INTACT FORESTS

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INTACT FORESTS

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EDITORIAL
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Editorial: Intact Forests

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Editorial on the Research Topic

Intact Forests

INTRODUCTION

Earth's forests cover an area approximately equal to Africa and Europe's landmasses combined (Keenan et al., 2015) and play vital roles in the global carbon, water, and energy cycles. But there is growing evidence that intensive, industrialized human uses reduce forest ecological integrity and damage these and other processes. It is increasingly clear that the most intact forests, i.e., those free from significant human-induced degradation, tend to support the highest levels of many important ecosystem values and services (Watson et al., 2018). As such they require particular attention in policies and management.

This special issue of Frontiers in Forests and Global Change was inspired by the 2018 Oxford Conference on "Intact Forests in the Twenty First Century," which was held in part due to the increasing desire of the global conservation policy community to understand, map and conserve intact ecosystems. The issue contains fifteen papers which can inform global policy and practice in this critical area.

CLARIFYING DEFINITIONS AND METRICS

The term "intact forests" represent a special case of the broader concept of ecological integrity (or, equivalently, intactness); namely the degree to which the composition, structure and functions of an ecosystem are within their natural ranges of variability. This formed one of the foundational concepts of the 1992 Rio Declaration, but has proven difficult to operationalize beyond bottom-up, local approaches (Hansen et al., 2021). However, recent advances in remote sensing, big data and cloud computing have enabled new biome-wide or global metrics to be generated (Grantham et al., 2020; Hansen et al., 2020; Williams et al., 2020; Nicholson et al., 2021). Rapid further developments are anticipated, and these new tools have already helped to build the confidence of the global policy community that ecological integrity can be measured and monitored in practical ways. For example, an increasing number of countries are incorporating forest degradation data into their greenhouse gas reporting (Lee et al., 2018) and it seems likely that the Parties to the Convention on Biological Diversity (CBD) will include the maintenance of the integrity of forests and other natural ecosystems as a headline goal under the forthcoming Global Biodiversity Framework 2021–2050 (CBD, 2021).

Ecological integrity is a multi-dimensional concept (Nicholson et al., 2021) so scientists must be careful to define exactly which aspects of it they are measuring, and to recognize that different aspects of integrity may not be perfectly correlated. One key challenge is to specify the natural

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range of states where no integrity is considered to have been lost. In addition to data constraints, there are philosophical questions relating to what degree of human activity should be considered a part of the natural system and how ongoing changes in environmental conditions are treated (Ellis et al., 2021; Morel and Nogué). For example, Harvey et al. show that what ecosystem is considered 'intact' in the mountains of Guatemala depends in part on how far in the past the reference state is measured. A range of practical solutions exists (Hansen et al., 2021) as long as the issue is dealt with transparently, and as long as the sensitivity of results to the choice of approach is considered.

We note there is some debate over how best to qualify a forest as "intact" or "not intact," along a given dimension of integrity. Whilst binary categories are inherently attractive and can be potentially useful for policy design and communications (e.g., Potapov et al., 2017), it is important to recognize that they are usually simplifications of continuous gradients of variation. For example, Plumptre et al. found that even areas qualifying as Intact Forest Landscapes (IFLs) on structural grounds may not be wholly intact with respect to their vertebrate faunas, as some hunting-sensitive species are absent at some sites. A key insight here is that in the Anthropocene (Malhi, 2017) few, if any, forests still lie wholly within their natural ranges of variation on all dimensions (Malhi et al., 2014). Hence attempts to identify 'perfectly intact' forests are likely to be largely uninformative for policy and planning.

A more useful approach is to quantify the *degree* of integrity, and then to assess the levels of integrity below which particular environmental values are *significantly* reduced. This may in turn help to identify threshold levels for integrity which are relevant in a particular context. For example, Qie et al. (2017) found that average annual carbon sink values were consistently high across Bornean forest interiors but begin to drop off steeply within 450 m of a forest edge, indicating that below this particular threshold of structural integrity a significant change is observed in a key ecological function.

VALUES ASSOCIATED WITH HIGH INTACTNESS

A wide diversity of values and services tends to be found at higher levels in more intact forests of a given type. Biomass carbon stocks are a good example (Keith et al., 2009; Mackey et al., 2020), and forests and other ecosystems without a history of significant disturbance also collectively absorb around 30% of anthropogenic carbon emissions annually (Friedlingstein et al., 2020). Two papers in this volume (Leverett et al.; Moomaw et al.) highlight the carbon values of intact North American forests, and also draw attention to the strong carbon sequestration services provided by older regrowth forests as their integrity returns toward more natural levels. Moreover, other climate regulatory services also tend to be higher in more intact forests, including moderation of local and regional air and land temperatures, and the return of moisture to the air through evapotranspiration (Baker and Spracklen).

Many aspects of biodiversity tend to be higher in more intact forests. For example, loss of ecological integrity tends to increase the numbers of species at elevated risk of extinction in an ecosystem (Betts et al., 2017; Donald et al., 2019) and to reduce or eliminate populations of many species (Haddad et al., 2015), including top predators and other species with large area requirements or particularly specialized niches. Hill et al. map variation in the natural (undisturbed) biodiversity importance of forests, and also estimate reductions in these forest species populations due to pressure from nearby human populations.

Many Indigenous Peoples' livelihoods and cultural security are underpinned by the integrity of the forest and other ecosystems within their territories and are at risk as degradation and clearance proceed (Garnett et al., 2018; Fa et al., 2020). There is often a reciprocal relationship between such communities and the integrity of their lands, since many have actively protected the lands they benefit from against destructive pressures originating elsewhere (Wells et al.).

The current global pandemic has put a spotlight on the sources of recent emerging infectious diseases, over 40% of which have been associated with transmission from wild animal species (Jones et al., 2008). Loss of integrity in natural systems, especially along tropical forest frontier zones, is believed to be a key factor driving rising rates of human-livestock-wildlife contact, and hence disease outbreaks, in recent decades (Dobson et al., 2020; Petrovan et al., 2021).

Due to methodological challenges, much remains to be learnt on the determinants of long-term ecosystem resilience, and on short-term resilience to conditions that ecosystems have not faced during the recent observational record (Morel and Nogué). Nonetheless, several key aspects of ecological resilience (including related concepts such as resistance) have been shown to be higher in intact forests and reduced following degradation (Thompson et al., 2009), including sensitivity to drought (Alencar et al., 2015) and vulnerability to fire (Nikonovas et al., 2020). For example, palaeoecological techniques show that intact Bornean mangroves appeared resilient over long periods to a regime of occasional fires, but experienced lasting and detrimental changes once fires, combined with multiple other pressures, exceeded some critical threshold of intensity following European colonization (Cole et al.).

THREATS TO INTACT FORESTS

Past pressures have already reduced the intactness of many forests such that only around 40% still have high ecological integrity (Grantham et al., 2020) with even less existing in blocks large enough to qualify as IFLs (Potapov et al., 2017). Declines are continuing, as shown by the >9% decline in the global extent of IFLs during 2000–16 (Potapov et al., 2017 and updates thereto)[1] Integrity is also in decline within these larger blocks (Benítez-López et al., 2019) and in smaller primary forest fragments outside them (Sabatini et al., 2020).

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[1] http://intactforests.org/data.ifl.html

Many human activities are causing these declines, notably logging, infrastructure development, changes to natural fire and flood regimes, and fragmentation by expanding farms (Potapov et al., 2017; Scullion et al.) as well as less visible issues such as hunting, over-grazing, pollution, and invasive species. It is clear that these threats and their indirect drivers (economic, social, and demographic) will grow in the future. For example, Wells et al. summarize the vast and expanding industrial footprint of logging, hydropower, mining, and oil and gas across the North American boreal forests whilst Grantham et al. (2021) found that 20% of tropical IFLs are currently overlapped by licenses for exploration or extraction by the oil, gas and minerals sectors and Putz et al. (2012) famously noted that, aside from those in protected areas, most tropical forests have been or will be selectively logged. Over 25 million km of new roads will be built by 2050, many in currently intact areas (Laurance et al., 2014).

Detailed metrics allow the exact impacts of various processes to be explored at a range of scales—for example, first-cut selective logging in tropical forest typically leaves patches averaging almost 70% of the area allocated for harvesting undamaged, though this number may decline in subsequent cycles (Putz et al.). Osuri et al. highlight the differential impacts on faunal assemblages from hunting and from habitat disturbance, whilst Morgan et al. examine the fine-grain effects of certified logging on great ape habitats.

SOLUTIONS: HALTING AND REVERSING THE DECLINE OF INTACT FORESTS

Significant efforts are underway to halt both the deforestation and degradation of intact forests, and increasingly also to restore elements of integrity (e.g., rewilding). Proposed solutions are as diverse as the threats and drivers themselves (Scullion et al.). Wells et al. suggest a package of measures for the North American boreal zone whilst Moomaw et al. propose a refocusing on intact forest (which they term "proforestation") in the US context.

One group of solutions involves area-based conservation measures, which include state or private protected areas and a wide range of Indigenous- or community-led approaches, from protected areas to the broader-scale management of traditional territories. To be fully effective, area-based measures should be supported by legally recognized, multi-sectoral spatial plans. Few protected area systems currently meet the necessary thresholds for extent, representativeness or effectiveness due to a range of constraints (Maxwell et al., 2020). Resourcing, legal limitations and other factors also constrain Indigenous and community-led approaches from reaching their full potential scale or impact (RFN, 2021; Wells et al.). Furthermore, communities defending forests are being disproportionately targeted with violence and murder (Butt et al., 2019), making it urgent for the international community to recognize their contribution and intervene in these predominantly politically- and corporate-driven attacks.

A crucial complementary approach to area-based methods is to address the drivers of loss. For example, over the last decade there has been a swell of industry-led zero-deforestation supply chain commitments, but implementation is still lacking and many companies are yet to act (NYDF Assessment Partners, 2020). In addition, these efforts have been found to seldom target locations where the pressure on intact forests will be highest in future (Leggett and Lawrence, 2021). Kleinschroth et al. explore some of the challenges to using voluntary certification approaches to minimize the impacts of logging on intact forests. On deforestation, Haywood and Henriot argue that voluntary approaches are largely ineffective and that it is essential for the governments of forest countries to take the lead, setting and enforcing appropriate laws.

To be successful, both area-based and driver-based approaches require a range of enabling conditions across society, including an ambitious and well-designed policy framework with clear targets that make the retention of large areas of intact natural ecosystems a high priority at international and national levels across all sectors including climate, health, biodiversity, industry and rural development (Maron et al., 2018, 2020; Milner-Gulland et al., 2021). Other critical factors are the availability of credible evidence, high levels of public awareness and interest, sufficient financial resourcing, attention to human rights and stakeholder participation, and economic tools that promote more sustainable alternative forms of development (Díaz et al., 2020; Scullion et al.).

In conclusion, this special issue highlights the necessity to conserve intact forests for their unique role in maintaining a variety of ecological functions and values in the face of growing threats. Participants in the conference together wrote the Declaration on Intact Forests in the Twenty First Century[2] which subsequently attracted support from a wide diversity of scientists, practitioners, and advocates. It is clear that if today's intact forests are to survive into the twenty second century, then globally coordinated action is very much needed, at all scales from individual sites and the struggles of environmental defenders through to over-arching UN conventions such as the CBD and UNFCCC.

AUTHOR CONTRIBUTIONS

TE, JW, AM, and YM conceptualized the manuscript. TE drafted the manuscript. JW and AM provided extensive edits. All authors contributed to the article and approved the submitted version.

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[2] https://www.eci.ox.ac.uk/if21/

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Are We Capturing Faunal Intactness? A Comparison of Intact Forest Landscapes and the "Last of the Wild in Each Ecoregion"

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Efforts to designate priority areas for conservation have had a long history, with most modern initiatives focused on either designating areas important for biodiversity or those least impacted by direct human disturbance. Ecologically intact ecosystems are becoming increasingly limited on the planet, making their identification and conservation an important priority. Intact forest landscapes (IFL) are defined as forests that are mainly free of significant anthropogenic degradation and at least 500 km^2 in size. Here we define a new metric, the Last of the Wild in each Ecoregion (LWE), as a preliminary scoping of the most intact parts of each ecoregion. IFL and LWE are approaches among a broad family of techniques to mapping ecological integrity at the global scale. Although both implicitly include species integrity as a dimension of intactness, this is inferred rather than directly measured. We assessed whether IFL or LWE areas were better at capturing species where they are most abundant using species distribution data for a set of forest species for which range-wide data were available and human activity limits the range. We found that IFL and LWE methods identified areas where species we assessed are either absent or at too low an abundance to be ecologically functional. As such many IFL/LWE polygons did not have intact fauna. We also show that 54.7% of the terrestrial realm (excluding Antarctica) has at least one species recorded as extinct and that two thirds of IFL/LWE areas overlap with areas where species have gone extinct in the past 500 years. The results show that even within the most remote areas, serious faunal loss has taken place at many localities so direct species survey work is also needed to confirm faunal intactness.

Keywords: intact forest landscapes, ecoregions, faunal intactness, prioritization for conservation, species extinction

INTRODUCTION

Throughout history, the reasons why areas have been established for wildlife protection have varied considerably. Some of the oldest forms of wildlife protection occurred as a result of land being put aside by the nobility for hunting (Hamin, 2002). For example, the Białowieża Primeval Forest protected the European bison for royal hunts and its habitats persisted for over 500 years (Jędrzejewska and Jędrzejewski, 1998). Prioritization of conservation sites for other reasons started with the establishment of the first national parks in the late 1800s. Initially, concepts of natural wonders, spiritual refuge, and scenic beauty were the criteria used to identify these parks (Runte, 1997; Nash, 2001; Lewis, 2007). In Africa, many of the first protected areas in the early to mid-1900s were established to enable sport hunting with a focus on the conservation of large mammals (with big trophies), usually where it was observed that they were declining in numbers (Willock, 1964).

It wasn't until the mid-1970s and 1980s that the attention started to shift to biodiversity conservation and the idea of saving life on Earth in all its forms. In the mid-1990s, Centres of Plant Diversity were identified to map species-rich plant regions (Davis et al., 1994). This led to the identification of ecoregions (Olson et al., 2001), areas of similar floristic and faunal composition, and the prioritization of these into the Global 200 (Olson and Dinerstein, 1998). The definition of biodiversity hotspots (Mittermeier et al., 2004) also emerged—regions rich in endemic plant species that also suffered a high degree of human impact. However, these broad-scale prioritizations, while helpful in identifying general regions important for conservation investment, were not easily translated into conservation actions at a local scale, and were biased toward tropical regions of the planet (Noss et al., 2015).

The Important Bird Areas (IBA) program (Donald et al., 2018), established in the early 1980s, was one of the first site-based prioritization initiatives based on the diversity of all species within a taxon. When it was shown that prioritization for birds also led to a good percentage of other taxa being captured, IBAs became known as the Important Bird and Biodiversity Areas program (Donald et al., 2018). Numerous additional schemes to identify important sites for taxonomic or thematic subsets of biodiversity (e.g., Alliance for Zero Extinction sites (AZE) etc.) were independently created. These formed the basis of a consolidated approach: the Key Biodiversity Areas (KBA) framework and methodology (IUCN, 2016), the purpose of which was to bring a standard and comparable approach to the identification of the most important sites for biodiversity on Earth that could be applied across all taxa. Following extensive consultation within the conservation community, *A Global Standard for the Identification of Key Biodiversity Areas* was finalized (Potapov et al., 2009; IUCN, 2016). Sites of importance for the global persistence of biodiversity can be selected if they meet one of five higher level criteria that have been recognized in several site identification or conservation prioritization approaches: (A) Threatened species or ecosystems, (B) Geographically restricted species or ecosystems, (C) Ecological Integrity, (D) Biological processes or congregations, and (E) Irreplaceability (IUCN, 2016). The ecological integrity criterion (C) was designed to identify outstanding examples at the global scale of still-natural and intact areas that maintain fully functional ecosystems within each ecoregion, and are therefore critical for sustaining biodiversity in the face of human-induced change.

KBA Criterion C deliberately incorporates both intactness and biotic integrity (IUCN, 2016) into the KBA approach by calling for the delineation of wholly intact natural areas with minimal post-industrial anthropogenic disturbance, sufficiently large to accommodate most broad-scale ecological processes, and supported by evidence that all ecosystem components (including highly mobile predators and herbivores and long-lived structural plant species) still fulfill their functional roles (KBA Standards Appeals Committee, 2018). Because comprehensive assessments of biotic communities will be impractical in many areas with high ecological integrity, especially in remote ecoregions with few human settlements and limited access, direct measures of intact faunal communities would have to be accomplished using indicator species (KBA Standards Appeals Committee, 2018). We note that unfortunately many ecoregions will not have criterion C KBAs because they have been so heavily impacted by humans that no areas within them now satisfy a meaningful intactness requirement.

The effort to identify which parts of the planet are globally important for biodiversity has been paralleled with assessments of global threats, in particular the impact of humans on the environment. The Human Footprint (Sanderson et al., 2002; Venter et al., 2016a; Allan et al., 2017) aimed to map the variation in human influence around the world using remotely sensed and other geographic data, such as human population data, infrastructure, and lights visible to a satellite at night. Areas of the least human influence within biomes have been termed "Last of the Wild" areas (Sanderson et al., 2002; Watson et al., 2016). It is now clear that these are rapidly dwindling in size and connectivity (Watson et al., 2016; Jones et al., 2018) and at the same time our understanding is growing of the exceptional value of intact ecosystems for provision of ecosystem services (water, carbon, etc.), biodiversity conservation, indigenous peoples, and human health (Watson et al., 2018).

Intact Forest Landscapes (IFL) adopted a similar approach to "last of the wild," albeit restricted to forested ecosystems (Potapov et al., 2008, 2017). The methodology identifies large undeveloped forest areas through satellite-based mapping of tree canopy cover, with areas unfragmented by roads or other development of no smaller than 500 km^2, assumed to be large enough to "maintain all native biodiversity, including viable populations of wide-ranging species" (Potapov et al., 2008, 2009). This size threshold was developed to be globally generalizable, but has been critiqued for being arbitrary and without scientific basis with respect to meeting biotic expectations, given the space needs of many wide-ranging species (Venier et al., 2018).

Here we make a scoping of the wildest parts of each ecoregion, what we term the "last of the wild in each ecoregion (LWE)" and compare this with IFL. We focused the Last of the Wild approach (Sanderson et al., 2002) down to the ecoregion scale with the LWE method because of the value in conserving the most intact areas of each ecoregion, rather than the most intact areas of each biome. This method is also a first step in a scoping of potential KBA Criteria C sites. With a focus on forested ecosystems, we assessed whether either approach identifies areas of faunal intactness as a preliminary measure of a more comprehensive species intactness. LWE and IFL are two approaches in what is now a broad family of techniques to mapping ecological integrity at the global scale, identified through measures of degree of human impact or influence, rather than through mapping of intact faunal communities. Others include Wilderness Areas (McCloskey and Spalding, 1989), Frontier Forests (Bryant et al., 1997), Hinterland Forests (Tyukavina et al., 2016), and very recently the Human Modification map (Kennedy et al., 2019). One concern with all these approaches is that they do not map what the satellites cannot see. Defaunation (Dirzo and Miranda, 1990) in what appears to be intact forest has long been recognized, and often referred to as "empty forest" (Redford, 1992; Wilkie et al., 2011). Verification of defaunation would require complete biological inventories and intimate historical knowledge.

Because both KBA and IFL approaches implicitly include species integrity as a dimension of intactness, it is of significant interest to determine the extent to which measures of human impact truly correspond with locations of intact animal communities, given the absence of credible global measures of this mapping dimension (Martin et al., 2019). An initial scoping of KBA criteria C sites requires likely intact areas of each ecoregion to be identified. The LWE approach we document here uses one method that might be used to scope potential Criteria C sites by identifying the areas with lowest human impact as measured by the human footprint. Threats are often mapped at various scales, from local to global, using remote sensing products, but their value for identifying intact fauna is often assumed rather than tested. In this paper we use both IFL and LWE areas as two measures of low human impact to assess how well measures such as these, made using remote sensing products and global datasets, actually capture important areas for fauna. We test the areas with (1) data on large, forest-dwelling mammals for which there are global data that tend to be negatively affected by human pressures and are likely to be some of the first species lost from a site, and (2) a measure of species extinction.

METHODS

We compared two estimates of intact habitat: IFL and LWE. "Last of the Wild" (Sanderson et al., 2002; Watson et al., 2016) maps focused on the wildest areas within biomes; the largest such areas, not surprisingly, are inhospitable deserts and tundra areas, and inaccessible areas such as the Amazon. Rather than using biomes, we modified the "last of the wild" method (Sanderson et al., 2002) to select within ecoregions rather than biomes. Ecoregions are more ecologically fine-grained and representative of biodiversity than biomes, as well as potentially compatible with the KBA Criterion C. Other similar published metrics (e.g., hinterland forests - Tyukavina et al., 2016) have an overlap of 92% with IFL maps.

Scoping of LWE Areas

We undertook a scoping of candidate LWE areas by identifying the five most intact areas for each ecoregion of the world. We overlaid the most recent human footprint map (Venter et al., 2016a,b) on the most recent map of ecoregions of the world (Dinerstein et al., 2017). The human influence index (HII) can range between 0 and 50; for the purposes of this analyses we identified the best 10% of each ecoregion (lowest footprint scores), and within this subset selected the 5 largest intact polygons. HII has been widely used relative to more recent datasets of human modification (e.g., Kennedy et al., 2019) and therefore offered opportunities to compare our results with previous literature. A similar approach was used for the "Last of the Wild" (Sanderson et al., 2002), except this assessed the 10 largest areas within the best 10% of each Biome. In order to avoid polygons that had a lot of "gaps" resulting from pockets of high human activity in otherwise non-impacted landscapes, we applied a 5 km smoothing buffer to the HII map (each pixel representing the average HII score within the buffer radius). We selected this buffer radius from a range between 0 and 25 km, testing the result in ∼2.5 km increments. The 5 km buffer provided the best smoothing, and appeared to stabilize both the reduction in border effects and remnant habitat selection (median effects on area perimeter and shape did not substantially vary using larger buffers). This meant that fragmented and border habitats would experience an increase in HII, while core areas would remain unaffected.

We selected a subset of these areas, designated Forest LWE, which selected only those forested ecoregions that overlapped with IFL polygons. We used these polygons to intersect with global maps of species loss (see below).

Our rationale for using anthropogenic influence to identify LWE areas is that a reduced anthropogenic influence is likely to translate to a reduced ecological impact, including species loss. Global maps of anthropogenic influence, however, are not likely detailed enough in many places of the world to capture (directly or indirectly) all pressure types that might result in species loss, or if modern measures of anthropogenic influence can still capture historical impacts. Notable pressures that are unmapped to date include hunting/poaching and will have drastically altered species composition in large landscapes; regional or local-scale maps will capture more elements of the human footprint. The regions we identify will need to go through more stages of rigorous analysis, including on-the-ground evaluation before KBA criterion C sites can be positively identified. As such, this is a preliminary scoping of regions of the world where such sites are likely to exist.

Intersecting IFL and LWE Areas With Species Distributions

Species With Measures of Density

To assess how well these areas might capture faunal intactness we compiled range and, where possible, density maps for a small subset of tropical forest mammals that are sensitive to human disturbance. We assembled density data for the following species: jaguars (*Panthera onca*) (Jedrzejewski et al., 2018),

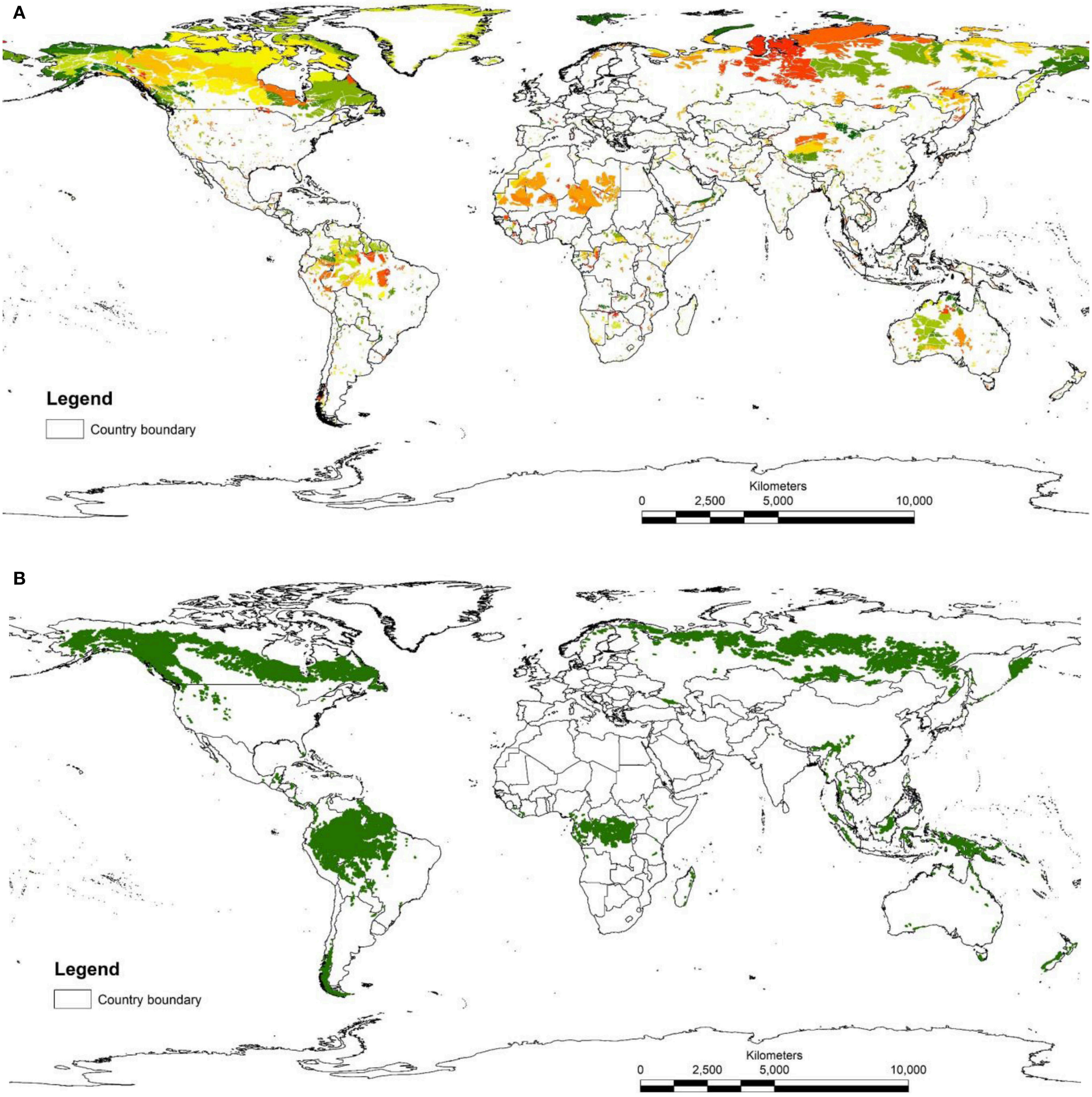

FIGURE 1 | (A) Map of LWE sites. These are the five largest parts of each ecoregion with the lowest 10% of human influence index scores. Different colors represent different ecoregions. **(B)** map of IFL sites.

African forest elephants (*Loxodonta africana cyclotis*) (Maisels et al., 2013), western lowland gorillas (*Gorilla gorilla gorilla*), central chimpanzees (*Pan troglodytes troglodytes*) (Strindberg et al., 2018), eastern chimpanzees (*P. t. schweinfurthii*) (Plumptre et al., 2010), eastern gorilla (*Gorilla beringei*) (Plumptre et al., 2016), Bornean orangutan (*Pongo pygmaeus*) (Voigt et al., 2018), Sumatran orangutan (*P. abelii*) (Wich et al., 2016), and Tapanuli orangutan (*P. tapanuliensis*) (Nater et al., 2017). For each of these maps we identified a threshold density separating high and low density populations using expert assessment of the relevant author's knowledge of each of the species. We then intersected the maps of IFL and the LWE areas with each species map to calculate areas of high density that were within these polygons and the area across the species range. We measured the percentage of the area of the LWE and IFL polygons that contained high density scores for a species and compared this

TABLE 1 | The area of suitable habitat, or area where the species was at high density (for species with density estimates), calculated within the LWE sites or IFL sites (where they overlap the species range), and within the global range of the species as a whole.

Species	LWE sites (km^2)	Intact forest landscapes (km^2)	Global extent of range (km^2)
RANGE WIDE PRIORITY MAPPING			
Asian black bear (*Ursus thibetanus*)	127,273 (24.3%)	83,341 (53.0%)	1,095,792 (28.5%)
Asian sun bear (*Helarctos malayanus*)	77,153 (23.3%)	79,297 (29.5%)	409,691 (17.5)
Brown bear (*Ursus arctos*)	4,565,655 (82.1%)	4,257,441 (84.8%)	14,214,665 (59.9%)
Sloth bear (*Melursus ursinus*)	52,796 (39.7%)	0 (0.0%)	352,042 (11.7%)
Snow leopard (*Panthera uncia*)	173,670 (36.0%)	19,668 (84.8%)	1,003,608 (44.3%)
Asian elephant (*Elephas maximus*)	60,750 (54.7%)	40,918 (74.3%)	526,101 (58.7%)
Peccary (*Tayassu pecari*)	102,403 (82.7%)	3,571,133 (90.1%)	5,899,639 (42.3%)
Tapir (*Tapirus terestris*)	50,267 (84.9%)	3,580,578 (91.1%)	5,830,185 (44.1%)
Tiger (*Panthera tigris*)	155,294 (71.5%)	116,950 (81.4%)	930,093 (78.1%)
DENSITY MAPS (WITH THRESHOLD DENSITY BETWEEN HIGH AND LOW IN PARENTHESES)			
African forest elephant (*Loxodonta africana cyclotis*) ($0.2/km^2$)	33,591 (16.4%)	37,078 (4.5%)	62,903 (3.8%)
Central chimpanzee (*Pan troglodytes troglodytes*) ($0.5/km^2$)	9,950 (7.3%)	18,136 (8.3%)	31,399 (5.5%)
Eastern chimpanzee (*Pan troglodytes shweinfurthii*) ($0.5/km^2$)	22,729 (22.7%)	156,371 (52.6%)	261,106 (28.8%)
Western lowland gorilla (*Gorilla gorilla gorilla*) ($1/km^2$)	44,574 (32.7%)	53,279 (24.4%)	85,056 (14.7%)
Grauers gorilla (*Gorilla beringei graueri*) ($0.5/km^2$)	0 (0.0%)	7,640 (9.9%)	14,000 (7.1%)
Jaguar (*Panthera onca*) ($2/100\ km^2$)	1,521,277 (60.5%)	2,569,571 (64.6%)	4,611,009 (49.4%)
Bornean orangutan (*Pongo pygmaeus*) ($0.5/km^2$)	8,945 (53.6%)	7,283 (41.0%)	89,138 (50.6%)
Sumatran orangutan (*Pongo abelii*) ($0.5/km^2$)	3,754 (86.0%)	5,695 (84.7%)	15,370 (91.6%)
Tapanuli orangutan (*Pongo tapanuliensis*) ($0.5/km^2$)	0.0 (0.0%)	0.0 (0.0%)	989 (96.0%)

The percentage of suitable/high density habitat of the total area within the LWE, IFL and global range is also given.

with the percentage area of high density scores across the species global range to assess whether the methods selected more of the area where species are considered to be likely to be at a functional density. We used this calculation because IFL and LWE areas have a great difference in extent, and failing to do so would have almost certainly indicated the larger areas to be more inclusive, despite the potential to also include large segments of low-density populations.

Species With Range-Wide Priority Setting

We also compiled maps from range-wide priority setting exercises that mapped areas where a species was definitely occurring, probably/possibly occurring and extirpated. We assembled maps for tigers (*Panthera tigris*) (Dinerstein et al., 2006), white-lipped peccary (*Tayassu pecari*), and tapir (*Tapirus terrestris*) (Taber et al., 2008), Asian black bear (*Ursus thibetanus*), brown bear in Asia (*Ursus arctos*), sloth bear (*Melursus ursinus*) and sun bear (*Helarctos malayanus*) (Garshelis et al., 2007), snow leopard (*Panthera uncia*) (McCarthy et al., 2016; Sanderson et al., 2016) and Asian elephant (*Elephas maximus*) (Hedges et al., 2009; Calabrese et al., 2017). Although large areas of IFL and LWE occur in boreal forest, analogous full range assessments of boreal species other than brown bear in Asia were not available. For the purposes of this analysis we assumed that where a species was definitely known, it was occurring at a reasonably functional density, because the species could be detected. Where a species was possible/probable it was at low density because it was uncertain whether the species was present. We use the term "suitable habitat" to define where a species definitely occurred in the rest of this paper. This will overestimate where a species is at functional density because there will be many sites where the species is known to occur, but only at low density, as well as known sink sites. We calculated the area of suitable habitat within the LWE and IFL polygons as well as within the species global range. We also assessed the percentage of the range of the species with suitable habitat and the percentage of this suitable habitat within LWE areas and within IFLs, to assess whether the method was selecting areas where the species was more likely to be at a higher density and more functional.

Intersecting IFL and LWE Areas With a Map of Where Species Have Gone Extinct

We assessed loss of faunal intactness by mapping the distribution of extinct ranges for species. We compiled maps of all species assessed from the IUCN Red List of Threatened Species (IUCN, 2018) and mapped the native range where a species was considered to be extinct or possibly extinct as classified under the range fields "Presence" for each species range polygon. The Red List assesses where species have gone extinct since the year 1500 AD, so does not include species that were extirpated prior to this date and there are recognized gaps in coverage as a result. It maps species that have gone extinct, and areas of range where extant species have lost range. We mapped all such ranges to assess the numbers of extinct species to obtain a measure of loss of faunal intactness across the world. We then intersected this map with the IFL and LWE/Forest LWE polygons to calculate the percentage area of polygons that had not lost any species using this measure.

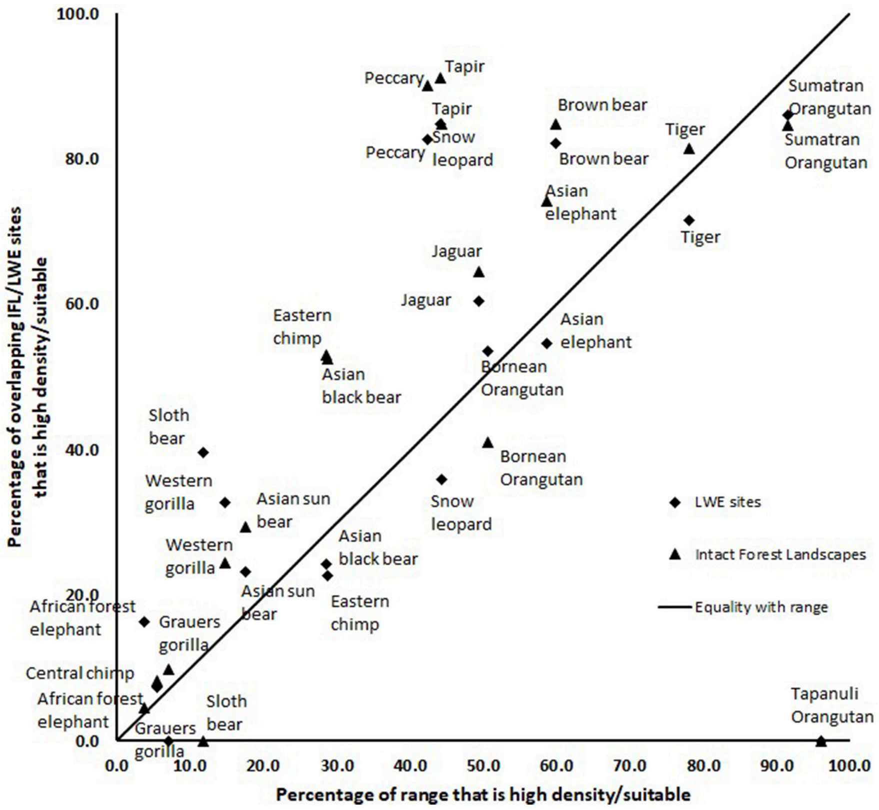

FIGURE 2 | A comparison of the percentage of "high density" or "suitable" habitat within a species range plotted against the percentage of the area within the LWE/IFL polygons that overlap the species range. Species below the 1:1 line have less suitable/high density habitat than available.

RESULTS

LWE Areas

The map of LWE areas is visually dominated by large areas of the northern ecoregions in tundra, taiga, and boreal forests (**Figure 1**). This is because the HII in these less populated ecoregions are mostly scored zero, so that when selecting the 10% of lowest scores, all cells with zero are selected. Human impacts in these regions include logging and other resource development (e.g., mining areas, seismic lines), but these are not available on global maps and therefore do not get incorporated in the HII (though see Kennedy et al., 2019). This highlights a compromise tied with using current global data sets, accepting data that may be of lower quality than locally available in order to reduce geographical bias across management units (countries or sub-national regions). For this reason, there have been several efforts to make regional human footprint maps (Leu and Hanser, 2008; Woolmer et al., 2008) What is clear is that for most of the ecoregions of the planet, the five most intact areas of each ecoregion are relatively small in size (average area was 6,323 km^2 but median area was only 696 km^2), reflecting the fine scale of many ecoregions and the density of human activity. Only 340 areas out of a total of 3,852 identified were larger than 10,000 km^2, the recommended minimum size for a KBA criterion C site (IUCN, 2016).

Intersection of Species Ranges and IFL/LWE Areas

The results of the intersection of the IFL and LWE areas with the ranges of the 16 species for which we had data on density or suitable habitat are shown in **Table 1** (**Figure S1** in supplementary material shows the overlap of LWE/IFL with suitable/high density habitat for all forest species). This table shows the areas of high density/suitable habitat in the LWE areas, the IFLs and the percentage of the species global range. On average 21% of high density/suitable habitat of a species range was captured within the LWE areas and 34% within IFLs. Given that all LWE areas (including those in non-forest ecoregions) cover only 2% of the surface covered by IFL (24.4 million km^2 vs. 1,163.3 million km^2), we also compared the relative percentages of high density/suitable habitat captured by each approach by plotting the percentage of high density/suitable habitat within the species range against the percentage of the area of the LWE/IFL polygons where there was overlap (**Figure 2**). For example, only 17% of the LWE areas that overlap African forest elephant range have high elephant densities, and this drops to only 4.5% in IFL polygons, similar to the global percentage across their range (3.8%). In some cases, the LWE areas capture more of a species' high-density range while for others the IFL do a better job. For the most part both capture a larger percentage than what

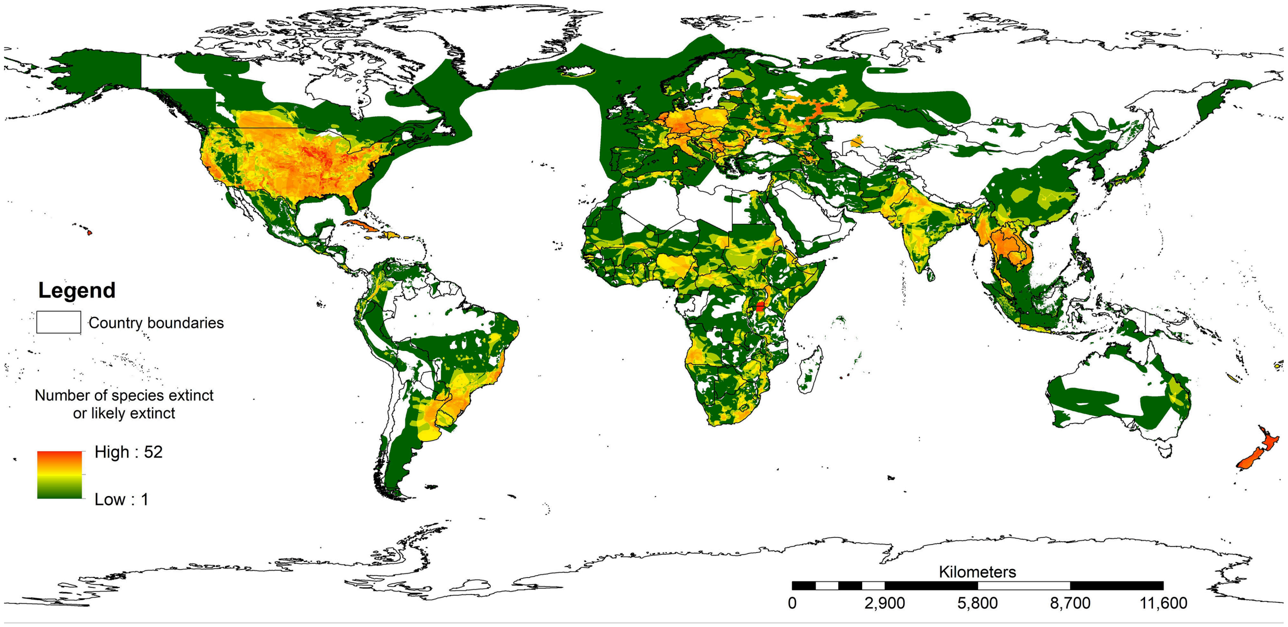

FIGURE 3 | The ranges where any species on the IUCN Red List of Threatened Species has been assessed as extinct or possibly extinct. Note that this map will be a significant underestimate because the IUCN Red List does not map species prior to 1500 AD and many extant species probably do not have their extinct ranges mapped.

is available within the species' range (species above the line of 1:1 –**Figure 2**), although many of the comparisons are close to what would be expected if polygons were allocated randomly (1:1 line—**Figure 2**). For many species, however, large areas of the IFL or LWE polygons do not have high density/suitable habitat. In these areas, the species are unlikely to be at a functional density or not even present. This was particularly true for those species measured using density, which were likely to better reflect functional integrity of a site. Note that the percentage areas of suitable habitat will be on the high side for the ranges determined by range wide priority setting because the assumption was made that definite/confirmed range or high quality range would have functional densities of the species, yet at many areas this may not be the case and they are simply recorded as being present which qualifies it as definite range. This assessment clearly shows that these species, which tend to be affected by human impact, will be at low and likely non-functional densities across large areas of either IFL or the LWE areas.

TABLE 2 | The results of intersecting the IFL, LWE, and Forest LWE polygons with the Extinct species map.

Intactness measure	Percentage of sites without extinct species (% area)
IFL sites	30.6
All LWE sites	33.3
Forest LWE sites	19.4

The percentage area of "intact" polygons are given, defined as area where no species are recorded as extinct.

Faunal Loss in IFL and LWE Areas

Figure 3 shows the results of mapping all species assessed on the IUCN Red List where a species has been extirpated or is possibly extirpated since 1500 AD. A total area of 54.7% of the terrestrial realm of the earth (excluding Antarctica) has at least one species with range recorded as extinct or possibly extinct. The white areas in Europe and central Asia would certainly have had species that had been lost prior to 1500 AD, such as bears (*Ursus arctos*), wolves (*Canis lupus*), and beavers (*Castor fiber*). It is important to note that within the IUCN Red List assessments, most records do not estimate where the species has lost part of its range. Therefore, this map will very much be an underestimate of species loss across the world. Yet it is still valuable in highlighting how much of the world has lost one or more species.

Intersecting all LWE areas with this map shows that 33% of the area of LWE polygons have no recorded extinctions, compared with 31% of IFL polygons. However, of the forested LWE areas only 19% of their total area have no extinctions recorded (**Table 2**).

DISCUSSION

What Do We Mean by Intactness?

Our results show that there are few places left on the planet that are faunally intact, a result that corresponds with many assessments of global biodiversity (e.g., Secretariat of the Convention on Biological Diversity United Nations Environment Programme, 2014; Wolf and Ripple, 2017). The two measures we assessed of intactness—the IFL measure and the LWE areas—encompass reasonably large areas of the globe. However, when we look at forest species that might be using the IFLs and LWE areas, for many there are large parts of these "intact areas" where they are absent or at low densities (**Figure 2**) that are not likely ecologically functional (*sensu* Sanderson, 2006). In extreme cases, species may be present, but ecologically extinct (Estes et al., 1989; Novaro et al., 2000). Assessment of species range loss or complete extinction also shows that a large area of the earth does not have a full complement of species and cannot be thought of as faunally intact (**Figure 3**). More than half of LWE areas had no species recorded as having gone extinct, but this would decrease if pre 1500 data were available for ecoregions in Europe in particular, and if extinction records in the IUCN Red List were more comprehensive in general. Comparison of forested areas demonstrated that more than half of IFL and forest LWE areas had lost at least one species.

Table 1 shows that areas of suitable habitat/high density range for the species we assessed were not captured by the IFL or LWE assessments, indicating that there are important areas for species where lack of intactness, as measured by HII or from anthropogenic alteration of forest cover, is still important for these species.

Estimates of human influence could be improved by using available local and regional data at the jurisdictional (e.g., national or subnational) level (e.g., Woolmer et al., 2008). Many smaller-scale analyses will reveal considerably higher levels of human impact, however, which could reduce the area of IFL polygons or LWE areas. Our use of a 10% threshold to select the least impacted areas of each ecoregion does limit the area where candidate LWE sites could occur in some ecoregions where human impacts are negligible throughout the ecoregion. In ecoregions with extensive scores of zero (northern tundra/taiga) LWE areas were large and included more than 10% of the area of the ecoregion, however for most ecoregions we were able to limit the analysis to the best 10% or smaller area of the ecoregion (if there were more than 5 candidate sites). There is a need to assess the potential impact of this on the identification of LWE areas in future.

In addition to regional-scale human pressures mapping, accurate assessments of faunal intactness will require (1) better models of direct pressures on biodiversity such as hunting intensity, which cannot be predicted using HII-like approaches, and (2) knowledge of the extent to which abundance levels have changed relative to historical baseline for multiple species throughout their ranges. How far a hunter will move into a forest will be determined by several factors such as the importance of hunting to their livelihood (e.g., poachers in wealthier vs. poorer countries), the relative reward obtained from hunting a species (e.g., ivory vs. bushmeat), the accessibility of a site (e.g., rugged terrain vs. flat), and the intensity and likelihood of penalties that might be incurred if caught (e.g., small fine vs. jail terms). Considerably more detail than traditional range maps will be necessary to evaluate the extent to which faunal communities have retained their integrity in the face of human disturbance. Only when we have a good handle on factors such as these will we be able to start modeling faunal intactness better. A recent study that was published as this paper went to press makes the first attempt to model hunting across tropical forests (López et al., 2019) which estimates large mammals have been lost in more than 50% of IFL. Global analyses, while being useful to help with planning for conservation, must also be supplemented with site evaluations for identification of evidence-based, intact areas for species, as specified by *Global Standard for the identification of Key Biodiversity Areas* with respect to criterion C sites.

Intactness as measured by global datasets and functional ecological integrity of biodiversity may not always co-occur and it is important to recognize that the two have a value for conservation independently. Some well-managed protected areas, for example, will inevitably have a high degree of anthropogenic influence, while at the same time retaining a full, or nearly full, complement of species at functional densities, exactly because they are being well protected and managed (e.g., Nairobi National Park on the outskirts of Nairobi city in Kenya (Ogutu et al., 2013). On the other hand, some intact areas may not currently contain species at functional densities but numbers might be recovered with management, so that areas become ecologically functional in the future. Areas, for instance, where a keystone species has been extirpated through hunting, and could meet KBA criterion C status after reintroduction and recovery of that species to functional levels.

The message highlighted from these analyses is that faunal intactness is highly rare in the remaining large areas on earth and that we cannot easily identify this from satellite images of seemingly intact forest canopy and human disturbance (the IFL method) nor from assessments using the HII (the LWE areas). Recent papers have highlighted the small percentage of remaining wilderness or intact sites (Watson et al., 2016, 2018; Potapov et al., 2017) and yet our results indicate that truly intact sites with a full complement of species are likely to be much rarer still.

AUTHOR CONTRIBUTIONS

AP and DB made the analyses described in this paper. AP drafted the paper. WJ, HK, FM, MV, ES, SS, and SW provided data sets and contributed to the writing and JR contributed ideas and to the writing of the paper.

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Intact Forests in the United States: Proforestation Mitigates Climate Change and Serves the Greatest Good

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Climate change and loss of biodiversity are widely recognized as the foremost environmental challenges of our time. Forests annually sequester large quantities of atmospheric carbon dioxide (CO_2), and store carbon above and below ground for long periods of time. Intact forests—largely free from human intervention except primarily for trails and hazard removals—are the most carbon-dense and biodiverse terrestrial ecosystems, with additional benefits to society and the economy. Internationally, focus has been on preventing loss of tropical forests, yet U.S. temperate and boreal forests remove sufficient atmospheric CO_2 to reduce national annual *net* emissions by 11%. U.S. forests have the potential for much more rapid atmospheric CO_2 removal rates and biological carbon sequestration by intact and/or older forests. The recent *1.5 Degree Warming Report* by the Intergovernmental Panel on Climate Change identifies *reforestation* and *afforestation* as important strategies to increase negative emissions, but they face significant challenges: afforestation requires an enormous amount of additional land, and neither strategy can remove sufficient carbon by growing young trees during the critical next decade(s). In contrast, growing existing forests intact to their ecological potential—termed *proforestation*—is a more effective, immediate, and low-cost approach that could be mobilized across suitable forests of all types. Proforestation serves the greatest public good by maximizing co-benefits such as nature-based biological carbon sequestration and unparalleled ecosystem services such as biodiversity enhancement, water and air quality, flood and erosion control, public health benefits, low impact recreation, and scenic beauty.

Keywords: biodiversity crisis, Pinchot, afforestation, reforestation, forest ecosystem, biological carbon sequestration, old-growth forest, second-growth forest

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INTRODUCTION

Life on Earth as we know it faces unprecedented, intensifying, and urgent imperatives. The two most urgent challenges are (1) mitigating and adapting to climate change (Intergovernmental Panel on Climate Change, 2013, 2014, 2018), and (2) preventing the loss of biodiversity (Wilson, 2016; IPBES, 2019). These are three of the Sustainable Development Goals, Climate, Life on Land and Life under Water (Division for Sustainable Development Goals, 2015), and significant international resources are being expended to address these crises and limit negative impacts on economies, societies and biodiverse natural communities. The recent *1.5 Degree Warming Report* of the Intergovernmental Panel on Climate Change (2018) was dire and direct, stating the need for "rapid, far-reaching and unprecedented changes in all aspects of society." We find that growing additional existing forests as intact ecosystems, termed *proforestation*, is a low-cost approach for immediately increasing atmospheric carbon sequestration to achieve a stable atmospheric carbon dioxide concentration that reduces climate risk. Proforestation also provides long-term benefits for biodiversity, scientific inquiry, climate resilience, and human benefits. This approach could be mobilized across all forest types.

Forests are essential for carbon dioxide removal (CDR), and the CDR rate needs to increase rapidly to remain within the 1.5 or 2.0°C range (Intergovernmental Panel on Climate Change, 2018) specified by the Paris Climate Agreement (2015). Growing existing forests to their biological carbon sequestration potential optimizes CDR while limiting climate change and protecting biodiversity, air, land, and water. Natural forests are by far the most effective (Lewis et al., 2019). Technologies for direct CDR from the atmosphere, and bioenergy with carbon capture and storage (BECCS), are far from being technologically ready or economically viable (Anderson and Peters, 2016). Furthermore, the land area required to supply BECCS power plants with tree plantations is 7.7 million km^2, or approximately the size of Australia (Intergovernmental Panel on Climate Change, 2018). Managed plantations that are harvested periodically store far less carbon because trees are maintained at a young age and size (Harmon et al., 1990; Sterman et al., 2018). Furthermore, plantations are often monocultures, and sequester less carbon more slowly than intact forests with greater tree species diversity and higher rates of biological carbon sequestration (Liu et al., 2018). Recent research in the tropics shows that natural forests hold 40 times more carbon than plantations (Lewis et al., 2019).

Alternative forest-based CDR methods include *afforestation* (planting new forests) and *reforestation* (replacing forests on deforested or recently harvested lands). Afforestation and reforestation can contribute to CDR, but newly planted forests require many decades to a century before they sequester carbon dioxide in substantial quantities. A recent National Academy study titled *Negative Emissions Technologies and Reliable Sequestration: A Research Agenda* discusses afforestation and reforestation and finds their contribution to be modest (National Academies of Sciences, 2019). The study also examines changes in conventional forest management, but neglects proforestation as a strategy for increasing carbon sequestration. Furthermore, afforestation to meet climate goals requires an estimated 10 million km^2–an area slightly larger than Canada (Intergovernmental Panel on Climate Change, 2018). The massive land areas required for afforestation and BECCS (noted above) compete with food production, urban space and other uses (Searchinger et al., 2009; Sterman et al., 2018). More importantly, neither of these two practices is as effective quantitatively as proforestation in the next several decades when it is needed most. For example, Law et al. (2018) reported that extending harvest cycles and reducing cutting on public lands had a larger effect than either afforestation or reforestation on increasing carbon stored in forests in the Northwest United States. In other regions such as New England (discussed below), longer harvest cycles and proforestation are likely to be even more effective. Our assessment on the climate and biodiversity value of natural forests and proforestation aligns directly with a recent report that pinpointed "stable forests" – those not already significantly disturbed or at significant risk – as playing an outsized role as a climate solution due to their carbon sequestration and storage capabilities (Funk et al., 2019).

Globally, terrestrial ecosystems currently remove an amount of atmospheric carbon equal to one-third of what humans emit from burning fossil fuels, which is about 9.4 GtC/y (10^9 metric tons carbon per year). Forests are responsible for the largest share of the removal. Land use changes, i.e., conversion of forest to agriculture, urban centers and transportation corridors, emit ~1.3 GtC/y (Le Quéré et al., 2018). However, forests' potential carbon sequestration and additional ecosystem services, such as high biodiversity unique to intact older forests, are also being degraded significantly by current management practices (Foley et al., 2005; Watson et al., 2018). Houghton and Nassikas (2018) estimated that the "current gross carbon sink in forests recovering from harvests and abandoned agriculture to be −4.4 GtC/y, globally." This is approximately the current gap between anthropogenic emissions and biological carbon and ocean sequestration rates by natural systems. If deforestation were halted, and secondary forests were allowed to continue growing, they would sequester −120 GtC between 2016 and 2100 or ~12 years of current global fossil carbon emissions (Houghton and Nassikas, 2018). Northeast secondary forests have the potential to increase biological carbon sequestration between 2.3 and 4.2-fold (Keeton et al., 2011).

Existing proposals for "Natural Climate Solutions" do not consider explicitly the potential of proforestation (Griscom et al., 2017; Fargione et al., 2018). However, based on a growing body of scientific research, we conclude that protecting and stewarding intact diverse forests and practicing proforestation as a purposeful public policy on a large scale is a highly effective strategy for mitigating the dual crises in climate and biodiversity and ultimately serving the "greatest good" in the United States and the rest of the world. **Table 1** summarizes some of the key literature supporting this point.

A SMALL FRACTION OF U.S. FORESTS IS MANAGED TO REMAIN INTACT

Today, <20% of the world's forests remain intact (i.e., largely free from logging and other forms of extraction and development). Intact forests are largely tropical forests or boreal forests in Canada and Russia (Watson et al., 2018). In the U.S.—a global pioneer in national parks and wildlife preserves—the percentage of intact forest in the contiguous 48 states is only an estimated 6–7% of total forest area (Oswalt et al., 2014), with a higher proportion in the West and a lower proportion in the East. Setting aside a large portion of U.S. forest in Inventoried Roadless Areas (IRAs) was groundbreaking yet only represents 7% of total forest area in the lower 48 states—and, ironically,

TABLE 1 | Comparison of climate and biodiversity benefits of *intact* (either old-growth forest or younger forest managed as Gap 1 or Gap 2, and thus protected from logging and other resource extraction) and traditionally *managed* forests for multiple forest types in the United States.

	Location	Forest type	Forest condition with greater value	References
ECOSYSTEM CHARACTERISTICS				
Density of large trees (>60 cm DBH)	Eastern US	mid-Atlantic oak-hickory forests, northern hemlock-hardwood forests, and boreal spruce-fir forests	Intact (81% greater)	Miller et al., 2016
Proportion of old forest	Eastern US	Same as above	Intact	Miller et al., 2016
Basal area of dead standing trees	Eastern US	Same as above	Intact	Miller et al., 2016
Coarse woody debris volume	Eastern US	Same as above	Intact (135% greater)	Miller et al., 2016
Carbon storage	Pacific Northwest US	Douglas fir and western hemlock;	Intact (75–138% greater)	Harmon et al., 1990
Carbon storage	Northeastern US	Northern hardwood conifer	Intact (39–118% greater)	Nunery and Keeton, 2010
Forest fire burn severity	Western US	Pine and mixed conifer forests	Managed (two SEs greater)	Bradley et al., 2016
BIODIVERSITY				
Tree species richness	Eastern US	mid-Atlantic oak-hickory forests, northern hemlock-hardwood forests, and boreal spruce-fir forests	Intact	Miller et al., 2018
Proportion rare tree species	Eastern US	Same as above	Intact	Miller et al., 2018
Bird species richness and abundance	Northeastern Minnesota	Hemi-boreal	Intact (12–20% greater)	Zlonis and Niemi, 2014
Trunk bryophyte and lichen species richness	Northwestern Montana	Grand-fir	Intact (33% greater)	Lesica et al., 1991
Salamander density	Ozark Mountains, Missouri	Oak-hickory	Intact (395–9,500% greater)	Herbeck and Larsen, 1999
Probability of occurrence of invasive plant species	Eastern US	Deciduous and mixed forest	managed	Riitters et al., 2018

Intact forests range in size and previous disturbance history but they are not under active management and have been allowed to continue growing according to the procedures described for proforestation.

management of some IRAs allows timber harvest and road building (Williams, 2000), a scenario happening currently in the Tongass National Forest in Alaska (Koberstein and Applegate, 2018). These scant percentages worldwide and particularly in the U.S. are insufficient to address pressing national and global issues such as rising CO_2 levels, flooding, and biodiversity loss, as well as provide suitable locations for recreation and associated public health benefits (Cordell, 2012; Watson et al., 2018). In heavily populated and heavily forested sub-regions in the Eastern U.S., such as New England, the total area dedicated as intact (i.e., primary management is for trails and hazard removals) is even more scarce, comprising only ∼3% of land area. Just 2% of the region is legally protected from logging and other resource extraction (**Figure 1**). A large portion of forest managed currently as intact or "reserved forest" – and thus functioning as "stable forest" (Funk et al., 2019) – is designated solely by administrative regulations that can be altered at any time.

Intact forests in the U.S. include federal wilderness areas and national parks, some state parks, and some privately-owned holdings and conservation trust lands. Recent studies reveal that intact forests in national parks tend to be older and have larger trees than nearby forests that are not protected from logging (Miller et al., 2016; **Table 1**). Scaling up protection of intact forests and designating and significantly expanding reserved forest areas are public policy imperatives that are compatible with public access and with the country's use of forest products. Identifying suitable forest as intact (for carbon sequestration, native biodiversity, ecosystem function, etc.) can spawn new jobs and industries in forest monitoring, tourism and recreation, as well as create more viable local economies based on wood reuse and recycling. Public lands with significant biodiversity and proforestation potential also provide wildlife corridors for climate migration and resilience for many species.

PROFORESTATION INCREASES BIOLOGICAL CARBON SEQUESTRATION AND LONG-TERM STORAGE IN U.S. FORESTS

Net forest carbon reflects the dynamic between gains and losses. Carbon is lost from forests in several ways: damage from natural disturbances including insects and pathogens ("pests"), fire, drought and wind; forest conversion to development or other non-forest land; and forest harvest/management. Together, fires, drought, wind, and pests account for ∼12% of the carbon lost in the U.S.; forest conversion accounts for ∼3% of carbon loss; and forest harvesting accounts for 85% of the carbon lost from forests each year (Harris et al., 2016). Forests in the Southern US have the highest percentage of carbon lost to timber harvest (92%) whereas the Western US is notably lower (66%) because of the

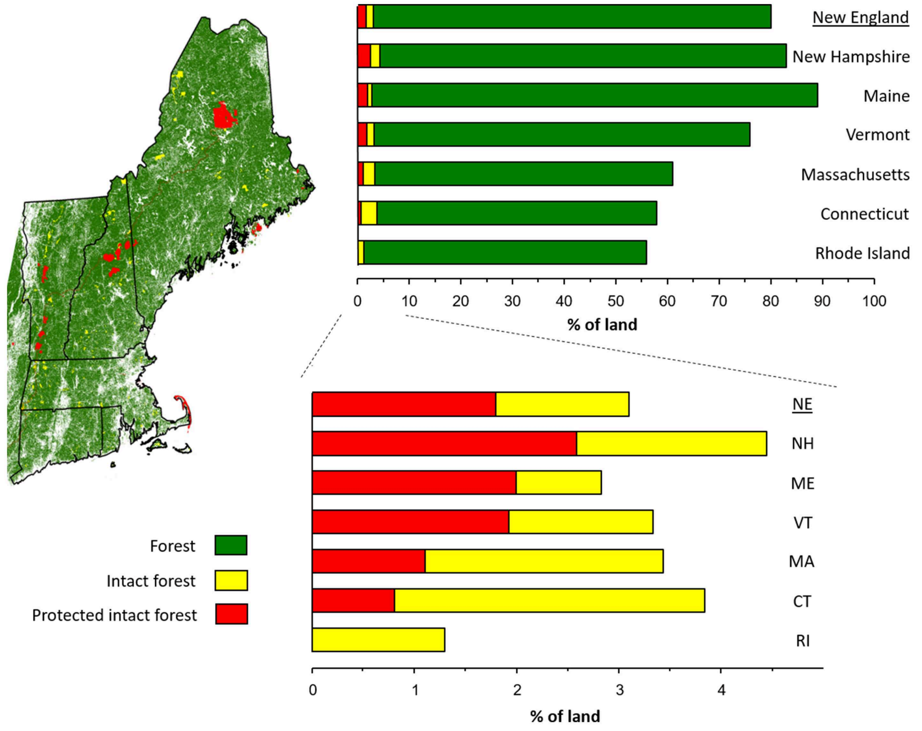

FIGURE 1 | Distribution of forest cover and intact "wildland" forest across six New England states. At left, map of overall forest cover (green) vs. forest protected legally (red) or managed currently (yellow) as intact in New England. At right, regional and state specific % forest cover (green), % managed as intact Gap 1 (limited intervention other than trails and hazard removals) but not protected legally (yellow), and % legally protected as intact forest (red, designated U.S Geological Survey (USGS) Gap 1 or Gap 2 and primarily federal and state wilderness areas, and certain national parks). Adapted and compiled from National Conservation Easement Database (2014); United States Geological Survey (2019a,b), and the University of Montana (2019). USGS Gap level 1 or 2 lands receive the highest level of protection from logging and other resource extraction and generally correspond with IUCN protected categories 1a, 1b, and II (https://gapanalysis.usgs.gov/blog/iucn-definitions/).

greater contribution of fires to carbon removal. The Northern U.S. is roughly equivalent to the national average at 86% (Harris et al., 2016).

Proforestation produces natural forests as maximal carbon sinks of diverse species (while supporting and accruing additional benefits of intact forests) and can reduce significantly and immediately the amount of forest carbon lost to non-essential management. Because existing trees are already growing, storing carbon, and sequestering more carbon more rapidly than newly planted and young trees (Harmon et al., 1990; Stephenson et al., 2014; Law et al., 2018; Leverett and Moomaw, in preparation), proforestation is a near-term approach to sequestering additional atmospheric carbon: a significant increase in "negative emissions" is urgently needed to meet temperature limitation goals.

The carbon significance of proforestation is demonstrated in multiple ways in larger trees and older forests. For example, a study of 48 undisturbed primary or mature secondary forest plots worldwide found, on average, that the largest 1% of trees [considering all stems $\geq$1 cm in diameter at breast height (DBH)] accounted for half of above ground living biomass (The largest 1% accounted for $\sim$30% of the biomass in U.S. forests due to larger average size and fewer stems compared to the tropics) (Lutz et al., 2018). Each year a single tree that is 100 cm in diameter adds the equivalent biomass of an entire 10–20 cm diameter tree, further underscoring the role of large trees (Stephenson et al., 2014). Intact forests also may sequester half or more of their carbon as organic soil carbon or in standing and fallen trees that eventually decay and add to soil carbon (Keith et al., 2009). Some older forests continue to sequester additional soil organic carbon (Zhou et al., 2006) and older forests bind soil organic matter more tightly than younger ones (Lacroix et al., 2016).

If current management practices continue, the world's forests will only achieve half of their biological carbon sequestration potential (Erb et al., 2018); intensifying current management practices will only decrease living biomass carbon and increase soil carbon loss. Forests in temperate zones such as in the Eastern U.S. have a particularly high untapped capacity for carbon storage and sequestration because of high growth and low decay rates (Keith et al., 2009) and because of recent recovery from an extensive history of timber harvesting and land conversion for agriculture in the 18th, 19th, and early 20th centuries (Pan et al., 2011; Duveneck and Thompson, 2019). In New England, median forest age is about 75 years of age (United States Forest Service, 2019), which is only about 25–35% of the lifespan of many of the common tree species in these forests (Thompson et al., 2011). Much of Maine's forests have been harvested continuously for 200 years and have a carbon density less than one-third of the forests of Southern Vermont and New Hampshire, Northwestern Connecticut and Western Massachusetts—a region that has not been significantly harvested over the past 75–150 years (National Council for Air Stream Improvement, 2019). Western Massachusetts in particular has a significant portion classifed as Tier 1 matrix forest, defined as "*large contiguous areas whose size and natural condition allow for the maintenance of ecological processes*" (Databasin, 2019). However, forests managed as intact do not need to be large or old in absolute terms to have ecological value: disturbances create gaps and young habitats, and the official policy of the Commonwealth of Massachusetts Department of Environmental Management (now Department of Conservation and Recreation) considers an old-growth forest of at least 2 hectares ecologically significant (Department of Environmntal Management, 1999).

As shown in **Table 1**, ecosystem services accrue as forests age for centuries. Far from plateauing in terms of carbon sequestration (or added wood) at a relatively young age as was long believed, older forests (e.g., >200 years of age without intervention) contain a variety of habitats, typically continue to sequester additional carbon for many decades or even centuries, and sequester significantly more carbon than younger and managed stands (Luyssaert et al., 2008; Askins, 2014; McGarvey et al., 2015; Keeton, 2018). A recent paper affirmed that letting forests grow is an effective way to sequester carbon—but unlike previous studies it suggested that sequestration is highest in "young" forests (Pugh et al., 2019). This conclusion is problematic for several reasons. One confounding factor is that older forests in the tropics were compared to young forests in temperate and boreal areas; temperate forests in particular have the highest CO_2 removal rates and overall biological carbon sequestration (Keith et al., 2009) but this high rate is not limited to young temperate and boreal forests. The age when sequestration rates decrease is not known, and Pugh et al. defined "young" as up to 140 years. As noted above, Keeton et al. (2011) estimate that secondary forests in the Northeast have the potential to increase their biological carbon sequestration several-fold. More field work is needed across age ranges, species and within biomes, but the inescapable conclusion is that growing forests is beneficial to the climate and maintaining intact forest has additional benefits (**Table 1**). We conclude that proforestation has the potential to provide rapid, additional carbon sequestration to reduce *net* emissions in the U.S. by much more than the 11% that forests provide currently (United States Environmental Protection Agency, 2019). A recent report on natural climate solutions determined that negative emissions could be increased from 11 to 21% even without including proforestation (Fargione et al., 2018). Quantified estimates of increased forest sequestration and ecosystem services were based on re-establishing forests where possible and lengthening rotation times on private land; they explicitly did not account for proforestation potential on public land.

Although biological carbon storage in managed stands, regardless of the silvicultural prescription, is generally lower than in unmanaged intact forests (Harmon et al., 1990; Ford and Keeton, 2017)—even after the carbon stored in wood products is included in the calculation—stands managed with reduced harvest frequency and increased structural retention sequester more carbon than more intensively managed stands (Nunery and Keeton, 2010; Law et al., 2018). Such an approach for production forests, or "working" forests—balancing resource extraction with biological carbon sequestration—is often termed "managing for net carbon" or "managing for climate change" and an approach that should be promoted alongside dedicating significant areas to intact ecosystems. Oliver et al. (2014) acknowledge a balance between intact and managed forest and suggest that long term storage in "efficient" wood products like wood building materials (with the potential for less carbon emissions compared to steel or concrete, termed the "avoidance pathway") can offer a significant carbon benefit. To achieve this, some questionable assumptions are that 70% of the harvested wood is merchantable and stored in a lasting product, all unmerchantable wood is removed and used, harvesting occurs at optimum intervals (100 years) and carbon sequestration tapers off significantly after 100 years. Forestry models underestimate the carbon content of older, larger trees, and it is increasingly clear that trees can continue to remove atmospheric carbon at increasing rates for many decades beyond 100 years (Robert T. Leverett, pers. comm. Stephenson et al., 2014; Lutz et al., 2018; Leverett et al., under review). Because inefficient logging practices result in substantial instant carbon release to the atmosphere, and only a small fraction of wood becomes a lasting product, increasing market forces and investments toward wood buildings that have relatively short lifetimes could increase forest extraction rates significantly and become unsustainable (Oliver et al., 2014).

HABITAT PROTECTION, BIODIVERSITY AND SCIENTIFIC VALUE OF PROFORESTATION

Large trees and intact, older forests are not only effective and cost-effective natural reservoirs of carbon storage, they also provide essential habitat that is often missing from younger, managed forests (Askins, 2014). For example, intact forests in Eastern U.S. national parks have greater tree diversity, live and dead standing basal area, and coarse woody debris, than forests that are managed for timber (Miller et al., 2016, 2018; **Table 1**). The density of cavities in older trees and the spatial and structural heterogeneity of the forest increases with stand age (Ranius et al., 2009; Larson et al., 2014), and large canopy gaps develop as a result of mortality of large trees, which result in dense patches of regeneration (Askins, 2014). These complex structures and habitat features support a greater diversity of lichens and bryophytes (Lesica et al., 1991), a greater density and diversity of salamanders (Petranka et al., 1993; Herbeck and Larsen, 1999), and a greater diversity and abundance of birds in old, intact forests than in nearby managed forests (Askins, 2014; Zlonis and Niemi, 2014; **Table 1**). Forest bird guilds also benefit from small intact forests in urban landscapes relative to unprotected matrix forests (Goodwin and Shriver, 2014). Several bird species in the U.S. that are globally threatened—including the wood thrush, cerulean warbler, marbled murrelet, and spotted owl are, in part, dependent on intact, older forests with large trees (International Union for Conservation of Nature, 2019). Two species that are extinct today—Bachman's warbler and Ivory-billed woodpecker—likely suffered from a loss of habitat features associated with old forests (Askins, 2014).

Today, forest managers often justify management to maintain heterogeneity of age structures to enhance wildlife habitat and maintain "forest health" (Alverson et al., 1994). However, early successional forest species (e.g., chestnut-sided warbler and New England cottontail) that are common targets for forest management may be less dependent on forest management than is commonly believed (cf. Zlonis and Niemi, 2014; Buffum et al., 2015). Management also results in undesirable consequences such as soil erosion, introduction of invasive and non-native species (McDonald et al., 2008; Riitters et al., 2018), loss of carbon—including soil carbon (Lacroix et al., 2016), increased densities of forest ungulates such as white-tailed deer (Whitney, 1990)—a species that can limit forest regeneration (Waller, 2014)—and a loss of a sense of wildness (e.g., Thoreau, 1862).

Forest health is a term often defined by a particular set of forestry values (e.g., tree regeneration levels, stocking, tree growth rates, commercial value of specific species) and a goal of eliminating forest pests. Although appropriate in a commercial forestry context, these values should not be conflated with the ability of intact natural forests to continue to function and even thrive indefinitely and provide a diversity of habitats on their own (e.g., Zlonis and Niemi, 2014). Natural forests, regardless of their initial state, naturally develop diverse structures as they age and require from us only the time and space to self-organize (e.g., Larson et al., 2014; Miller et al., 2016).

Intact forests provide irreplaceable scientific value. In addition to a biodiverse habitat an intact forest provides an area governed by natural ecological processes that serve as important scientific controls against which to compare the effects of human activities and management practices (Boyce, 1998). Areas without resource extraction (i.e., timber harvesting, hunting), pest removal, or fire suppression allow for a full range of natural ecological processes (fire, herbivory, natural forest development) to be expressed (Boyce, 1998). Only if we have sufficient natural areas can we hope to understand the effects of human activities on the rest of our forests. Additional research and monitoring projects that compare ecological attributes between intact and managed forests at a range of spatial scales will also help determine how effective protected intact forests can be at conserving a range of biota, and where additional protected areas may need to be established (e.g., Goodwin and Shriver, 2014; Jenkins et al., 2015).

PROFORESTATION AND FOREST FIRES

Given the increase in forest area burned in the United States over the past 30 years (National Interagency Fire Center, 2019), it is important to address the relationship between forest management and forest fires. There is a widely held perception that the severity and size of recent fires are directly related to the fuels that have accumulated in the understory due to a lack of forest management to reduce these fuels (i.e., pulping, masticating, thinning, raking, and prescribed burning; Reinhardt et al., 2008; Bradley et al., 2016). However, some evidence suggests that proforestation should actually *reduce* fire risk and there are at least three important factors to consider: first, fire is an integral part of forest dynamics in the Western U.S.; second, wildfire occurrence, size, and area burned are generally not preventable even with fuel removal treatments (Reinhardt et al., 2008); and third, the area burned is actually far less today than in the first half of the twentieth century when timber harvesting was more intensive and fires were not actively suppressed (Williams, 1989; National Interagency Fire Center, 2019). Interestingly, in the past 30 years, intact forests in the Western U.S. burned at significantly *lower* intensities than did managed forests (Thompson et al., 2007; Bradley et al., 2016; **Table 1**). Increased potential fuel in intact forests appear to be offset by drier conditions, increased windspeeds, smaller trees, and residual and more combustible fuels inherent in managed areas (Reinhardt et al., 2008; Bradley et al., 2016). Rather than fighting wildfires wherever they occur, the most effective strategy is limiting development in fire-prone areas, creating and defending zones around existing development (the wildland-urban interface), and establishing codes for fire-resistant construction (Cohen, 1999; Reinhardt et al., 2008).

PROFORESTATION AND ECOSYSTEM SERVICES: SERVING THE GREATEST GOOD

In 1905 Gifford Pinchot, Chief of the U.S. Forest Service, summarized his approach to the nation's forests when he wrote "...where conflicting interests must be reconciled, the question will always be decided from the standpoint of the greatest good of the greatest number in the long run." This ethos continues to define the management approach of the U.S. Forest Service from its inception to the present day. Remarkably, however, even in 2018 the five major priorities of the Forest Service do not mention biodiversity, carbon storage, or climate change as major aspects of its work (United States Forest Service, 2018).

Today, the needs of the nation have changed: emerging forest science and the carbon and biodiversity benefits of proforestation demand a focus on growing intact natural public and private forests, including local parks and forest reserves (Jenkins et al., 2015). There is also a growing need across the country, and particularly within reach of highly populated areas, for additional local parks and protected forest reserves that serve and provide the public with solitude, respite, and wild experiences (e.g., Thoreau, 1862). Detailed analysis of over one thousand public comments regarding management of Hoosier National Forest, a public forest near population centers in several states, revealed a strong belief that wilderness contributes to a sense of well-being. Responses with the highest frequency reflected an interest in preservation and protection of forests and wildlife, a recognition of the benefits to human physical and mental health, a sense of ethical responsibility, opposition to damage and destruction, monetary concerns, and a preponderance of sadness, fear and distress over forest loss (Vining and Tyler, 1999).

Quantifiable public health benefits of forests and green spaces continue to emerge, and benefits are highest in populations with chronic and difficult-to-treat conditions like anxiety, depression, pain and post-traumatic stress disorder (Karjalainen et al., 2010; Frumkin et al., 2017; Hansen et al., 2017; Oh et al., 2017). In the United Kingdom "growing forests for health" is the motto of the National Health Service Forest (2019) and there is a recognized need for evidence-based analysis of human health co-benefits alongside nature-based ecosystem services (Frumkin et al., 2017).

POLICY RECOMMENDATIONS

To date, the simplicity of the idea of proforestation has perhaps been stymied by inaccurate or non-existent terminology to describe it. Despite a number of non-binding international forest agreements (United Nations Conference on Environment Development, 1992; United Nations Forum on Forests, 2008; Forest Declaration, 2014) and responsibilities by a major UN organization [Food and Agriculture Organization (FAO)], current climate policies lack science-based definitions that distinguish forest condition—including the major differences between young and old forests across a range of ecosystem services. Lewis et al. (2019) further note that broad definitions and confused terminology have an unfortunate result that policymakers and their advisers mislead the public (Lewis et al., 2019). Most discussions concerning forest loss and forest protection are in terms of percentage of land area that has tree canopy cover (Food and Agriculture Organization, 2019). This lack of specificity significantly hampers efforts to evaluate and protect intact forests, to quantify their value, and to dedicate existing forests as intact forests for the future. For example, the UN Framework Convention on Climate Change and the FAO consider and group tree plantations, production forests, and mature intact forests equally under the general term "forest" (Mackey et al., 2015). In addition, "forest conservation" simply means maintaining "forest cover" and does not address age, species richness or distribution—or the degree that a forest ecosystem is intact and functioning (Mackey et al., 2015). The erroneous assumption is that all forests are equivalently beneficial for a range of ecosystem services—a conclusion that is quantitatively inaccurate in terms of biological carbon sequestration and biodiversity as well as many other ecosystem services.

Practicing proforestation should be emphasized on suitable public lands as is now done in U.S. National Parks and Monuments. Private forest land owners might be compensated to practice proforestation, for sequestering carbon and providing associated co-benefits by letting their forests continue to grow. At this time, we lack national policies that quantify and truly maximize benefits across the landscape. At a regional scale, however, some conservation visions do explicitly recognize and promote the multiple values and services associated with forest reserves or wildlands (e.g., Foster et al., 2010) and climate offset programs can be used explicitly to support proforestation. For example, a recent project by the Nature Conservancy protected 2,185 hectares (5,400 acres) in Vermont as wildland and is expected to yield ∼$2 M over 10 years for assuring long-term biological carbon storage (Nature Conservancy, 2019). Burnt Mountain is now protected by a "forever wild" easement and part of a 4,452 hectare (11,000 acre) preserve. More public education and similar incentives are needed.

CONCLUSIONS

To meet any proposed climate goals of the Paris Climate Agreement (1.5, 2.0° C, targets for reduced emissions) it is essential to simultaneously *reduce greenhouse gas emissions from all sources* including fossil fuels, bioenergy, and land use change, and *increase CDR* by forests, wetlands and soils. Concentrations of these gases are now so high that reducing emissions alone is insufficient to meet these goals. Speculation that untested technologies such as BECCS can achieve the goal while allowing us to continue to emit more carbon has been described as a "moral hazard" (Anderson and Peters, 2016). Furthermore, BECCS is not feasible within the needed timeframe and CDR is urgent. Globally, existing forests only store approximately half of their potential due to past and present management (Erb et al., 2018), and many existing forests are capable of immediate and even more extensive growth for many decades (Lutz et al., 2018). During the timeframe while seedlings planted for afforestation and reforestation are growing (yet will never achieve the carbon density of an intact forest), proforestation is a safe, highly effective, immediate natural solution that does not rely on uncertain discounted future benefits inherent in other options.

Taken together, proforestation is a rapid and essential strategy for achieving climate and biodiversity goals and for serving the greatest good. Stakeholders and policy makers need to recognize that the way to maximize carbon storage and sequestration is to grow intact forest ecosystems where possible. Certainly, all forests have beneficial attributes, and the management focus of some forests is providing wood products that we all use. But until we acknowledge and quantify differences in forest status (Foster et al., 2010), we will be unable to develop policies (and educate landowners, donors, and the public) to support urgent forest-based benefits in the most effective, locally appropriate and cost-effective manner. A differentiation between production forests and natural forest ecosystems would garner public support for a forest industry with higher value products and a renewed focus on reducing natural resource use—and for recycling paper and wood. It could also spur long-overdue local partnerships between farms and forests—responsible regional composting keeps jobs and resources within local communities while improving soil health and increasing soil carbon (Brown and Cotton, 2011). The forest industry as a whole can benefit from proforestation-based jobs that focus on scientific data collection, public education, public health and a full range of ecosystem services.

In sum, proforestation provides the most effective solution to dual global crises—climate change and biodiversity loss. It is the only practical, rapid, economical, and effective means for atmospheric CDR among the multiple options that have been proposed because it removes more atmospheric carbon dioxide in the immediate future and continues to sequester it long-term. Proforestation will increase the diversity of many groups of organisms and provide numerous additional and important ecosystem services (Lutz et al., 2018). While multiple strategies will be needed to address global environmental crises, proforestation is a very low-cost option for increasing carbon sequestration that does not require additional land beyond what is already forested and provides new forest related jobs and opportunities along with a wide array of quantifiable ecosystem services, including human health.

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Intact Forest in Selective Logging Landscapes in the Tropics

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The selective logging that characterizes most timber extraction operations in the tropics leaves large patches of logging blocks (i.e., areas allocated for harvesting) intact, without evidence of direct impacts. For example, in ∼10,000 ha sampled in 48 forest management enterprises in Africa (Gabon, Republic of Congo, and the Democratic Republic of Congo), Indonesia, Suriname, and Mexico, an average of 69% (range 20–97%) of the area in logging blocks was not directly affected by timber harvests. The proportion of intact forest within logging blocks decreased very slightly with increases in harvest intensity in the accessed portion of the logging blocks (9–86 m^3 ha^{-1}) but decreased strongly with harvest intensity in entire logging blocks (0.3–48.2 m^3 ha^{-1}). More forest was left intact in areas farther from roads, on slopes >40%, and within 25 m of perennial streams, but the effect sizes of each of these variables was small (∼8%). It is less clear how much of the intact forest left after one harvest will remain intact through the next. Conservation benefits without reductions in timber yields will derive from better management planning so that sensitive and ecologically critical areas, such as steep slopes and riparian buffers, constitute large and permanent proportions of the intact forest in selectively logged landscapes in the tropics.

Keywords: conservation, land-use planning, reduced-impact logging, sparing-sharing, tropical forestry

INTRODUCTION

Heightened concerns about tropical forest fates and limited funds for their conservation are reasons to strive for efficiency and effectiveness in investments in environmental protection. Where forests are threatened by agricultural conversion, insights have been derived from contrasts of the ends of the land-use continuum that runs from forest sparing via agricultural intensification in small areas through land-sharing with extensive wildlife-friendly agricultural practices (e.g., Phalan et al., 2011). This dichotomous approach proved less appropriate where productive land uses do not result in biodiversity decimation, such as natural forest management based on selective logging (e.g., Edwards et al., 2014; Griscom et al., 2018; Runting et al., 2019). Here we elaborate on the forest sparing-sharing discourse by focusing on forest spared from logging's direct impacts in landscapes allocated for timber production. By direct impacts, we mean logging-induced changes in vegetation and soils such as forest clearing and soil scarification for road building, soil compaction on skid trails, and canopy opening in felling gaps. We refer to these spared stands as "intact" in full recognition that they may have lost or might soon lose their fauna, may be hydrologically compromised, or suffer other forms of degradation such as from pollution and invasive exotic species. In other words, we focus only on the direct or primary impacts of selective logging in full recognition of the often critical secondary impacts associated with the access provided by logging roads.

Due to differences in market acceptability and commercial species stocking, logging intensities also vary substantially among regions (e.g., Putz et al., 2001; Ellis P. W. et al., 2019). For example, in the forest management enterprises (FMEs) analyzed in this study, logging intensities ranged from 0.3 and 1.1 m^3 ha^{-1} in two Mexican ejidos (i.e., community-based FMEs; Ellis E. A. et al., 2019) to 53.3 and 56.5 m^3 ha^{-1} in two industrial concessions in Indonesia (Griscom et al., 2019). Understanding how the intensity of timber trees removal affects the intactness of forest within a logging block is critical for future management planning.

Due to the spatial aggregation of commercially valuable timber trees in most tropical forests, coupled with topographical impediments and other biophysical/economic constraints, selective logging is notoriously patchy. This aggregation means that values for intensity that are averaged over large areas often poorly reflect conditions on the ground. For example, in 32 plots of 1 ha set up prior to logging in East Kalimantan, Indonesia, (Sist et al., 1998) reported that logging intensities averaged 86.9 m^3ha^{-1} (nine trees ha^{-1}) but ranged 9–247 m^3 ha^{-1} with 1–17 trees ha^{-1} harvested. In Gabon, where overall logging intensities averaged 8.11 m^3ha^{-1} and 0.82 trees ha^{-1}, five of the ten 1 ha plots established in the logging area yielded no timber, and two of those were also not traversed by skid trails (Medjibe et al., 2011). Reported levels of spatial variance are noticeably lower in studies in which plots were set up post-logging to represent a range of logging intensities (e.g., Ewers and Banks-Leite, 2013; Riutta et al., 2018), but can nevertheless be substantial, especially when sampled at sub-hectare scales (e.g., Pfeifer et al., 2016; Senior et al., 2017).

In discussions of intactness, the issues of spatial scale and characteristics of surrounding habitats should loom large. We fully endorse appropriate forms of protection for as much of the remaining large swaths of intact tropical forests as possible; those areas are of irreplaceable environmental and spiritual value. Smaller areas of forest might not support viable populations of forest interior species and may not provide people with wilderness experiences. Nevertheless, even small patches of undisturbed forest are functionally intact for some processes and fully suitable for some species while they maintain gene pools and serve as seed sources (e.g., Turner and Corlett, 1996; Arroyo-Rodríguez et al., 2009). Furthermore, the ecological value of small intact areas is augmented if the surroundings are selectively logged and not cleared, especially if the harvests are low intensity and conducted using reduced-impact (RIL) logging practices. In regards to the permanence of the status of intact patches of forest in selectively logged landscapes, we argue that even temporary reprieves from deforestation or degradation are of value, given the rate of wholesale forest destruction. An analogous situation pertains to "wildfire refugia," those patches of unburned forest in landscapes subjected to mixed-severity fires (e.g., Kolden et al., 2017).

Although the shape and temporal permanence of intact forest patches in logged landscapes are not considered in our analysis, we recognize that intactness is as multidimensional a concept as forest degradation (e.g., Thompson et al., 2013) and similarly deserving of local definitions (e.g., Vásquez-Grandon et al., 2018). What makes defining intactness particularly challenging is that its dimensions are not all orthogonal, linear, continuous, and constant, nor can they all be objectively delineated. Proclaimed definitions or benchmarks (e.g., >500 km^2; Potapov et al., 2017) are easily communicated and can be politically expedient, but the fact remains that intactness is not a binary trait. We argue that intact forest in logged landscapes ranges in size from small and isolated patches of remnant trees through contiguous strips of riparian forest, to unlogged high-conservation value areas of hundreds or thousands of hectares.

Here we describe the spatial heterogeneity of selective logging impacts in tropical Southeast Asia, Africa, and the Americas with field data collected with identical protocols and analyzed in a uniform manner. We explore why intact forest was retained in logged landscapes such as due to regulatory constraints (e.g., riparian buffer zones), remoteness, steepness, low soil trafficability, inaccessibility (e.g., surrounded by rocky cliffs), or low stocking. This last-mentioned condition may be permanent, if due to adverse conditions, or temporary. With some reluctance because this study was not designed to assess the impacts of Forest Stewardship Council (FSC) certification [for a description of how such studies should be designed see (Romero et al., 2017)], we also present a naïve comparison of the proportions of logged blocks left intact in the 12 certified FMEs with the 36 non-FSC FMEs. We note that a similar analysis for the same FMEs revealed no association between FSC certification and carbon emissions from selective logging (Ellis P. W. et al., 2019).

CAVEAT

Before proceeding, we want to clarify that we are not unquestioning advocates of logging, especially not in primary forest. Nevertheless, we accept that tropical forests will continue to be logged and recognize the geopolitical and economic justifications for use of renewable natural resources. This justification is bolstered by the failure of environmentalists to secure the funds needed to make protection a financially attractive option for all but a few forests. Our main goal is improved timber stand management, as appropriate for maintenance of ecological integrity, in tropical forests that will be logged. We also assert that intact forest within logging landscapes deserve recognition and that there are environmental as well as economic benefits to be derived from better spatial planning of tropical forest management. That said, we do not equate relatively small patches of unlogged forest in selectively logged landscapes with the extensive (i.e., >500 km^2) areas free from substantial human impacts that qualify as "Intact Forest Landscapes," as defined by Potapov et al. (2008) and mapped and tracked by international organizations including such as World Resources Institute and Greenpeace (http://www.intactforests.org/; Potapov et al., 2017). We point out, however, that selectively logged landscapes maintain substantial proportions of their biodiversity and carbon stocks (e.g., Sist and Nguyen-Thé, 2002; Putz et al., 2012; Edwards et al., 2014), especially if logging intensities are low (i.e., <8 trees ha^{-1}; Burivalova et al., 2014), reduced-impact logging practices are employed (e.g., Pinard and Putz, 1996; Bicknell et al., 2014), and hunting is limited (e.g., Roopsind et al., 2017).

METHODS

Blocks of forest with active logging operations in each country were selected at random from strata defined by forest management enterprise (FME) size, soils, elevation, and certification status (i.e., FSC certified or not). The sampled countries (Indonesia, Gabon, Democratic Republic of Congo, Republic of Congo, Suriname, and Mexico) represent a wide range of selective logging intensities, harvesting methods, ecological conditions, and socio-political contexts. In Indonesia field data were collected in recently logged areas with the reduced-impact logging for climate (RIL-C) method described by Griscom et al. (2014, 2019), while in other geographies a refined RIL-C protocol was used as described by Ellis P. W. et al. (2019). We deviate from the RIL-C protocol only insofar as we defined accessed areas individually for each country based on delineation of skid trail buffers at the 95th percentile of the distance from stumps of harvested trees to the nearest skid trail; buffers ranged from 9.8 m in RoC to 32.7 m in Indonesia (Ellis P. W. et al., 2019; see **Figure 1**). Basically, to map skid trails in 42 of the 48 logging blocks sampled (one per FME except in Indonesia), field crews equipped with wide-area augmentation system-enabled Garmin GPS receivers mapped an average of 6 km of skid trails and measured the widths of 5 km of logging roads (distance between the trunks of standing trees >10 cm DBH) in recently logged blocks of 38–415 ha (see Ellis P. W. et al., 2019 for further description of field and analytical methods). In the remaining six logging blocks in Indonesia, we collected medium density (mean = 4.5 points m^{-2}), discrete return lidar data from a standard altitude of 650 m in April 2013 and used those data to map logging impacts in 5,620 ha that included six annual cutting areas encompassing 54 logging blocks in five FMEs following methods described in Ellis et al. (2016) to avoid pseudoreplication, we used mean logging block statistics from each annual cutting area.

The hypothesis that intact forest is farther from the nearest haul road than areas that were accessed by loggers was tested by comparing the means of the Euclidian distances between the closest haul road section and the accessed and intact forest areas in each logging block with a paired *t*-test. Two blocks were excluded due to computational difficulties and additional four were excluded because no haul roads crossed the blocks. Data included in this analysis were from 42 logging blocks in six countries, with six in Indonesia, eight in Mexico, six in Suriname, eight in DRC, eight in Gabon, and six in ROC.

To determine whether loggers avoided steep slopes, we first classified steep forest areas as those with slopes >40% (21.8°) based on a 1 arc second (30 m) digital elevation model (DEM) constructed with SRTM data (USGS, 2004). We then used the proportions of entire logging blocks left intact to generate the expected proportions of intact steep pixels and then compared this expected proportion with the observed values for blocks with >15% steep pixels. We used a similar approach to test the hypothesis that loggers avoided riparian areas, which we defined as being within 25 m of a stream. Of the many ways to identify streams, we employed a basic approach using Esri's Hydrology toolset. First, we located each logged block within a Level 12 HydroSHEDS Basin (Lehner et al., 2008) and used this to bound our analysis area. We identified and filled sinks within each 30 m DEM, and then used a D8 flow method to compute flow directions. Finally, we calculated the accumulated flow within each watershed and then used the mean flow accummulation for the watershed as the threshold to identify the head of the drainage network (Tang et al., 2001).

All geospatial analyses were conducted in ArcGIS v10. 10.3.1 (ESRI, 2015) and statistical analyses with base packages in R v 3.5.0 (R Development Core Team, 2016), unless mentioned otherwise.

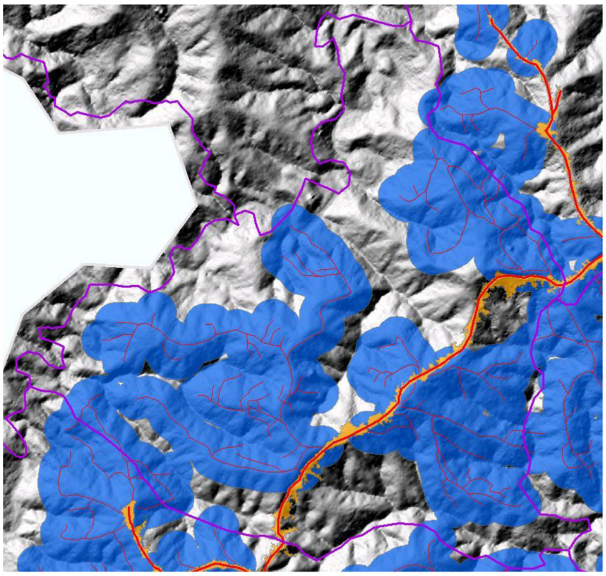

FIGURE 1 | Lidar-delimited (1:10,000) skidding/felling (blue) and haul-road (orange) impact zones in an FME in Kalimantan, Indonesia with purple lines demarcating the logging block boundaries, ridges are indicated by dark shading, valleys with light shading, and the logging road in red (reprinted with permission from Ellis et al., 2016). Note that timber in the area to the northwest was not yet harvested.

RESULTS

Intact forest covered a mean of 69% (range 20–97%) of the 48 logged blocks in six tropical countries (**Figure 2**). When data from all regions are combined, we detected a small but statistically insignificant decrease in the proportion of forest left intact in logged blocks with harvest intensity in the accessed area (% intact = 0.78–0.0026 * harvest intensity; SE$_b$ = 0.0014, df =

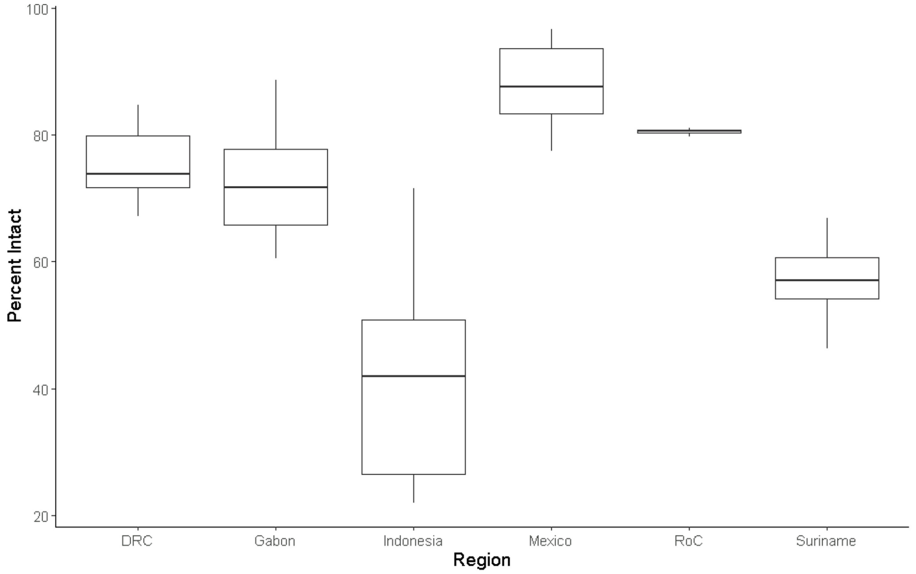

FIGURE 2 | Proportions of intact forest in selectively logged harvest blocks (DRC, Democratic Republic of Congo; RoC, Republic of Congo).

45, $P = 0.06$, adjusted $R^2 = 0.055$; **Figure 3A**). In contrast, if harvest intensities are assumed to represent conditions in entire logging blocks, which is commonly assumed, there was a more marked decrease in intact area with harvest intensity (% intact = 0.83–0.0109 * harvest intensity per cutting block; $SE_b = 0.0015$, df = 46, $P < 0.001$, adjusted $R^2 = 0.529$; **Figure 3B**). In the 42 logging blocks in six countries with road data, as expected, intact areas averaged a larger distance (289.6 m, SD = 25.54 m) from the nearest haul-road than accessed areas (231 m, SD = 20.6 m; $t = 4.0$, $P < 0.01$). Distances to haul-roads ranged 64–722 m for intact areas and 56–662 m for accessed areas. There was no apparent difference in the proportion of forest left intact in the 12 FSC-certified (65 ± 21% SD) and the 36 non-certified FMEs (71 ± 17% SD, $t = 0.77$, $P = 0.45$; **Figure 4**; see supplementary data table for complete results and logging block statistics).

Analyses of the effects of steep slopes and stream buffers on the distribution of logging were limited by the presence of these conditions in the surveyed harvest blocks. Steep areas (>40% slope) covered <15% of the logging blocks in Suriname and the Democratic Republic of Congo while there were no streams in the Mexican blocks due to subterranean drainage. Of the 13 logged blocks with their area >15% on slopes >40%, forest was left intact in 76% of the steep pixels and 60% of the less steep pixels (SD = 27 and 22%, respectively; $t = 6.8$, $P < 0.001$; **Figure 5A**). In the 26 blocks with streams, an average of 73% (S.D. = 24%) of pixels < 25 m from a stream were intact in contrast to 61% of pixels farther from streams (SD = 26%; $t = 3.5$; $P < 0.001$; **Figure 5B**).

DISCUSSION

In the six tropical countries in which we assessed spatial variation in selective logging impacts, more than half of the forest in blocks allocated for logging experienced no direct impacts of timber harvests. This finding indicates that studies that describe the impacts of logging based on data collected only where harvests actually occurred exaggerate those impacts by a factor of two. Depending on the spatial distributions of intact forest in logged landscapes and the permanence of those refugia, opportunities abound for both conservation and silvicultural intensification. Ideally, standing forest should be retained in riparian and other ecologically sensitive areas. Conversely, for both ecological and economic reasons, silvicultural treatments prescribed to increase the stocking and growth of commercial timber should be concentrated near existing roads and on suitable terrain. If appropriate spatial planning regulations were developed and then followed, both economic and ecological benefits could be secured, but tropical forestry has proven itself incredibly resistant to regulatory reform (e.g., Fraser, 2019).

Many factors influenced how much forest was left unscathed by loggers and the locations of the fractions that escaped felling, skidding, and hauling damage. Surprisingly, logging intensity, as expressed in terms of timber volumes harvested from the accessed portions of logging blocks, explained little of the variance in the proportions of intact forest retained. For example, logging refugia were scarce in the intensively logged forests of Indonesia, but were also scarce in Suriname where logging intensities were low. This finding is partially explained by the relatively small sizes of individual trees harvested in Suriname, which meant that for the same volumetic yields, more trees were harvested. To a small but statistically significant extents, loggers avoided areas on steep slopes, near streams, and far from haulroads. Harvesting costs obviously increase with distance but also increase with slope basically due to the need to overcome gravitational forces (Putz et al., 2018). Whether riparian area avoidance was due to regulations, physical constraints on timber extraction, low stocking, or some combination of these factors,

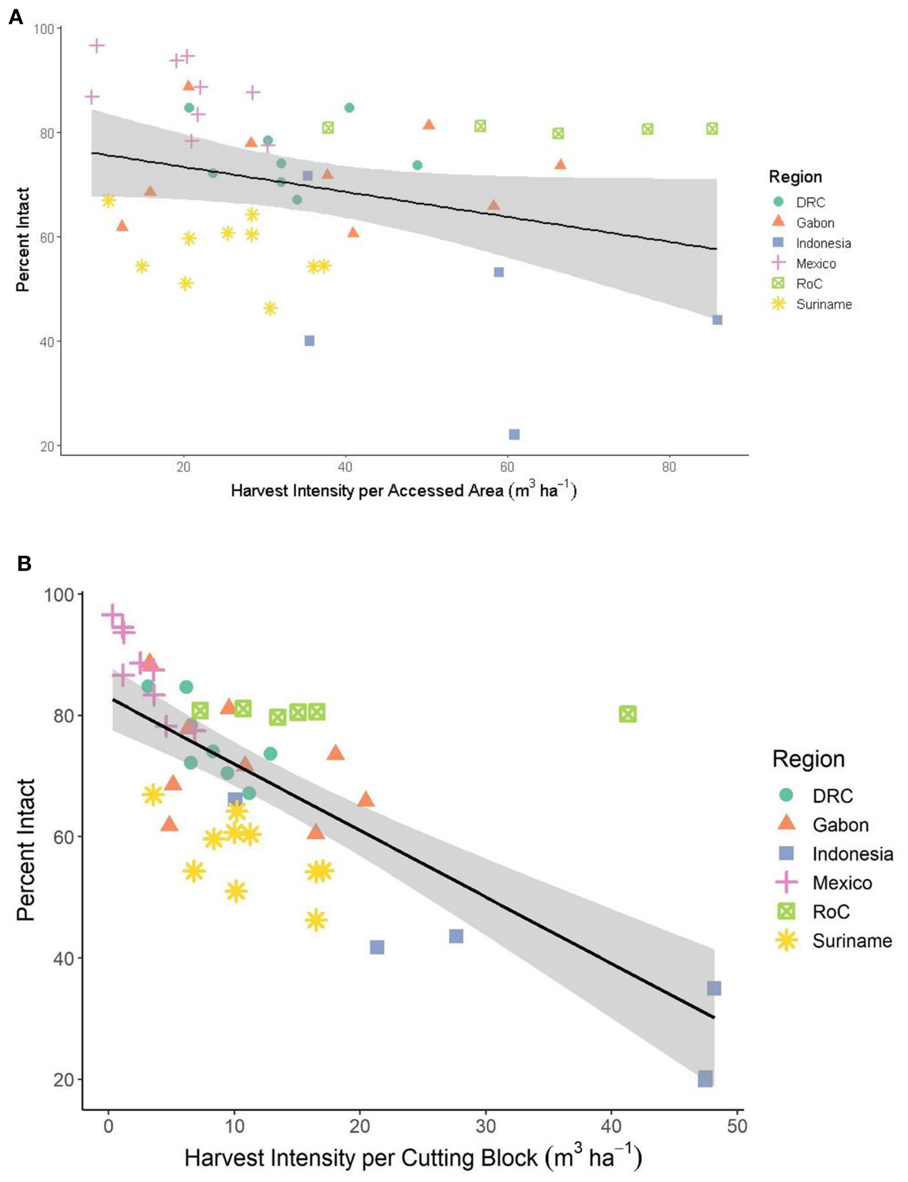

FIGURE 3 | The extents of intact forest (%) in selectively logged forests as a function of harvest intensities (m^3 ha^{-1}) in accessed areas **(A)** and across entire logging (cutting) blocks **(B)**.

the result is clearly environmentally beneficial. We note that in the lidar-sampled FMEs in Indonesia, Ellis et al. (2016) found that above-ground biomass in steep and riparian areas did not differ from elsewhere in the logging blocks, which suggests that timber scarcity was not the predominant cause of these findings.

Given concerns about forest degradation and the fact that selective logging in the tropics is the major cause of that degradation (e.g., Asner et al., 2005; Hosonuma et al., 2012; Pearson et al., 2017), it behooves conservationists to be abundantly clear in their analyses of the impacts of timber harvests and other interventions. Based on the findings presented in this paper, forest degradation analyses (e.g., Vásquez-Grandon et al., 2018) need to consider the spatial patterns of reduced basal area or biomass, loss of species, domination by pioneer species, or lack of regeneration. Clearly, the ecological consequences of a 50% reduction in biomass are different if that change is spatially uniform than if half the area is clear-cut while the other half remained unscathed. It also matters whether the unscathed portion is a continuous band of riparian forest or small, isolated patches of standing trees in an otherwise deforested landscape. Edge effects also deserve consideration but are likely modest and temporary in selectively logged forests except along the main haul roads, which typically cover <2% of logging areas in the tropics (Malcolm and Ray, 2000; Kleinschroth and Healey, 2017). Our analyses demonstrate that the impacts of selective logging are not spatially uniform in the tropics, which is also

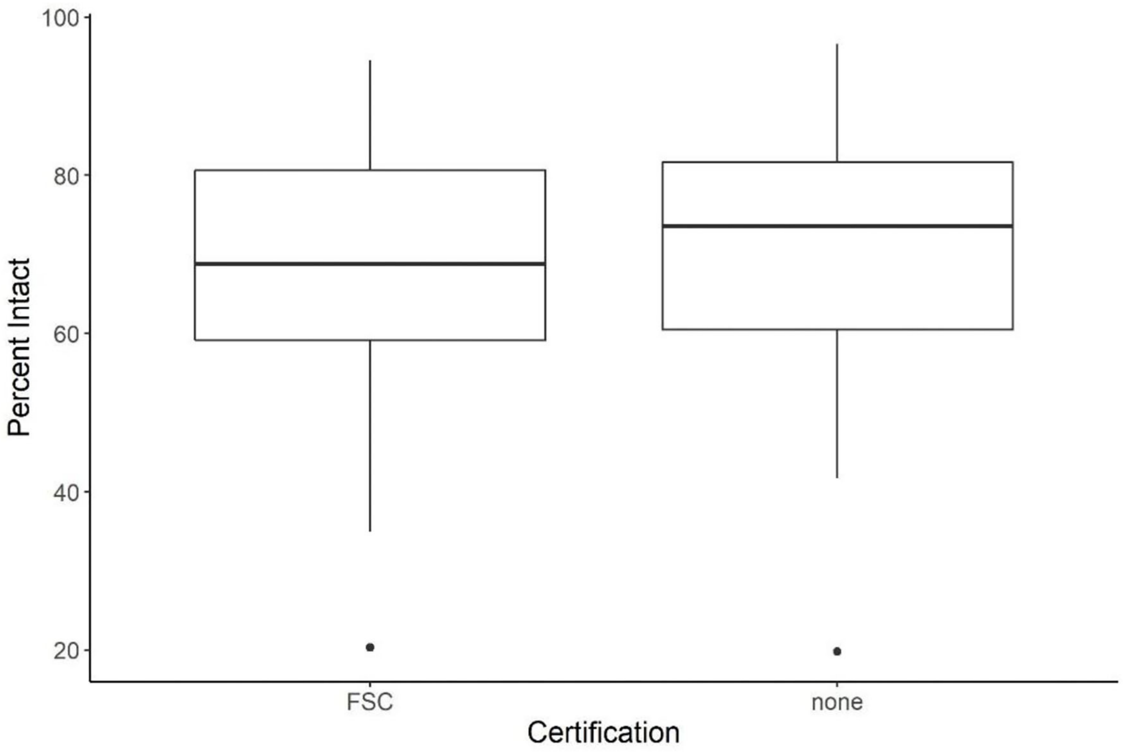

FIGURE 4 | A naïve comparison of the proportions of intact forest in Forest Stewardship Council (FSC; *N* = 12) and non-certified forest management enterprises (*N* = 36). Box plot hinges correspond to first and third quartiles, and whiskers extend to highest and lowest values.

apparently the case in similarly treated temperate forests (e.g., Grushecky and Fajvan, 1999).

Comparison of our results with other published measures of logging impacts is challenging due to methodological differences, but the patterns we observed are similar to other reports in the literature. For example, based on field measurements of ground disturbance by selective logging in South America reported for 17 plots in six different published studies, Feldpausch et al. (2005) reported that 46–88% of the forest was not affected directly by logging. Those same authors reported that intact forest area decreased with logging intensity and was much smaller for conventional logging than RIL. In a more recent study of a forest subjected to RIL in Belize at a block-wide intensity of 2.9 m^3 ha^{-1} (2.7 trees ha^{-1}), Arevalo et al. (2016) reported that 93% of the 350-ha harvest block experienced no direct impacts of logging. That value is much higher than the global average of 69% intact reported here, but is similar to the 77–97% intact forest found in logging blocks in Mexico where harvest intensities were also low (0.24–3.15 trees/ha). Similarly, in a pantropical review of the literature on logging roads, Kleinschroth and Healey (2017) reported a median impact of 1.7% of the ground surface. Studies based on remote sensing, especially those that employed canopy-penetrating lidar and wall-to-wall sampling of logged blocks, often report considerably higher proportions of intact forest than field studies (e.g., Ellis et al., 2016). Despite the opportunities for lidar to detect accessed areas accurately (Melendy et al., 2018), larger scale studies using canopy-penetrating lidar have yet to reveal the spatial patterns of intactness in landscapes designated for logging beyond the scale of individual harvest blocks, which could have large implications for meta-population dynamics.

Considerations of the impacts of selective logging in the tropics need to reflect its tremendous spatial variation at all scales. If large portions of logged areas are not directly affected by logging, any data collected on or adjacent to roads, skid trails, or felling gaps (i.e., in the impact zones) needs to be adjusted accordingly. Failure to adjust the results to account for the areas not directly affected clearly exaggerates the impacts of logging. For example, the much- cited study by Thiollay (1997) on the influence of selective logging on birds in French Guiana was based on point counts centered on skid trails and in logging gaps. More recently, Blonder et al. (2018) reported substantially higher temperatures in moderately and heavily logged forests than in old growth, but the two logged hectare plots lost 53 and 86% of their biomass, respectively. It would be dangerous to extend these results to other selectively logged tropical forests that lose, on average, only 11% of their biomass (Ellis P. W. et al., 2019).

Maximizing intact forest in areas designated for logging might, from a landscape-level environmental perspective, be counter-productive especially if by so doing, timber yields decline. Instead, we advocate first of all for scrupulous use of RIL practices and for yield maintenance in designated portions of the logging landscape that are ecologically and economically

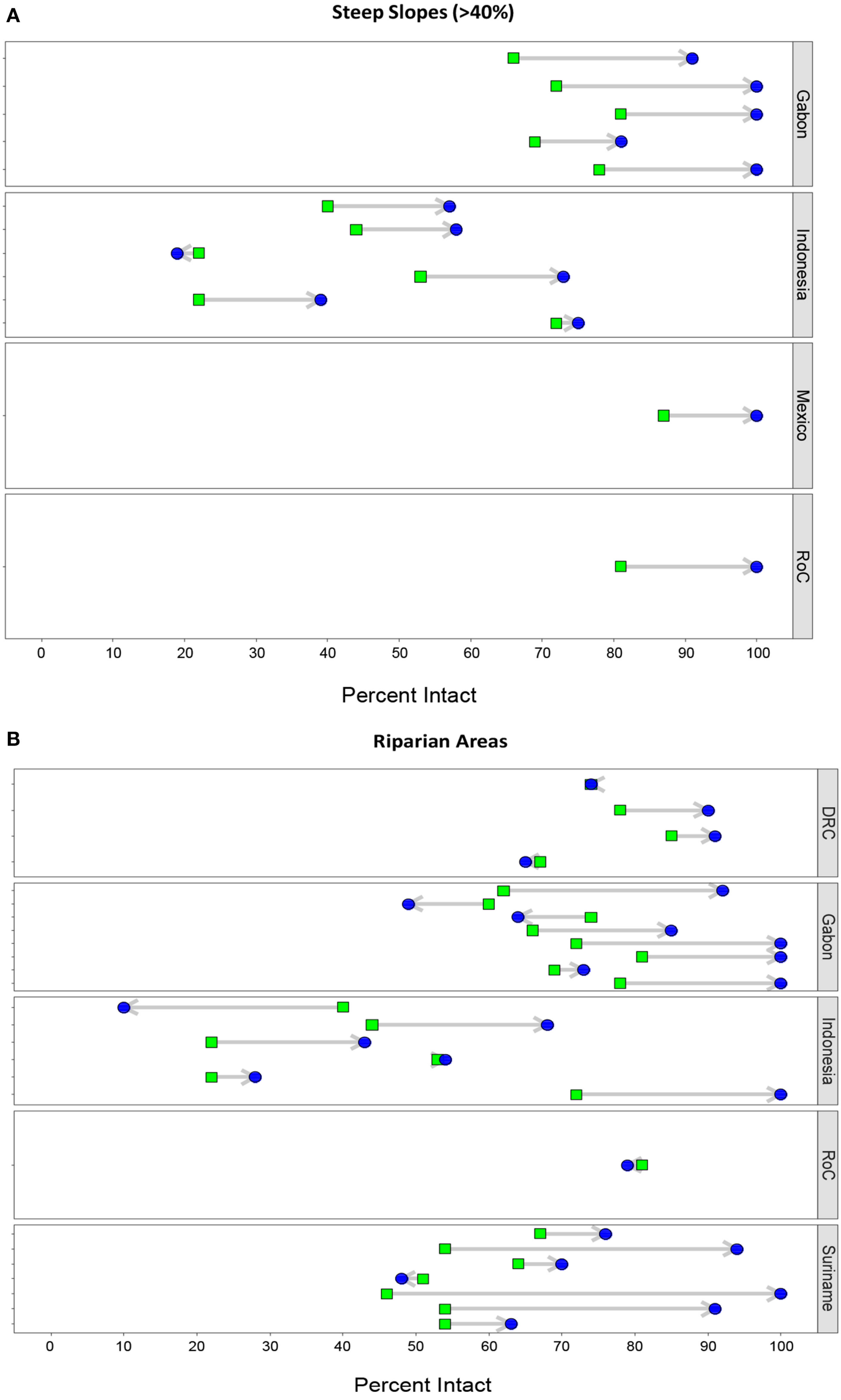

FIGURE 5 | Percentages of 30 m pixels in logged blocks left intact by loggers on **(A)** steep slopes (>40%) and **(B)** <25 m of permanent streams. Green squares show the percent of intact forest in entire logged blocks, blue dots show percent intact on steep slopes and in riparian zones, and gray arrows represent the residual effect size.

appropriate. We also endorse at least gentle silvicultural intensification with interventions designed to increase growth and yield, such as cutting lianas on future crop trees (e.g., Putz and Romero, 2015; Mills et al., 2019). In addition to accessibility, site capability, and environmental or cultural constraints, spatial planning of management in logging landscapes in the tropics should also consider adjacency, connectivity, and patch size (e.g., Llorente et al., 2017).

Improvements in tropical forest management require better spatial planning, but such plans, if properly implemented, might reduce the area of intact forest in logged blocks unless accompanied by clear demarcation and better protection of ecologically sensitive areas. Better planning of logging operations might explain why our naïve comparison on FSC certified and non-certified FMEs did not differ in amounts of intact forest retained. Indeed, one of the benefits of proper planning and implementation of RIL operations is that fewer trees and logs are missed by harvest crews (Holmes et al., 2002). Our results also show that loggers already avoid steep areas and riparian zones to some extent, but they also seem to skip patches of forest with standing commercial timber apparently because they are unaware of its existence, despite their preparation of government-required stand maps. The reliability and actual use of those maps in Suriname (Zalman et al., 2019) may explain the scarcity of intact forest in the relatively lightly logged harvest blocks in that country (**Figure 2**). Alternatively, perhaps trees were left standing in patches of intact forest after loggers reached the volumetric quotas set by government or the industries they supply.

RIL is promoted as leakage-free insofar as yield reductions are not required, and as more cost-effective than conventional logging, despite the mixed support for these claims in the literature (Medjibe and Putz, 2012; Sasaki et al., 2016). The claim of being leakage-free is admittedly not supported when scrupulous adherence to RIL guidelines results in no logging on steep slopes, in riparian areas, in inaccessible enclaves, and during wet weather (Healey et al., 2000). Logic supports the claim that RIL is more profitable than conventional logging, but the data are far from consistent. The model studies on this topic, both conducted in Amazonian Brazil by Barreto et al. (1998) and Holmes et al. (2002), reported that RIL was, respectively, 35 and 18% more profitable than conventional logging. The principal financial benefits derived from worker training, harvest planning, and close supervision were from higher timber recovery in RIL areas. Directional felling by trained workers toward pre-planned skid trails coupled with better bucking and less felling damage to commercial logs should all also result in more efficient and less costly harvests, but this assumption is not consistently supported by research (Medjibe and Putz, 2012). Given the deficiencies in the experimental designs of many cost-benefit analyses of RIL and the variety of conditions under which selective logging is carried out in the tropics, the financial consequences of adoption of improved logging practices remain unclear. What is made clear by the lack of adoption of RIL (e.g., Ellis P. W. et al., 2019) is that the decision-makers in tropical forestry operations, be they concession owners, crew bosses, or chain saw operators, clearly do not recognize the financial benefits of RIL. An obvious need is for more and better research that tracks the costs and benefits by specific operation (e.g., tree felling, log skidding, and worker training) and from the perspectives of the various relevant stakeholders (e.g., chainsaw operators, crew bosses, and concession owners; Putz and Romero, 2012). Alternatively, given the existence of an accurate and inexpensive way to monitor logging impacts with the RIL-C protocol (e.g., Ellis P. W. et al., 2019), where there are reliable regulatory authorities, FMEs could be rewarded for demonstrated improvements in their forest management practices relative to established baselines.

RECOMMENDATIONS

The environmental benefits of the intact forest in logged landscapes would be greatly enhanced by spatial planning with enforcement of restrictions on access to sensitive habitats. If the observed proportions of selectively logged forest were left intact near streams and on steep slopes, the deleterious environmental impacts of logging would be greatly diminished (Griscom et al., 2019). In addition to the hydrological benefits, protection of riparian corridors would enhance connectivity for wildlife. Any reductions in timber yields could be easily compensated for with silvicultural treatments in accessible stands (e.g., Ruslandi et al., 2017). Enforcement of spatial planning regulations could be enhanced if governmental and certification body auditors included comprehensive GPS tracks in their reports on inspections of logging locations and practices.

To reduce the deleterious environmental impacts of selective logging in steep areas, we endorse long-line cable yarding with modified excavators (e.g., LogFishers: http://www.logfisher.com/contact.html). Such machines move easily along ridge-top roads so that almost every log follows a different path of up to 200 m upslope. Even in the absence of data, we are confident that this approach, at least compared to cutting switchbacks with bulldozers, results in reductions in soil damage, carbon emissions, and costs. We advocate this approach to cable yarding in full recognition of the massive but little documented environmental destruction caused by unregulated high-lead cable yarding in Malaysian Borneo and the Philippines during the 1970s and 1980s (reviewed by Ewel and Conde, 1981). While it would be environmentally preferable to not log steep slopes, few countries have such prohibitions (Putz et al., 2018). Furthermore, if slope restrictions were enacted and enforced, yields from the increasingly steep lands being allocated for logging would decline and risks of activity-shifting leakage (i.e., loggers go elsewhere for timber) would increase.

Data limitations make it difficult to assess the permanence of the intact forests in logged landscapes. We were surprised to learn the extent to which governmental agencies ultimately responsible for the forest and FME managers both lacked reliable records of the locations of previous episodes of timber extraction. Be that as it may, if the intact patches retained through the first harvest are logged after only 25–30 years, the reprieves are not durable. Perhaps worse, if hunters travel the logging roads to access intact areas and wipe out wildlife, that dimension of intactness will disappear. Furthermore, just as species differ in the degree to which their biology is disrupted by selective logging, the impacts of that intervention are not all immediate—some increase in response to elevated post-logging tree mortality rates while others decrease as forest recovers.

The emphasis of many environmental scientists on describing in ever-increasing detail the problems associated with selective logging in the tropics needs to shift toward finding solutions to those problems. Researchers and environmental advocates need to accept that, at least in much of the remaining tropical forest of the world, as long as there is merchantable timber to be harvested, logging is likely. Whether that logging is carried out by private forest owners, entrepreneurial rural communities and indigenous groups, or the employees of large corporations, there will be impacts. Understanding these impacts is essential, but given that many are obvious already well described, attention should be directed toward finding financially viable and ecologically sound ways to manage tropical forests sustainably. To this end, more full-fledged silviculturalists, mensurationists, forest engineers, and forest economists are essential, but well-trained ecologists can also re-train in those more applied disciplines. More to the main point of this study, improved spatial planning of logging and other silvicultural interventions will help increase the sustainability of natural forest management in the tropics.

AUTHOR CONTRIBUTIONS

The study was designed by FP and PE based on data provided by BG, EE, JZ, and PU. TB, TG, and PE did much of the data analysis, with input from R and AR. All authors commented on earlier versions of this article.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2019.00030/full#supplementary-material

Supplementary Table 1 | Summary statistics for the logged blocks assessed in this study.

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CORRECTION
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Corrigendum: Intact Forest in Selective Logging Landscapes in the Tropics

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Keywords: conservation, land-use planning, reduced-impact logging, sparing-sharing, tropical forestry

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A Corrigendum on

Intact Forest in Selective Logging Landscapes in the Tropics
by Putz, F. E., Baker, T., Griscom, B. W., Gopalakrishna, T., Roopsind, A., Umunay, P. M., et al. (2019). Front. For. Glob. Change 2:30. doi: 10.3389/ffgc.2019.00030

In the original article, there was a mistake in **Figure 3B** as published. There was a mistake (underestimates) in calculations of the proportion of cutting blocks left intact. The corrected **Figure 3B** appears below.

In the original article, there was a mistake in **Figure 4** as published. There was a mistake (underestimates) in calculations of the proportion of cutting blocks left intact. The corrected **Figure 4** appears below.

In the original article, there was a systematic error in calculations that resulted in underestimations of the proportions of logging blocks not directly affected by timber harvests.

In the original article, there was a mistake in the Abstract. It read as "an average of 57% (range 22–97%) of the area in logging blocks was not directly affected by timber harvests." The corrected sentence should read as "an average of 69% (range 20–97%) of the area in logging blocks was not directly affected by timber harvests."

In the original article, there were two mistakes in the first paragraph of the Results section. It read as "Intact forest covered a mean of 57% (range 22–93%) of the 48 logged blocks in the six tropical countries we sampled (**Figure 2**)". The corrected sentence should read as "Intact forest covered a mean of 69% (range 20–97%) of the 48 logged blocks in six tropical countries (**Figure 2**)." The second mistake reads as "There was no apparent difference in the proportions of forest left intact in the 12 FSC-certified (53 ± 19% SD) and the 36 non-certified FMEs (85 ± 17% SD, $t = 1.54$, $P = 0.13$; **Figure 4**; see Supplementary Table 1 for complete results and logging block statistics)." The corrected sentence should read as "There was no apparent difference in the proportion of forest left intact in the 12 FSCcertified (65 ± 21%SD) and the 36 non-certified FMEs (71 ± 17% SD, $t = 0.77$, $P = 0.45$; **Figure 4**; see supplementary data table for complete results and logging block statistics)."

In the original article, there was a mistake in paragragh 4 of the Discussion section. It read as "That value is much higher than the global average of 57% intact reported here, but is similar to the 77–97% intact forest found in logging blocks in Mexico where harvest intensities were also low (0.24–3.15 trees/ha)." The corrected sentence should read as "That value is much higher than the global average of 69% intact reported here, but is similar to the 77–97% intact forest found in logging blocks in Mexico where harvest intensities were also low (0.24–3.15 trees/ha)". The corrected paragraphs appear below.

ABSTRACT

The selective logging that characterizes most timber extraction operations in the tropics leaves large patches of logging blocks (i.e., areas allocated for harvesting) intact, without evidence of direct impacts. For example, in ∼10,000 ha sampled in 48 forest management enterprises in Africa (Gabon, Republic of Congo, and the Democratic Republic of Congo), Indonesia, Suriname, and Mexico, an average of 69% (range 20–97%) of the area in logging blocks was not directly affected by timber harvests. The proportion of intact forest within logging blocks decreased very slightly with increases in harvest intensity in the accessed portion of the logging blocks (9–86 m^3 ha^{-1}) but decreased strongly with harvest intensity in entire logging blocks (0.3–48.2 m^3 ha^{-1}). More forest was left intact in areas farther from roads, on slopes >40%, and within 25 m of perennial streams, but the effect sizes of each of these variables was small (∼8%). It is less clear how much of the intact forest left after one harvest will remain intact through the next. Conservation benefits without reductions in timber yields will derive from better management planning so that sensitive and ecologically critical areas, such as steep slopes and riparian buffers, constitute large and permanent proportions of the intact forest in selectively logged landscapes in the tropics.

Results (paragraph 1):

Intact forest covered a mean of 69% (range 20–97%) of the 48 logged blocks in six tropical countries (**Figure 2**). When data from all regions are combined, we detected a small but statistically insignificant decrease in the proportion of forest left intact in logged blocks with harvest intensity in the accessed area (% intact = 0.78–0.0026 * harvest intensity; $SE_b = 0.0014$, df = 45, $P = 0.06$, adjusted $R^2 = 0.055$; **Figure 3A**). In contrast, if harvest intensities are assumed to represent conditions in entire logging blocks, which is commonly assumed, there was a more marked decrease in intact area with harvest intensity (% intact = 0.83–0.0109 * harvest intensity per cutting block; $SE_b = 0.0015$, df = 46, $P < 0.001$, adjusted $R^2 = 0.529$; **Figure 3B**). In the 42 logging blocks in six countries with road data, as expected, intact areas averaged a larger distance (289.6 m, SD = 25.54 m) from the nearest haul-road than accessed areas (231 m, SD = 20.6 m; $t = 4.0$, $P < 0.01$). Distances to haul-roads ranged 64–722 m for intact areas and 56–662 m for accessed areas. There was no apparent difference in the proportion of forest left intact in the 12 FSC-certified (65 ± 21% SD) and the 36 non-certified FMEs (71 ± 17% SD, $t = 0.77$, $P = 0.45$; **Figure 4**; see supplementary data table for complete results and logging block statistics).

Discussion (paragraph 4):

Comparison of our results with other published measures of logging impacts is challenging due to methodological differences, but the patterns we observed are similar to other reports in the literature. For example, based on field measurements of ground disturbance by selective logging in South America reported for 17 plots in six different published studies, Feldpausch et al. (2005) reported that 46–88% of the forest was not affected directly by logging. Those same authors reported that intact forest area decreased with logging intensity and was much smaller for conventional logging than RIL. In a more recent study of a forest subjected to RIL in Belize at a block-wide intensity of 2.9 m^3 ha^{-1} (2.7 trees ha^{-1}), Arevalo et al. (2016) reported that 93% of the 350-ha harvest block experienced no direct impacts of logging. That value is much higher than the global average of 69% intact reported here, but is similar to the 77–97% intact forest found in logging blocks in Mexico where harvest intensities were also low (0.24–3.15 trees/ha). Similarly, in a pantropical review of the literature on logging roads, Kleinschroth and Healey (2017) reported a median impact of 1.7% of the ground surface. Studies based on remote sensing, especially those that employed canopy-penetrating lidar and wall-to-wall sampling of logged blocks, often report considerably higher proportions of intact forest than field studies (e.g., Ellis et al., 2016). Despite the opportunities for lidar to detect accessed areas accurately (Melendy et al., 2018), larger scale studies using canopy-penetrating lidar have yet to reveal the spatial patterns of intactness in landscapes designated for logging beyond the scale of individual harvest blocks, which could have large implications for meta-population dynamics.

The authors apologize for these errors and state that they do not change the scientific conclusions of the article in any way. The original article has been updated.

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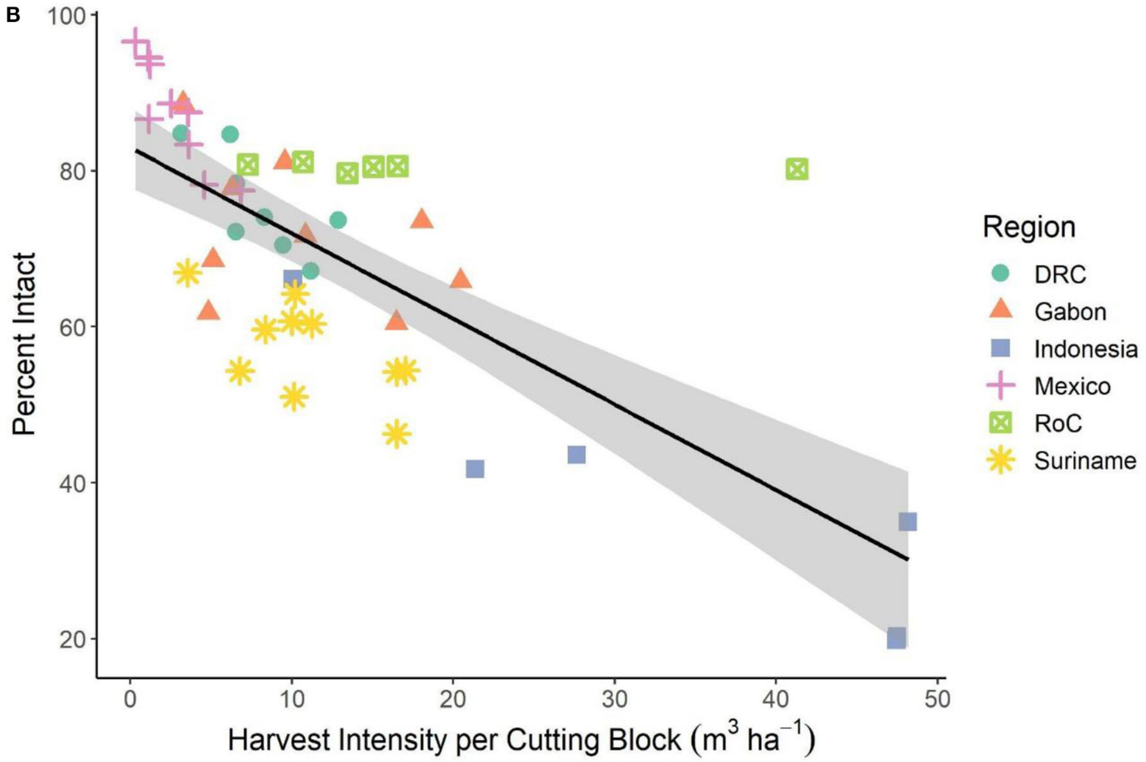
B
100
80
60
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Percent Intact
0
10
20
30
40
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Harvest Intensity per Cutting Block (m^3 ha^{-1})
Region
DRC
Gabon
Indonesia
Mexico
RoC
Suriname

FIGURE 3 |

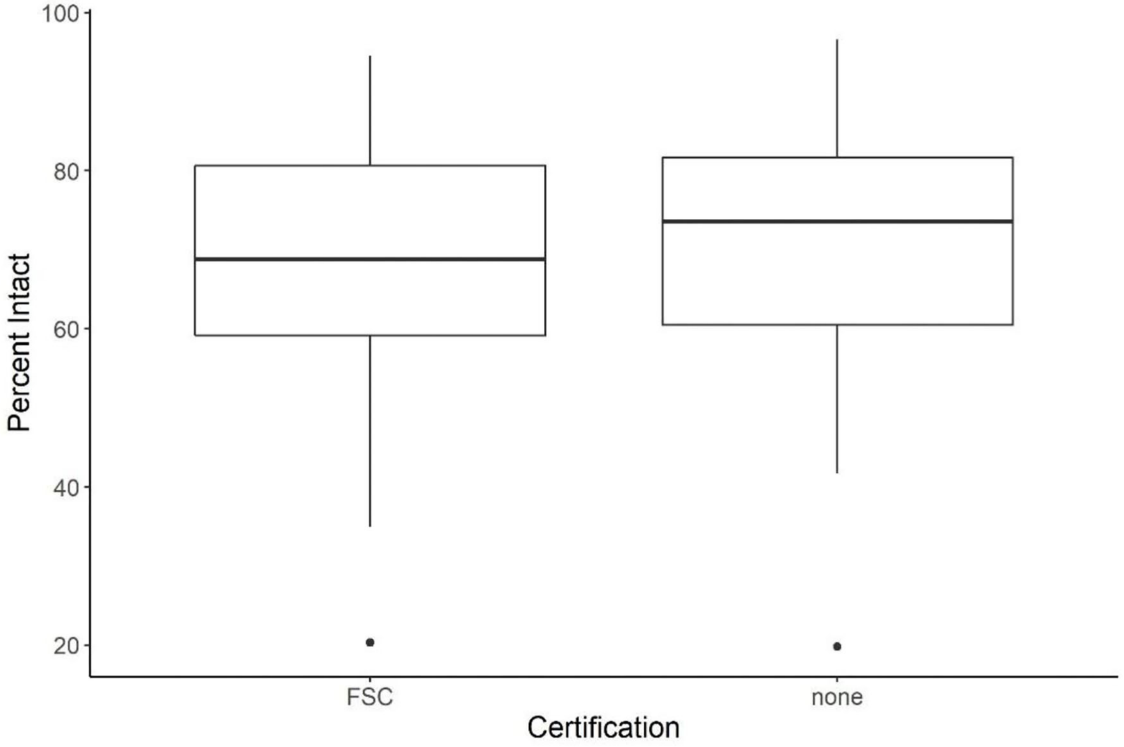

FIGURE 4 |

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The Legacy of Pre–Columbian Fire on the Pine–Oak Forests of Upland Guatemala

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Mountain tropical forests of the Southern Maya Area (Pacific Chiapas and Guatemala, El Salvador, and Northern Honduras) predominantly comprise pine and oak formations, which form intricate mosaics and complex successional interactions following large–scale fire. These forests have been transformed by the peoples of the Maya civilization through practices of horticulture, agriculture, and architectural developments over thousands of years. Anthropogenic impacts and the extent of early human interaction with these upland forests is currently poorly understood. In this study we identify: (i) the natural baseline vegetation of the region; (ii) when human impact and agrarian practices began in the Maya uplands; and (iii) what impacts the Maya had on forest structure, composition, and successional regeneration. Past vegetation, anthropogenic use of fire, and faunal abundance were reconstructed using proxy analysis of fossil pollen, macroscopic charcoal, microscopic charcoal, and dung fungal spores (*Sporormiella*). Three phases of forest succession were identified from 4000B.C.E. to 1522CE that broadly overlap with the well–defined archaeological periods of (i) the Archaic (10,000–2000B.C.E.); (ii) Pre–Classic (2000B.C.E.−100C.E.); (iii) Terminal Pre–Classic (100–250C.E.); (iv) Classic (250–950C.E.); and (v) Post–Classic (950–1522C.E.). These results also include the earliest evidence for agriculture within the Southern Maya Area through presence of peppers (*Capsicum*) from 3850B.C.E. and the rise of maize cultivation (Zea mays) from 970B.C.E. Persistent high intensity burning driven by agricultural practices and lime production during the Late–Pre-Classic (400–100B.C.E.) to Classic Period resulted in a compositional change of forest structure c.150B.C.E. from oak (Quercus) dominated forests to pine (Pinus) dominated forests. The legacy of Pre–Columbian anthropogenically driven fire in these mountain tropical forests demonstrates the resilience and thresholds for fire driven succession. These findings are particularly relevant for addressing current land use and management strategies involving agriculture, fire, and forest management in the mountain tropical forests of the Southern Maya Area.

Keywords: fire, pine-oak forest, *Zea mais*, early agriculture, *Capsicum*, *Sporormiella*, palaeoecocology, Maya

INTRODUCTION

Unlike the Amazon or boreal regions, Central America does not have large tracts of intact forests (Watson et al., 2018), and further reductions in the extent of intact forests are a concern. Potapov et al. (2017), for example, determined that forest cover declined by 13.3% in Guatemala between 2000 and 2013C.E. Mountain tropical forests (MTF) are important for the provision of ecosystem services, particularly biodiversity and water (Martínez et al., 2009), and loss of intactness has serious implications for these ecosystem services. Given the current high international interest in the effects of human actions that cause degradation of forests and subsequent loss of ecological function, the development of long–term ecological data will provide insight on how forests were influenced by anthropogenic and natural factors during pre–history and thereby help inform potential future responses to similar actions and/or occurrences. For Central America such long–term ecological datasets are scarce and are rarely considered in modern conservation discussions (Jeffers et al., 2015). In particular, the Middle to Late Holocene (6000–2000B.C.E.) vegetation history of the Central American uplands (>1,000 m.a.s.l.) is not well-documented but is essential to our understanding of early human impacts and prehistoric land use across the Maya Area (Neff et al., 2006). Filling these temporal and spatial gaps in knowledge is essential for understanding the function and protection of intact forests in this region and more generally.

The Maya occupied three separate areas: the Southern Uplands, and the Central, and Northern Lowlands (<1,000 m) (**Figure 1**). Our research area lies within the Southern Uplands, which includes the highlands of Guatemala and adjacent Chiapas (Coe and Houston, 1966). There are altitudinal gradients in temperature and precipitation, with annual mean temperatures ranging between 14 and 25°C and annual rainfall ranging between 900 and 3,700 mm per year (Kappelle, 2006). The vegetation inhabiting this upland area typically comprises tropical and subtropical mixed deciduous and coniferous forests, known as mountain tropical forest (MTF) formations, which start in the Sierra Madre de Chiapas (Southern Mexico) and extend down to Northern Nicaragua (Dinerstein et al., 2017).

PREVIOUS WORK IN THE MAYA AREA

Early human populations across Central America are suggested to have increasingly interacted with their surrounding environment from 6000B.C.E., aided by progressively more favorable climatic conditions (Turner and Miksicek, 1984; Colunga–GarcíaMarín and Zizumbo–Villarreal, 2004; Ford and Nigh, 2009). In palaeoecology records from Maya sites, anthropogenic impacts to vegetation are typically inferred from the: (i) presence of known cultigens, such as *Capsicum* (peppers), Cucurbitaceae (gourds), *Maranta arundinacea* (arrowroot), *Phaseolus* (beans), and *Zea mays* (Maize) (White, 1999); (ii) presence of "weedy taxa," such as, Amarathaceae, Compositae, and *Polygonum* (Dull, 2004a; Franco-Gaviria et al., 2018); (iii) reductions in all or select arboreal taxa, such as *Quercus* (Dull, 2004a,b, 2007; Velez et al., 2011); and (iv) increases in local and regional burning (e.g., Dull, 2004a,b, 2007; Anderson and Wahl, 2016).

Archaic (10,000–2000B.C.E.) anthropogenic impacts and the extent of early human interaction with the upland forests of the Maya Area are currently poorly understood. There have been 11 palaeopalynological studies conducted in the southern Maya Area (**Figures 1**, **2**), and only five of these reconstructions have been undertaken in the uplands (Dull, 2004a; Caffrey et al., 2011; Velez et al., 2011; Franco-Gaviria et al., 2018). Interpretations of fossil pollen and charcoal records from Laguna Verde (El Salvador) and Lago Amatitlan (Guatemala) identify extensive human alteration of the upland vegetation between 2550 and 625B.C.E. (Dull, 2004a; Velez et al., 2011). Likewise, records from Lake San Lorenzo and Lake Esmeralda (Chiapas) provide evidence that anthropogenic and climatic impacts drove vegetation changes from *c.*450B.C.E. (Franco-Gaviria et al., 2018). In contrast, palynological data from Miqul Meadow (Guatemala) indicates that climate is the sole driver of vegetation change (Caffrey et al., 2011). These records are mostly low in resolution (more than 200 years between samples: e.g., Laguna Verde and Miqul Meadow) and poorly chronologically constrained (e.g., Miqul Meadow), limitations that prevent conclusive assessment of questions related to the timing of events. In order to reconstruct the impacts of disturbance events in MTF and forest succession, palaeoecological datasets must be sampled at a resolution higher than that of the rate of succession, which is up to 200 years in MTF (Kappelle, 2006). In addition, many of these studies rely on geographically distant proxy records to infer the impacts of climate on vegetation dynamics (e.g., La Yeguada, Panama: (Bush et al., 1992) and Peten Itza, Guatemala: Islebe et al., 1996). Given the spatial heterogeneity in precipitation patterns across Central America through time (e.g., Metcalfe et al., 2015), it is critical to include local palaeoclimate records for comparison with vegetation reconstructions.

FOREST SUCCESSION

Currently the arboreal canopy of MTF predominantly comprise a combination of coniferous forest taxa (e.g., *Pinus* and *Abies*) and mixed hardwood forest (MHWF) taxa (e.g., *Quercus*, *Alnus*, and *Liquidambar*), which are well-adapted to variable climatic conditions and natural fires (Corrales et al., 2015). These MTF are a combination of pine forests (PF), pine–oak forests (POF), mountain–pine–oak forests (MPOF), oak forests (OF), pine–oak–*Liquidambar* forests (POLF), mountain rain forests (MRF), and cloud forests (CF) (Kappelle, 2006). These typically overlap in floristic composition but vary in species abundance (Miranda, 1952; Breedlove, 1981; Kappelle, 2006; Figueroa-Rangel et al., 2008, 2010, 2012). POF form intricate mosaics and complex successional interactions, especially at higher elevations, which extend up into the broad–leaved evergreen CF (Rzedowski, 2006). Altitudinally, MPOF in Chiapas are found above 1,500 m, while POF have an extensive range from 500 to 3,400 m.a.s.l., with strong turnovers between species along altitudinal gradients (Kappelle, 2006). There are over 150 species of *Pinus* and *Quercus* that can be found across the uplands of Guatemala

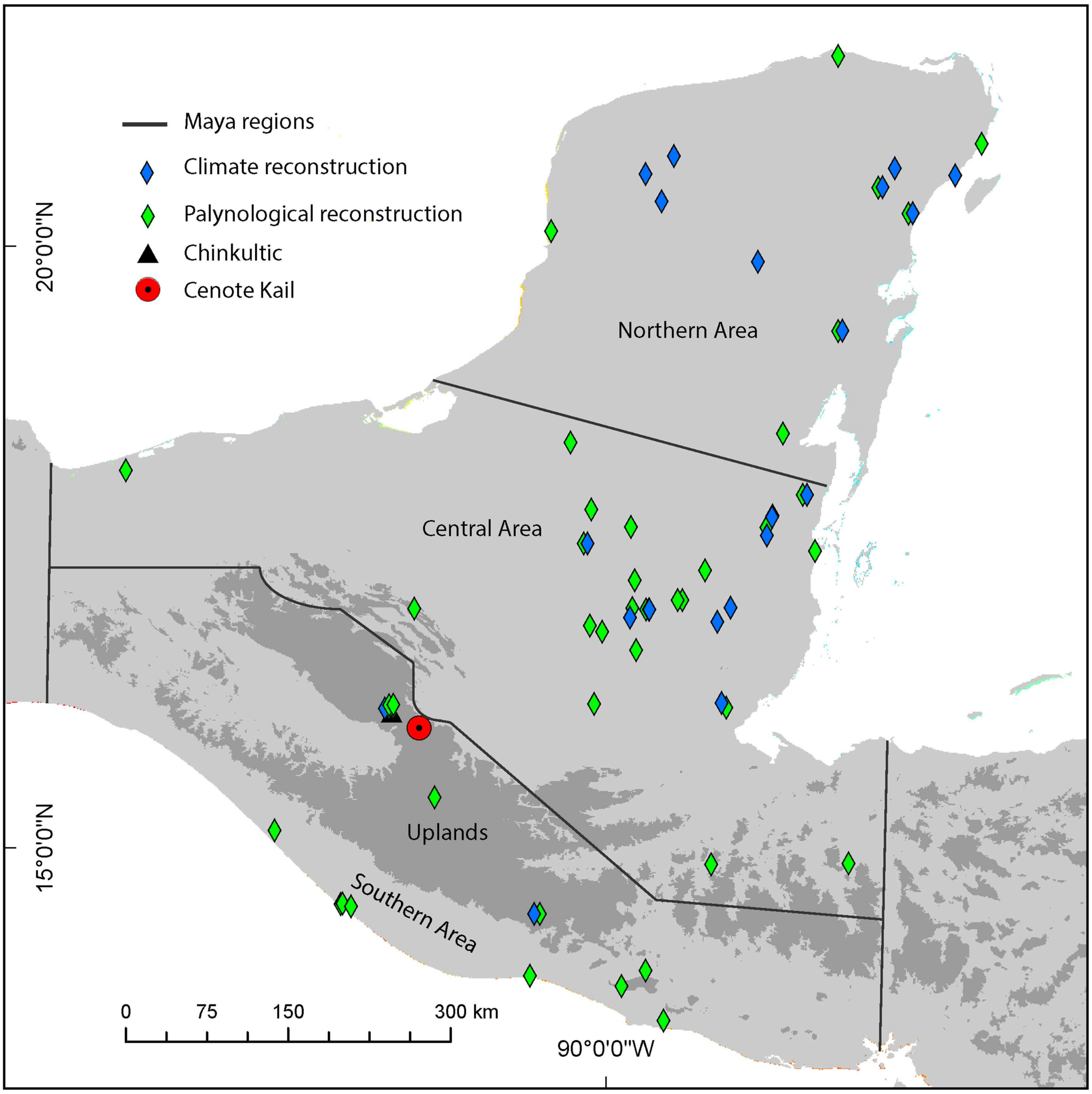

FIGURE 1 | Topographic map of Central America depicting (i) Maya regions; (ii) independent climate proxies (blue diamonds); (iii) previous vegetation reconstructions in the Maya Area (green diamonds); (iv) location of archaeological complex Chinkultic (black triangle); and (v) location of Cenote Kail (red circle). Dark gray shading represents elevation >1,000 m.a.s.l. (see **Supplementary Information** for sites).

(Muller, 1942; Kappelle, 2006). Only 47% of forest cover (1990–2000C.E.) remains, and it is highly fragmented due to high human population densities and land modification for subsistence farming (Corrales et al., 2015).

Drivers of POF dynamics have been previously investigated in upland Guatemala (Velez et al., 2011), neighboring Chiapas (Domínguez-Vázquez and Islebe, 2008), Pacific Mexico (Figueroa-Rangel et al., 2008, 2010, 2012) and Costa Rica (Islebe and Hooghiemstra, 1997), detailing the climatic and anthropogenic mechanisms that contribute toward changes in POF composition through time (Kappelle, 2006). In these studies fire has been identified as the dominant driver of structural and successive turnover within POF systems. However, there is disagreement as to what factors are driving these fires, changes in burning are controlled by complex interactions of fire, fuel load, climate, and humans (Cochrane and Barber, 2009; Bowman et al., 2011; Anderson and Wahl, 2016). While it is not possible wholly to differentiate between anthropogenic and naturally occurring fires (Anderson and Wahl, 2016), inferences can be made by combining multiple lines of evidence such as fossil charcoal with the presence of known agricultural grains (e.g., *Zea mays*) (Dull, 2004a,b, 2007), or with climatic proxy data, to infer known shifts in precipitation, which can impact fuel loads and ignitions (Bowman et al., 2011).

Research conducted on the Pacific coast of Mexico (Figueroa-Rangel et al., 2008, 2010, 2012) and in Costa Rica (Islebe and Hooghiemstra, 1997) suggests that fire within POF are primarily climatically driven; whereas palynological work in

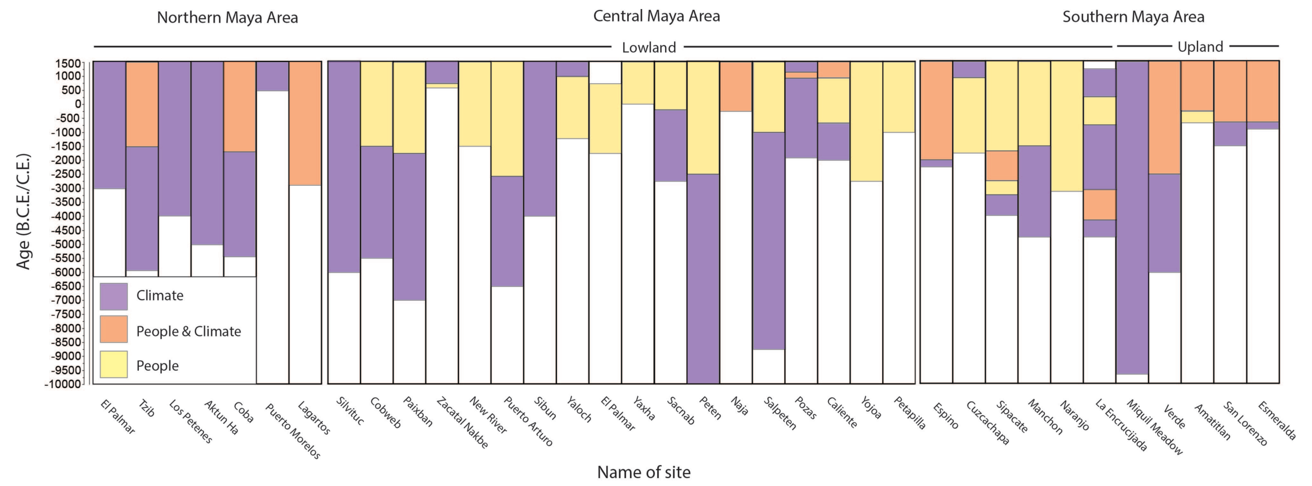

FIGURE 2 | Summary of reported vegetation drivers and impacts to the vegetation from the Maya Area during the Pre–Columbian Holocene, as reported by authors from palynological reconstructions (see **Supplementary Information** for sites).

Guatemala and Chiapas (Domínguez-Vázquez and Islebe, 2008; Velez et al., 2011) indicates a more intertwined relationship of climate and people. Other factors considered to affect the structure and successional regeneration of POF are overall climate (temperature and precipitation), soil (type, nutrient availability), and anthropogenic activities (timber extraction and agriculture) (Kappelle, 2006). In addition, herbivory can cause deviations in successional pathways through sapling browsing and seed dispersal (Baker et al., 2016; Arroyo-Rodríguez et al., 2017).

It has been suggested that without further disturbances natural recovery will return a fallow field to a POF within *c.*80 years (Figueroa-Rangel et al., 2008). Sustained low–intensity and long-duration human disturbance leads to a deviation from this natural sequence resulting in slowed recovery, and more intensive anthropogenic or climatic disturbances can reverse or reset recovery times (Kappelle, 2006). However, these are theoretical timelines and to date there is very little evidence on recovery rates from different types of disturbances (fire, human, climate) in this region, nor on how this varies according to altitude.

This study seeks to identify (i) the natural baseline vegetation of the region; (ii) when human impact and agrarian practices began in the Maya uplands; and (iii) what impacts the Maya had on forest structure, composition, and successional regeneration. To address the potential impacts of anthropogenic influences and herbivory upon the biota of upland Guatemala, a proxy reconstruction of changes in vegetation, burning, and animal populations from 4000B.C.E. to 1522C.E. was developed using fossil pollen, macroscopic charcoal ($>150\,\mu$m), microscopic charcoal ($<150\,\mu$m), and fossil dung fungal spore (*Sporormiella*), from Cenote Kail, a lake situated in the uplands of the Southern Maya Area. These records were then compared with local and regional climatic archives and information on human population dynamics collected from nearby archaeological sites.

METHODS

Study Site: Cenote Kail

Cenote Kail (150 m diameter) is located within the uplands of the Southern Maya Area (N16°00′00.0″W91°33′14.4, 1,534 m.a.s.l.) and situated 28 km away from the well-documented archaeological complex Chinkultic (Ball, 1980; **Figure 1**). This city was established sometime between 50B.C.E and 75C.E. and occupied until 300–350C.E. The city was then abandoned between 350 and 700C.E. before being occupied again from 700 to 1,250C.E. (Ball, 1980). The lake is presently surrounded by a coniferous forest mosaic best described as POF or MPOF. Vegetation is distributed between densely populated mixed deciduous and coniferous forested patches, and large open shrub/grasslands.

Field and Sampling Techniques

In 2015 a 545 cm–long composite sediment core, with overlapping sections, was extracted from Cenote Kail using a Livingstone piston corer (Livingstone, 1955). Forty-six samples (1g wet weight) were extracted at 10 cm intervals for biological proxy analysis of macroscopic charcoal ($>150\,\mu$m), microscopic charcoal ($<150\,\mu$m), pollen, and coprophilous fungal spores (*Sporormiella*).

Chronology

An age depth model was constructed using 38 calibrated radiocarbon dates obtained from charcoal and terrestrial leaf fragments, which represent a single event or from one to two seasons of growth (**Table 1**). Samples were pre–treated using standard acid–base–acid protocols (Abbott and Stafford, 1996). Radiocarbon dates were generated at the W.M. Keck Carbon Cycle Accelerator Mass Spectrometry Laboratory at the University of California, Irvine. The IntCal13 radiocarbon

TABLE 1 | Measured, calibrated, and modeled radiocarbon ages for Cenote Kail.

Lab#	Measured age (C14 B.P.)		Depth	2σ Calibrated age range (B.C.E./C.E.)		Median 2σ calibrated age (B.C.E./C.E.)	OxCal 2σ modeled age (B.C.E./C.E.)		Median 2σ modeled agev (B.C.E/C.E.)	Model agreement index
146795	385	±20	106.5	1,445	1,620	1,532.5	1,560	1,633	1,596.5	99.9
209175	260	±20	118.75	1,528	1,797	1,662.5	1,515	1,595	1,555	99.2
209176	560	±25	138.75	1,311	1,425	1,368	1,312	1,425	1,368.5	105.7
209177	870	±20	160.75	1,052	1,220	1,136	1,061	1,224	1,142.5	102.3
146797	1,080	±30	192	894	1,018	956	895	1,017	956	114.4
169170	1,380	±80	229.8	433	865	649	431	767	599	107.3
146798/146799	1,975/2,115	±20/45	267	−44	53	4.5	−40	61	10.5	55.9
209178	2,070	±30	299.25	−174	−1	−87.5	−188	−50	−119	85.5
209179	2,235	±25	318.75	−385	−206	−295.5	−389	−210	−2,995	103
209180	2,515	±25	332.75	−791	−543	−667	−789	−543	−666	101.2
146800	2,585	±20	342	−805	−772	−788.5	−806	−770	−788	64.8
209181	2,990	±50	355.75	−1,391	−1,054	−1,222.5	−1,371	−1,023	−1,197	116.6
209182	3,220	±20	378.75	−1,527	−1,439	−1,483	−1,596	−1,436	−1,516	130.8
209183	3,350	±35	382.75	−1,739	−1,531	−1,635	−1,728	−1,529	−1,628.5	118.4
209184	3,405	±20	387.75	−1,749	−1,642	−1,695.5	−1,745	−1,654	−1,699.5	102.9
209185	3,415	±20	390.75	−1,767	−1,658	−1,712.5	−1,757	−1,667	−1,712	110.1
209186	3,590	±20	394.5	−2,018	−1,889	−1,953.5	−2,015	−1,886	−1,950.5	106.8
209188	3,700	±60	407.75	−2,284	−1,928	−2,106	−2,196	−1,984	−2,090	103.9
209189	3,750	±40	412.75	−2,286	−2,035	−2,160.5	−2,270	−2,046	−2,158	95.6
209190	3,750	±25	413.75	−2,278	−2,041	−2,159.5	−2,273	−2,052	−2,162.5	100.4
146802	3,940	±25	428.5	−2,561	−2,345	−2,453	−2,466	−2,310	−2,388	98.9
209191	3,875	±25	431.25	−2,465	−2,286	−2,375.5	−2,468	−2,343	−2,405.5	101.1
209193	4,315	±30	467.25	−3,013	−2,888	−2,950.5	−3,011	−2,888	−2,949.5	96.1
209195	4,475	±25	484.25	−3,338	−3,030	−3,184	−3,303	−3,025	−3,164	93
209196	4,570	±25	498.25	−3,491	−3,119	−3,305	−3,361	−3,118	−3,239.5	92.6
193048	4,545	±25	508.8	−3,366	−3,106	−3,236	−3,367	−3,146	−3,256.5	102.5
146803	4,570	±20	519	−3,485	−3,126	−3,305.5	−3,659	−3,194	−3,426.5	100.8
193050	4,900	±25	521.7	−3,709	−3,643	−3,676	−3,708	−3,642	−3,675	106.9
193051	4,995	±25	532.9	−3,927	−3,704	−3,815.5	−3,913	−3,705	−3,809	100.7
193052	5,100	±20	536.9	−3,965	−3,804	−3,884.5	−3,961	−3,798	−3,879.5	13.9
193054	5,130	±30	543.7	−3,990	−3,804	−3,897	−3,989	−3,811	−3,900	66
*209187	3,485	±25	404.75	−1,886	−1,703	−1,794.5	−2,164	−1,759	−1,961.5	42
*209192	4,275	±25	438.25	−2,916	−2,879	−2,897.5	−2,916	−2,369	−2,642.5	28.1
*209194	4,185	±40	472.25	−2,892	−2,633	−2,762.5	−3,145	−2,755	−2,950	22.8
*209197	5,020	±60	499.25	−3,958	−3,674	−3,816	−3,386	−3,116	−3,251	6.9
*193049	5,090	±20	516.33	−3,961	−3,801	−3,881	−3,872	−3,281	−3,576.5	16.5
*193053	5,330	±25	541.3333	−4,245	−4,051	−4,148	−4,197	−3,805	−4,001	19.8

**Omitted dates identified by the general outlier model.*

dataset (Reimer et al., 2013) was used to calibrate the measured radiocarbon dates, and OxCal (v.4.3) was used to construct an age–depth model applying a Bayesian approach (Ramsey, 2009). Outliers were identified using the general outlier model implementing an outlier probability of 0.05 (Ramsey, 2008). Sedimentation rates were calculated using this age-depth model.

Fossil Pollen and Sporormiella Analysis

Fossil pollen was used to reconstruct the abundance and composition of past vegetation dynamics. Fossil pollen extraction and preparation followed standard palynological procedures applying the Oxford Long–Term Ecology Laboratory (OxLEL) protocol (OxLEL, 2016). Silicone oil was used as the mounting agent to allow for the rotation of grains, easing identification. Samples were spiked with known concentrations of an exotic marker, *Lycopodium* spores (batch No. 20848 or 9666), to calculate pollen accumulation rates. Pollen influx was calculated using pollen accumulation rates and sedimentation rate (Bennett and Willis, 2001). Counting and identification of pollen grains were conducted at 400x and 1000x magnification. For each level a minimum of 300 terrestrial pollen grains were counted (**Data Sheet 1**). Morphological identification was achieved using (i) pollen databases (APSA, 2007; Bush and Weng, 2007; Martin and Harvey, 2017); (ii) published plates: (Roubik and Moreno, 1991; Willard et al., 2004); and (iii) botanical reference materials from the OxLEL reference collection. In order to interpret the relative composition of the forest, coniferous and mixed—hard—wood forest (MHWF) canopy taxa were compared as a ratio. The abundance of *Sporormiella* spores was used to indicate herbivorous animal presence and abundance. *Sporormiella* spores were counted and morphologically identified on the same slides (Davis and Shafer, 2006; Baker et al., 2016).

Charcoal Analysis

Macroscopic fossil charcoal fragments (150 μm), were used to infer past occurrences of local fires where local is taken to represent burning within a 10 km radius of the catchment area (Gavin et al., 2003; Lynch et al., 2004; Higuera et al., 2007, 2011; Peters and Higuera, 2007; Anderson and Wahl, 2016). All fragments over 150 μm in the 1 g samples were counted at 10x magnification.

Microscopic charcoal (<150 μm), representing a regional signal of up to 100 km (see Clark, 1988), were also counted on the same slides, applying the point counting method at 400x magnification (Clark, 1982). Microscopic charcoal counts were recorded until a minimum of 50 *Lycopodium* spores and 200 fields of view were encountered for each level to allow for influx of microscopic charcoal (cm^2 per year) to be calculated.

Data Handling

Pollen counts were converted to percentages, while S*porormiella,* macroscopic, and microscopic charcoal are presented as annual influx (Maher, 1981; Bennett, 1994; Bennett and Willis, 2001; Whitlock and Larsen, 2002; Baker et al., 2016). To identify discrete zones in the resulting palynological diagrams, constrained hierarchical clustering upon the palynological assemblage was applied following the broken stick model (Bennett, 1996).

Statistical analysis and presentation of data were performed using packages Vegan (Oksanen et al., 2015) and Rioja (Juggins, 2009) in base R (R. Core Team, 2012). Before preforming all ordination analyses, the percentage data were square–root transformed to normalize the distribution and for variance stabilization (Bennett and Willis, 2001; Legendre and Legendre, 2012). A square root transform was chosen because it can be applied to data sets containing zero values. Detrended Correspondence Analysis (DCA) was conducted upon the palynological assemblage data to check if it was appropriate to apply a linear or unimodal ordination method (Ter Braak and Prentice, 1988). The site scores for the first axis of the DCA were then extracted to calculate the species turnover. Next, a Principal Component Analysis (PCA) was used to infer similarities between samples and the change in trajectories of composition of taxa through time, applying a singular value decomposition of the centered, but not scaled, data matrix. Finally, a Canonical Correspondence Analysis (CCA) was performed to quantify the relationship between environmental variables (fire and herbivory) and the palynological assemblage data. Ellipses representing the discrete Zones were calculated using standard parameterization (cos(theta + d/2), cos(theta – d/2)), where cos(d) is the correlation of the parameters (see Murdoch and Chow, 1996).

RESULTS

Chronology and Resolution

The age–depth model indicates that the sediment sequence (545–105 cm) continuously (i.e., without hiatus) spans 4000B.C.E. to 1522C.E. (**Figure 3**). The general outlier model (see Ramsey, 2008) identified six dates as outliers and thus were removed from the overall age–depth model (**Table 1**). The overall model agreement index was high (96.7), indicating there is very little variance between the modeled ages and the observational data. The sedimentation rate is on average 1.2 mm per year.

Palaeoecological Trends

Three statistically significant Zones were identified using the broken stick model (**Figures 4**, **5**). Seventy–six taxa were recognized in the palynological sequence extracted from Cenote Kail (see **Supplementary Information**). Throughout this sequence *Pinus, Quercus* and *Morella cerifera* dominate the arboreal component while Compositae and Poaceae are the most abundant herbaceous taxa (**Figure 5**). Temporal spacing between samples is as follows: (i) Zone 1 represents an average spacing of 130 years spanning 1800 years (with a range of 68–415 years); (ii) Zone 2 represents an average spacing of 137 years spanning 2300 years (with a range of 53–192 years); and, (iii) Zone 3 represents an average of 90 years spanning 1400 years (with a range of 68–160 years).

Results from the CCA show that microscopic and macroscopic charcoal are significant environmental variables most associated with Zones 2 and 3, while *Sporormiella* is most associated with Zone 1 and is not statistically significant (**Figure 4A**). The PCA displays a distinct gradient and several associations between taxa and samples (**Figure 4B**). The first axis represents 20.2% of the variation, while axis two represents 10.5% of the variation. The arch between samples suggests that there is only one clear gradient. When the independently calculated palynological Zones are superimposed upon these quadrants, the top, and bottom right quadrants are most associated with Zone 1, the top left quadrant is most associated with Zone 2 and the bottom left quadrant is most associated with Zone 3 (**Figure 4B**). The first taxonomic association comprises canopy taxa *Quercus*, understory taxa Leguminosae, *Myrica*, Ericaceae, and the herbaceous and agrarian taxa *Capsicum*, which is most associated with Zone 1. The second taxonomic association comprises of understory taxa *Juniperus* and *Terminalia*, herbaceous taxa Polygalaceae, Apiaceae, Compositae *Aphelandra*, and agrarian taxa Capsicum most associated with Zone 2. The third taxonomic association comprises canopy taxa *Pinus, Alnus*, and *Liquidambar* together with understory taxa *Morella cerifera*, and herbaceous taxa Poaceae, and Campanulaceae, which is most associated with Zone 3 (**Figure 4B**).

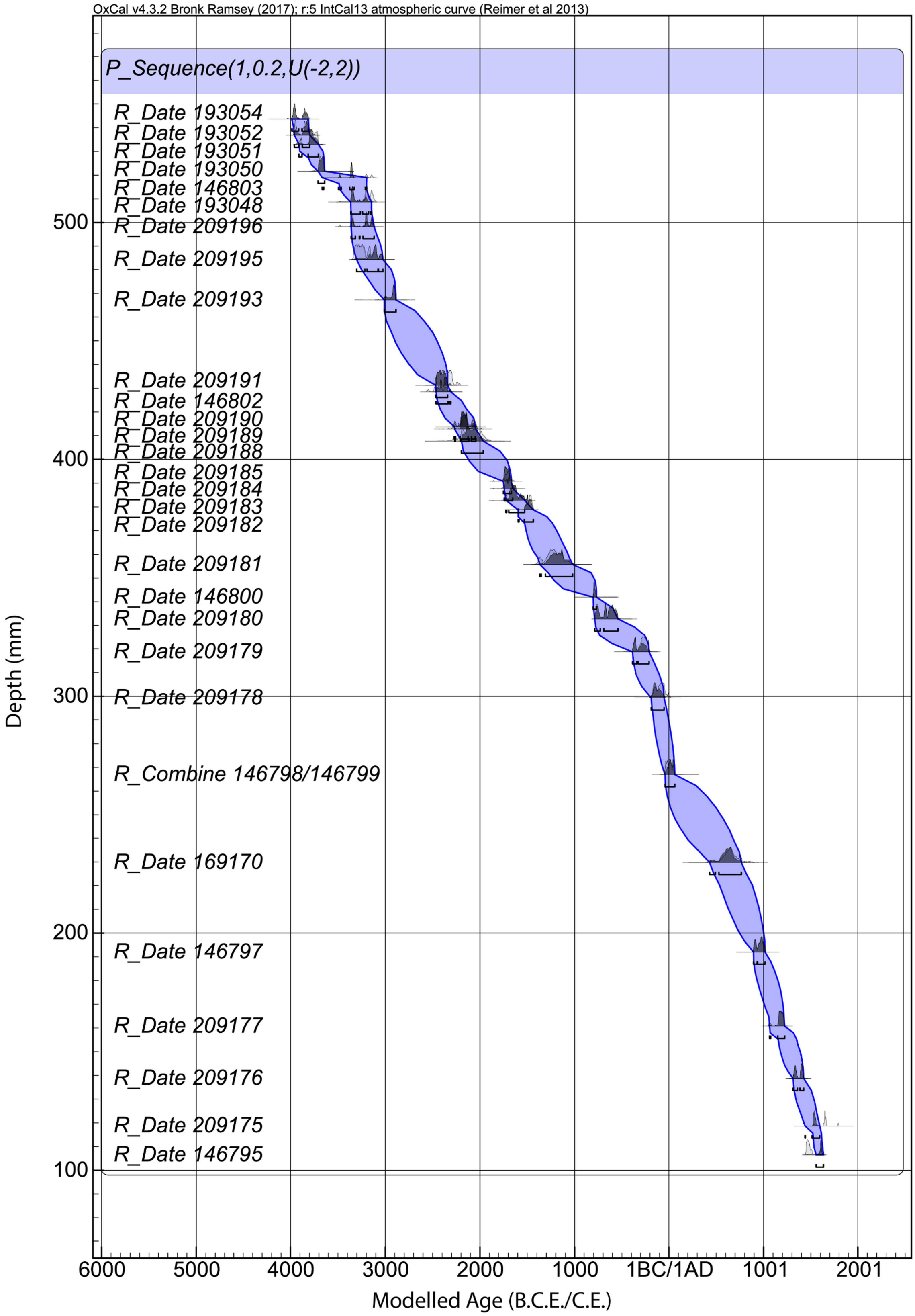

FIGURE 3 | Age depth model for Cenote Kail.

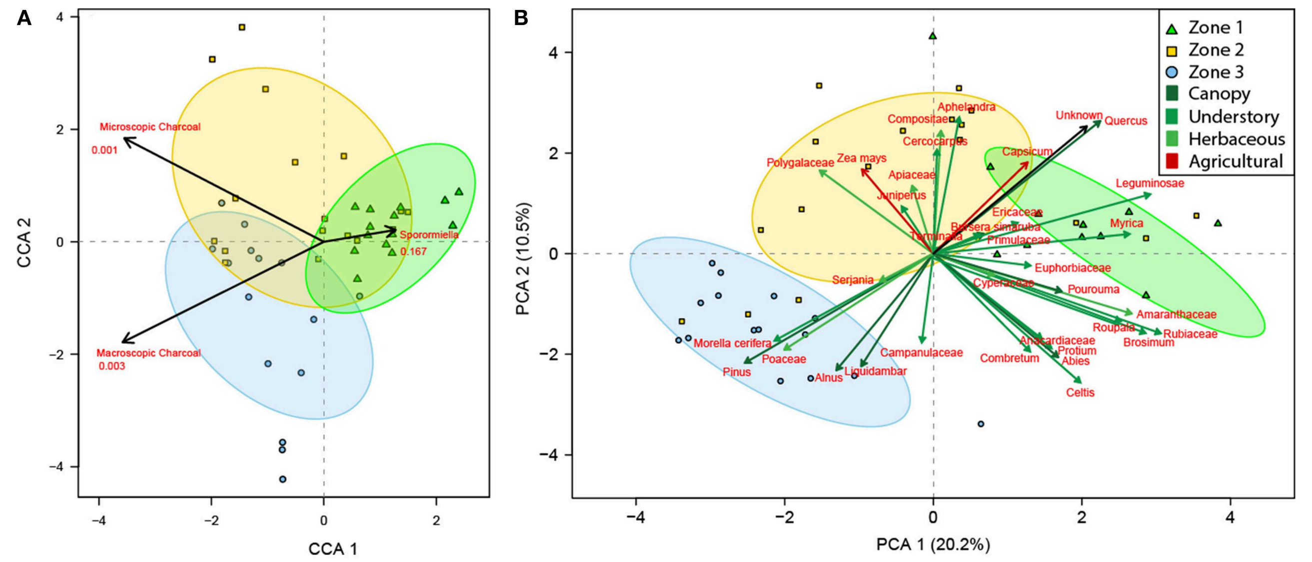

FIGURE 4 | Canonical correspondence analysis of the palaeopalynological data set ordinated against independent environmental indicators of local fire (macroscopic charcoal), regional fire (microscopic charcoal), and herbivory (*Sporormiella*) **(A)**. Principal component analysis of the palaeopalynological data set **(B)**. Zones are derived from the broken stick model and are represented by ellipses at a confidence of 95%. Zone 1 = green triangles; Zone 2 = yellow squares; Zone 3 = blue circles.

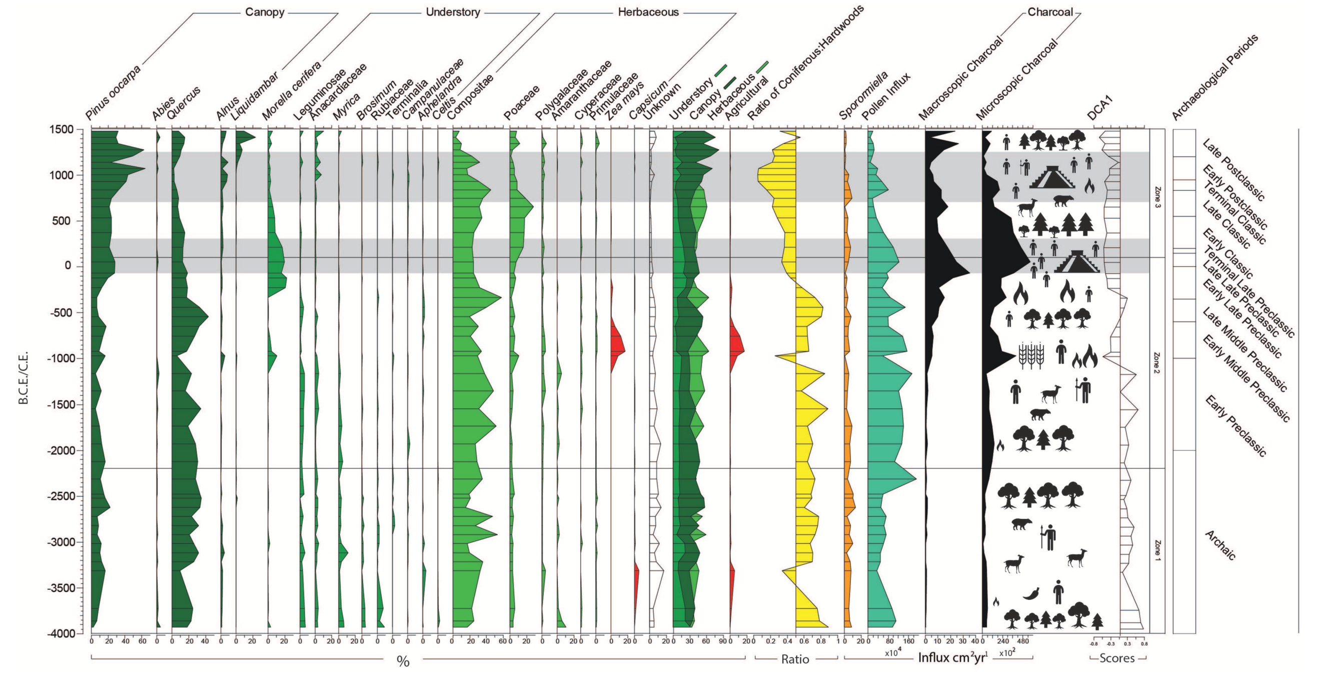

FIGURE 5 | Palynological percentage diagram of taxa appearing in an abundance >2%; forest structure; coniferous to hardwood ratio; pollen influx; macroscopic and microscopic influx; DCA axis 1; and Occupation of Chinkultic (dark bands). The palynological data are expressed as a percentage of total land pollen.

Zone 1 (545.75–421 cm, 14 samples, 4000–2200B.C.E.) spans *c.*1800 years concurrent with the last 2000 years of the Archaic Period (10,000–2000B.C.E.) (**Figure 5**). This Zone is predominantly defined by POF taxa *Quercus* (25.9%) and *Pinus* (11%) alongside herbaceous taxa Compositae (27.6%). Between 4000 and 3300 B.C.E. there is evidence for a decline in canopy taxa (from 61.3 to 37.3% of the total pollen sum), particularly *Quercus* (18–9.7%). In contrast, *Pinus* became abundant during this period, rising from 4000B.C.E. (2.3%) to 3300B.C.E. (16.7%). *Myrica* and *Alnus* are mostly present throughout this Zone, peaking at 3100B.C.E. (15.3%). *Brosimum* (0–4.3%), Anacardiaceae (0.3–4.3%), Leguminosae (0–6.3%), *Morella cerifera*, and Rubiaceae (0–9%) are present in low abundance and on average decrease from 4000 to 2200B.C.E. The ratio of coniferous to MHWF is on average 30:70. The coniferous to MHWF ratio changes from 25:75 to 66:34 between 3700 and 3300B.C.E. Compositae abundance increases between 4000 and 3200B.C.E. (17.3–35.3%) and peaks at 2900B.C.E. (53.3%) and 2700B.C.E. (47.3%). Amaranthaceae is present at 10.3% from 4000B.C.E. but subsequently declines leading up to 3700B.C.E. (1.3%). *Capsicum* appears and increases from 3850 to 3300 B.C.E. (0.3–5.3%), and Polygalaceae follows a similar trend, peaking at 3300B.C.E. (4.3%). Poaceae is stable and in low abundance throughout the record (2.3–5.6%). Pollen influx is low, decreasing from 4000 to 3300B.C.E. (965–344 grains x10^3 cm^2 per year) and increasing after 2300B.C.E. (1,919 grains x10^4 cm^2 per year). *Sporomiella* abundance is relatively high and stable (2.6–10.5%), falling below 4% abundance at 3100B.C.E. (2.6%), 2700B.C.E. (2.9%), and 2320B.C.E. (3.8%); there is a sustained high abundance of >10% between 2600 and 2500B.C.E. (10.2–13.3%). Macroscopic and microscopic charcoal are relatively low, decreasing between 4000 and 3000B.C.E. (macroscopic charcoal: 0.44–0.32 particles cm^2 per year; and, microscopic charcoal: 552–86 particles cm^{2}yr^1) then increasing through to 2300B.C.E (macroscopic: 1.2 particles cm^2 per year; and, microscopic: 770 particles cm^2 per year).

Zone 2 (412−263.5cm, 17 samples, 2200B.C.E−100C.E.) spans 2100 years, including the Early, Middle, and Late Pre–Classic Periods (2000–B.C.E.−100C.E.) and is defined by arboreal taxa *Quercus*, *Pinus* and *Morella cerifera* and herbaceous taxa Compositae, Poaceae, and *Zea mays* (**Figure 5**). *Quercus* continues to dominate the arboreal component (23%) but decreases between 1550 and 970B.C.E. (34–6%). After 970B.C.E. (6%) *Quercus* recovers until 550B.C.E. (43%) before decreasing rapidly by 350C.E. (17.3%) and stabilizing by 100C.E. (13%). *Pinus* continues to be persistently present and in stable abundance with slight increases between 1550 and 650B.C.E. (4.6–17.7%) and a larger increase from 340B.C.E.−100C.E. (6.3–28.3%). The low ratio of coniferous to MHWF taxa indicates relatively abundant MHWF, particularly *Quercus* (47:63), with a turnover to more coniferous taxa between 1150 and 970B.C.E. (17:83–74:26) and 230B.C.E.−50C.E. (4:6–7:3). *Morella cerifera first* substantially enters the record from 970B.C.E. (10.3%) but does not establish until 230B.C.E. where it rises to the second most abundant forest taxa through to 100C.E. (19.7%). Prior to the arrival of *Zea mays* (*c.*1000B.C.E.), Amaranthaceae abundance briefly increases c.1150B.C.E. (5.3%). The rise of *Zea mays* from 970B.C.E. (8.6%) peaks at 930B.C.E. (17%) and is abundant until 650B.C.E. (4.6%). Polygalaceae re–establishes between 1350 and 750B.C.E. (4–3.3%). Poaceae begins to increase from 1150B.C.E (2%) through to 100C.E. (11.5%), while Compositae remains the dominant herbaceous taxa (33.1%). Pollen influx is high overall during this Zone, peaking at 1150B.C.E. (175 × 10^4 grains cm^2 per year), with the exception of lower values at 970B.C.E. (577 × 10^3 grains cm^2 per year) and again between 650 and 550B.C.E. (810–781 × 10^3 grains cm^2 per year) and 340–130B.C.E. (881– 98 × 10^3 grains cm^2 per year). Macroscopic charcoal rises substantially after 1150B.C.E. (1.25 particles cm^2 per year) until 50C.E. (24.9 particles cm^2 per year). Microscopic charcoal follows a similar trend; however, it begins to increase from the beginning of this Zone (1,163 particles cm^2 per year) and peaks at 970B.C.E. (4,004 particles cm^2 per year), increasing again from 650 B.C.E. to 50C.E. (911–5,660 particles cm^2 per year). *Sporormiella* continues to be high in abundance and remains stable (0.6–8.8%) but on average is lower (4.4%) than in Zone 1 (7.2%). There are particularly high abundances of *Sporormiella* from 2100B.C.E. (7.4%) to 1750B.C.E. (8.8%), 930B.C.E (6.5%), and at 550B.C.E. (7.7%).

Zone 3 (254.5–114 cm, 15 samples, 100–1,522C.E.) encompasses *c.*1400 years and is defined by the arboreal components: *Pinus, Quercus, Morella cerifera,* and *Liquidambar,* and herbaceous components: Compositae and Poaceae (**Figure 5**). This zone is representative of the Terminal Preclassic (150–250C.E.), Classic (250–950C.E.) and Post–Classic Periods (950–1,522C.E.). *Quercus* and *Morella cerifera* decline between 200 and 1,070C.E. (30–4.7%) while *Pinus* increases (21.3–64%). *Liquidambar* establishes and rises from 1070C.E. (0.7%) through to 1522C.E. (9.3%). Of the remaining MHWF canopy taxa, *Alnus* increases after 850.C.E. (1.3%) through to 1150C.E. (6.3%) and then again from 1200 to 1,522.E. (0.7–6.3%). The coniferous to MHWF ratio increases between 100 and 1,522C.E. (78:22) in favor of coniferous taxa. Compositae remains in high abundance (22.9%) but decreases after 850C.E. (45.3%) through to 1522C.E. (7.7%). Poaceae increases from 200 to 650C.E. (15.7–28%). Pollen influx decreases from 200C.E. through to 1522C.E. (10 to 20 × 10^4 grains cm^2 per year). *Sporormiella* abundance increases from 70B.C.E. (0.9%) through to 200C.E. (7.1%) then decreases until the end of this Zone (4.1%). Overall *Sporormiella* abundance is comparatively lower (3.3%) than in Zone 2 (4.4%). Influx of macroscopic and microscopic charcoal decreases from 200 to 1000C.E. (macroscopic charcoal: 0.44–0.32 particles cm^2 per year; and, microscopic charcoal: 552–86 particles cm^2 per year).

DISCUSSION

The Natural Baseline Vegetation

This palaeoenvironmental sequence represents the vegetation dynamics of the Maya uplands of Guatemala from 4000B.C.E. to 1522C.E. Our data indicate that the natural baseline of this region is best described as OF to MPOF. This deciduous coniferous mosaic of oak dominated forests largely persisted from 4000 to 230B.C.E. after which, the vegetation assemblage deviates away from the natural baseline toward pine dominated forests. Deviation from the natural baseline was attributed to extensive and prolonged anthropogenic settlement and activities surrounding agrarian practices and use of fire for architectural developments (Anderson and Wahl, 2016). While our record suggests that this region has been predominantly forested through time, there is clear evidence for compositional changes in flora as a direct result of anthropogenic activities, particularly between 3700 and 3300B.C.E. and from 1000B.C.E.−1522C.E. (**Figure 5**). For example, the transition from MPOF in Zone 1 (4000–2200B.C.E.) through to PFs in Zone 3 (100–1522C.E.) is reflected in the taxonomic associations of the PCA and the environmental drivers presented in the CCA (**Figure 4**).

Anthropogenic Impacts and Agrarian Practices

Archaeological records have widely found that village farming became firmly established across the wider Maya Area after *c.*1800B.C.E. (Neff et al., 2006). This is reflected in the interpretations of the reconstructed palynological assemblages for both the Maya lowlands and the upland areas (**Figure 2**). Disturbance driven by anthropogenic activities, such as: (i) agricultural practices (e.g., Dull, 2004a,b, 2007); (ii) rearing livestock (Lovell, 1985); (iii) timber extraction (e.g., Dull, 2004a,b, 2007; Velez et al., 2011); and (iv) lime production (Anderson and Wahl, 2016), can initiate or maintain local vegetation succession impacting: (i) forest composition, (ii) structure, and (iii) regeneration (González-Espinosa et al., 1991).

Archaic populations from the Maya Area combined agriculture (e.g., pepper, beans, maize, squash, and chili) with hunting and gathering from as early as 5200B.C.E. (Pope et al., 2001). Evidence for agriculture from Centote Kail is first indicated by vegetation changes from 4000B.C.E. The observed changes include (i) a decline in canopy and understory taxa; (ii) increases in weedy disturbance taxa; (iii) a very small increase in local and regional burning; (iv) and the presence of cultivated taxa such as *Capsicum* (White, 1999), between *c.*3850 and 3300B.C.E. or *Zea mays* between *c.*970 and 550B.C.E. (**Figure 5**). A mixture of traditional hunter–gather practices combined with limited agriculture is exemplified by the abundance and variety of edible fruits and nuts (e.g., *Brosimum, Myrica*, and Anacardiaceae) and high abundance of fauna as indicated by the influx of *Sporormiella*.

Little is known about the Pre–Columbian human habitation of the upland Maya Areas, particularly during the Archaic, due to a scant archaeological record (MacNeish, 1982; Clark and Cheetham, 2002; Lohse et al., 2006; Lohse, 2009). Evidence from Cenote Kail suggests that people were manipulating the uplands of Guatemala from at least *c.*4000B.C.E. and practicing agriculture from *c.*3850B.C.E. This is the earliest palynological evidence for agriculture in the Southern Maya Area, preceding evidence from lowland Pacific Guatemala and from El Salvador, which all indicate agrarian practices established from *c.*3500B.C.E. (Dull, 2004a; Neff et al., 2006). Based on this evidence, we hypothesize that agriculture in the Southern Maya Area started in the uplands and spread to the lowlands, driven by increasingly favorable climatic conditions in the lowlands during the Holocene Thermal Maximum (6000–3000BC.E.) (Ford and Nigh, 2009). Human populations dispersed with the expansion of the lowland forests (Rosenmeier et al., 2002; Hillesheim et al., 2005; Neff et al., 2006; Wahl et al., 2006, 2014; Bush et al., 2009; Mueller et al., 2009; Escobar et al., 2012), increasingly interacting with the tropical forest ecosystem and gaining ethnobotanical knowledge (Ford and Nigh, 2009).

The start of the Pre–Classic (2000B.C.E.) is marked by the first appearance of state level settlements and an increased reliance on domesticated crops, particularly *Zea mays* (Neff et al., 2006). Settlements and agriculture were concentrated around water bodies, such as Cenotes, which provided reliable access to fresh water for sustenance and agriculture (Lucero et al., 2014). Although pollen records have been used to document the spread of maize agriculture in the Maya Area, most of these records are from the lowlands (**Figure 1**). Consequently, our understanding of the initial arrival of maize in the uplands of Central America is poor. Results from Cenote Kail are filling this gap. For example, traditional *Zea mays* agriculture is evident from 970B.C.E. in the Cenote Kail record. This is late compared to the uplands of El Salvador, *c.*2500B.C.E. (Dull, 2004a); however, the relative palynological abundance of *Zea mays* found in Cenote Kail, suggests that the expanse of agriculture in the Guatemala highlands was much greater. *Zea mays* agriculture is typically associated with *Milpa* (e.g., Dull, 2004a,b, 2007), which entails a 5–10 year cycle between periods of cultivation and fallow (Cowgill, 1962). Intensification of milpa cycling due to increasing human populations commonly leads to the depletion of nutrients in the soil (Ford and Nigh, 2009). We suggest that after 550B.C.E the agricultural settlement surrounding Cenote Kail was abandoned in favor of more productive soils in the lowlands.

By *c.*350B.C.E. large pyramids were being built across the Maya Area including the establishment of Chinkultic *c.*50B.C.E. (Ball, 1980). These pyramids were typically covered in plaster for architectural as well as decorative purposes (Anderson and Wahl, 2016). The production of this lime plaster involved the burning of powdered limestone (Oates, 2008). Monuments built during the Pre–Classic period were covered in this plaster (Hansen, 2001, 2012; Anderson and Wahl, 2016). Hansen (2012) reports that floor thickness alone could exceed 13cm. Anderson and Wahl (2016) explore the amount of fuel required to produce sufficient lime to meet the demands of this monument building and the impact that this might have had on the forest environment. They calculate 192 km^2 of forest would have been required for burning to create enough plaster for the construction of El Mirador in the central Maya Area. While Chinkultic is significantly smaller than El Mirador, the required plaster to create the complex of temples and ball courts would have been extensive. Agriculture in the Guatemala highlands culminated *c.*400 years before the Chinkultic settlement was established (Ball, 1980). Therefore, we suggest that the large increase of macroscopic and microscopic charcoal from *c.*200B.C.E. in Cenote Kail might relate to the production of lime plaster at Chinkultic, coinciding with its founding. The extraction of wood from the surrounding forests for burning is reflected in the structure of these POF as well as patterns for local and regional burning.

Forest Structure, Composition, and Successional Regeneration

Relatively equal abundances of canopy, understory, and herbaceous taxa from 4000 to 3700B.C.E. indicate a diverse and stratified forest structure comprising at least three vegetative levels. The high diversity of taxa, particularly in the understory (e.g., Leguminosae, Anacardiaceae, *Myrica*, and Rubiaceae), suggests a relatively low and open canopy allowing light to penetrate to the forest floor (Bush, 2000). This structure is typical of middle succession in mixed POF after a large clearance event (Peterson and Reich, 2001).

Weedy disturbance taxa (e.g., Amaranthaceae), reductions in canopy taxa (e.g., *Quercus*) and the creation of more open habitats exemplify anthropogenic disturbance prior to the agrarian establishment of *Zea mays* (e.g., Dull, 2004a,b, 2007). Anthropogenic impacts, as indicated by agricultural grains and reductions in forest taxa in Zone 1 occur at Cenote Kail between *c.*4000 and 3300B.C.E. Disturbance to the natural vegetation baseline was likely caused by settlement and agrarian practices directly surrounding Cenote Kail. After 3300B.C.E. cultivation ceases and arboreal taxa (understory and canopy) re–establish within *c.*100 years (3200–3100B.C.E.). This follows the expected recovery time of *c.*80 years for POF (Kappelle, 2006; Figueroa-Rangel et al., 2008). By 2600B.C.E. the mature structure of the POF are well-established and persist in relative equilibrium until further anthropogenic disturbance at 1150C.E. Deforestation, agrarian cultivar, and increased regional burning surrounding Cenote Kail all coincide at *c.*1000B.C.E. (**Figure 5**), and are attributed to the expansion and development of the Pre–Classic Maya (e.g., Neff et al., 2006). Increases in local and regional burning from the onset of Pre–Classic agriculture marks the sustained decline and eventual transition of POF to Pine dominated forests.

Plant community composition after burning is often explained by: (i) the sprouting ability of dominant species, (ii) the ability of subdominant species to increase in numbers, and (iii) the failure of invasive species to become established (Elliott et al., 1999, McDonald et al., 2003). Many species of oak rapidly sprout from their root collar after burning (e.g., *Quercus insignis, Q. skinneri*), dominating early successional stands (Barnes and Van Lear, 1998; Kirby and Watkins, 2015). However, several species of pine have also adapted to fire through the development of thick bark, serotiny, rapid growth, and sprouting, including *Pinus teocote* and *P. pseudostrobus* (Richardson, 2000; Rodríguez-Trejo and Fulé, 2003). The early successional formation of oak dominance is evident between 970 and 550B.C.E. (**Figure 5**). As the forest becomes more established, oak abundance typically diminishes under faster-growing conifers (Sheffer, 2012).

Extraction of wood, sustained land clearance, and most importantly burning has changed the structure of the POF from oak-dominated to pine-dominated (**Figure 5**). Additionally, herbivores, such as the white–tailed deer (*Odocoileus virginianus*) may also have impacted forest composition and regeneration through selective browsing on young saplings and individual species (Vera, 2000; Kirby and Watkins, 2015). We suggest that the coppice systems created by the Maya are particularly vulnerable to browsing from medium and large sized herbivores (Joys et al., 2004). Pines have been found to be preferentially browsed compared with other arboreal taxa (Blair and Brunett, 1980). While overall herbivore abundance decreases through time, their browsing impacts upon forest structure may have been particularly important to recovery after prolonged disturbance (Joys et al., 2004).

The pine-dominated forests become increasingly established between 150B.C.E. and 1070C.E. (**Figure 5**). When coniferous forests form closed stands, they change the environment beneath them. The most substantial changes involve the greater uptake of soil water and decrease of light reaching the ground (Jucker et al., 2014). The combination of these factors makes it almost impossible for other arboreal taxa to establish and grow (Kappelle, 2006). For example, most species of oak suffer increased reproductive failure under closed canopy conditions (Jucker et al., 2014), relying on the dispersal of acorns to forest edges or clearings through animal transport (Lopez-Barrera, 2003; Kappelle, 2006). Large herbivores, such as the Baird tapir (*Tapirus bairdii*), are important to the structure and diversity of recovering POF due to their role as long distance seed dispersers, ingesting whole seeds and dropping them intact with their feces (Bodmer, 1991; Rodrigues et al., 1993; Fragoso, 1997; Olmos, 1997; Lawton, 2000). The reduction of herbivore abundance during the transition of oak dominated POF to pine dominated POF at Cenote Kail (*c.*220B.C.E.) is likely to have contributed to the established rise in pine. Coniferous forest stands remain dominant until they are removed through felling or die of disease, insect attack or old age (Jones, 1974). The transition from pine dominated coniferous forests to MHWF is gradual and relies upon the breakup of the coniferous forest canopy to allow for secondary canopy taxa to rise through (Jones, 1974). The establishment of *Quercus, Liquidambar* and *Alnus* at Cenote Kail after *c.*850C.E. demonstrates this final transition back to MHWF dominance (**Figure 5**).

Results from this study indicate that fire has been the most important driver of vegetative change in this ecosystem throughout the last *c.*6000 years, particularly during the Pre–Classic and Classic periods (2000B.C.E.—950C.E.). Fire driven change from MHWF (oak–dominated) to coniferous forests (pine–dominated) has previously been attributed to climate driven aridity (e.g. Figueroa-Rangel et al., 2008, 2010, 2012); however, our study suggests that anthropogenic activity is the most likely source of burning and overall vegetative change. The predominantly anthropogenic signal for burning represented in Cenote Kail is inferred through the combined evidence of: (i) agricultural practices, (ii) reduction of MHWF taxa, and (iii) rapid increase of burning coinciding with the establishment and expansion of nearby Maya temples and settlements (e.g., Chinkultic).

Terrestrial hydroclimatic reconstructions from the upland Maya Area suggest that only modest changes in precipitation amounts occurred over the last several millennia. Climatic evidence from Lago Amatitlan indicates lower lake levels from 250B.C.E. to 125C.E. and 875 to 1375C.E., which has been attributed to a decline in water level resulting from either a drier climate and/or reforestation after anthropogenic abandonment (Velez et al., 2011). Also, evidence from San Lorenzo (Chiapas) indicates generally wetter conditions from *c.*1400–700B.C.E., 500–850B.C.E., and *c.*1200–1522C.E. interrupted by periods of drought from *c.*700–500B.C.E. and *c.*850–1200C.E. (Franco-Gaviria et al., 2018). These records suggest that although climate may have played an abetting role in driving forest dynamics, the timing of these hydroclimatic changes do not reflect the forest and fire dynamics reconstructed from Cenote Kail. Our findings suggest that anthropogenic activities revolving around agriculture and architectural developments have initiated and maintained successive regeneration of vegetation from mixed oak dominated forests to pine dominated forests. However, further work investigating past hydroclimate changes for this region will be required to fully understand the role of climate as an independent driver of the vegetation surrounding Cenote Kail.

CONCLUSIONS

The sedimentary sequence from Cenote Kail was continuously deposited from 4000B.C.E. to 1522C.E. and provides a record of past changes in vegetation and human impacts. We have found that POF within the Southern Maya area were transformed by Pre–Columbian human populations through practices of agriculture and architectural developments over thousands of years extending back into the Archaic Period (Betz, 1997; Piperno and Pearsall, 1998; Smith, 1998; Dull, 2004a; Neff et al., 2006). Three successional phases can be discerned following a combination of natural and anthropogenically modified successional pathways. The Archaic period is defined by light anthropogenic disturbance, centered around some land clearance for agriculture. *Zea mays* cultivation is prevalent from 970 to 550B.C.E., after which time sedentary agriculture does not appear to be widely practiced. Herbivorous animals, such as deer and tapir, are likely to have played an important role in forest recovery after disturbance; however, discerning their individual impacts would require further research. Persistent high intensity burning for lime production during the Late–Pre-Classic to Classic Period are suggested to have resulted in a turnover of forest structure *c.*150B.C.E. from oak-dominated POF to pine-dominated POF. Evidence for the fragmentation, degradation and subsequent recovery of these MTF over the past *c.*6000 years provides a valuable comparison for the present–day anthropogenic activities that are driving current changes in this region. To protect the remaining intact fragments of these MTF and to encourage the recovery of areas that have suffered past compositional or structural shifts, fire needs to be carefully managed.

AUTHOR CONTRIBUTIONS

WH conceived the presented idea with input from SN, KW, and GP. WH conducted all palaeoecological lab work, statistical analysis, and age-depth modeling. SN and KW verified the analytical methods. NS and BS conducted the field work. NS carried out the radiocarbon dating. KW, SN, NS, and GP helped supervise the project. WH drafted the final manuscript. All authors discussed the results contributing to the final manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2019.00034/full#supplementary-material

Supplementary Table 1 | Sites represented on **Figures 1** and **2**.

Supplementary Table 2 | Images of palynological taxa at 400x magnification identified from Cenote Kail.

Data Sheet 1 | Raw Palaeoecological Data.

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CORRECTION
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Corrigendum: The Legacy of Pre–Columbian Fire on the Pine–Oak Forests of Upland Guatemala

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A Corrigendum on

The Legacy of Pre–Columbian Fire on the Pine–Oak Forests of Upland Guatemala
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In the original article, there was an error. After discussions with the wider scientific community, the pollen taxa identified as *Corylus* is more likely to be *Myrica*; and the pollen taxa identified as *Cercocarpus* is more likely to be *Terminalia*.

A correction has therefore been made to the ***Results***, subsection ***Palaeoecological Trends***, paragraph two and three:

"Results from the CCA show that microscopic and macroscopic charcoal are significant environmental variables most associated with Zones 2 and 3, while *Sporormiella* is most associated with Zone 1 and is not statistically significant (**Figure 4A**). The PCA displays a distinct gradient and several associations between taxa and samples (**Figure 4B**). The first axis represents 20.2% of the variation, while axis two represents 10.5% of the variation. The arch between samples suggests that there is only one clear gradient. When the independently calculated palynological Zones are superimposed upon these quadrants, the top, and bottom right quadrants are most associated with Zone 1, the top left quadrant is most associated with Zone 2 and the bottom left quadrant is most associated with Zone 3 (**Figure 4B**). The first taxonomic association comprises canopy taxa *Quercus*, understory taxa Leguminosae, *Myrica*, Ericaceae, and the herbaceous and agrarian taxa *Capsicum*, which is most associated with Zone 1. The second taxonomic association comprises of understory taxa *Juniperus* and *Terminalia*, herbaceous taxa Polygalaceae, Apiaceae, Compositae *Aphelandra*, and agrarian taxa Capsicum most associated with Zone 2. The third taxonomic association comprises canopy taxa *Pinus, Alnus*, and *Liquidambar* together with understory taxa *Morella cerifera*, and herbaceous taxa Poaceae, and Campanulaceae, which is most associated with Zone 3 (**Figure 4B**)."

"Zone 1 (545.75–421 cm, 14 samples, 4000–2200B.C.E.) spans *c.*1800 years concurrent with the last 2000 years of the Archaic Period (10,000–2000B.C.E.) (**Figure 5**). This Zone is predominantly defined by POF taxa *Quercus* (25.9%) and *Pinus* (11%) alongside herbaceous taxa Compositae (27.6%). Between 4000 and 3300 B.C.E. there is evidence for a decline in canopy taxa (from 61.3 to 37.3% of the total pollen sum), particularly *Quercus* (18–9.7%). In contrast, *Pinus* became abundant during this period, rising from 4000B.C.E. (2.3%) to 3300B.C.E. (16.7%). *Myrica* and *Alnus* are mostly present throughout this Zone, peaking at 3100B.C.E. (15.3%). *Brosimum* (0–4.3%),

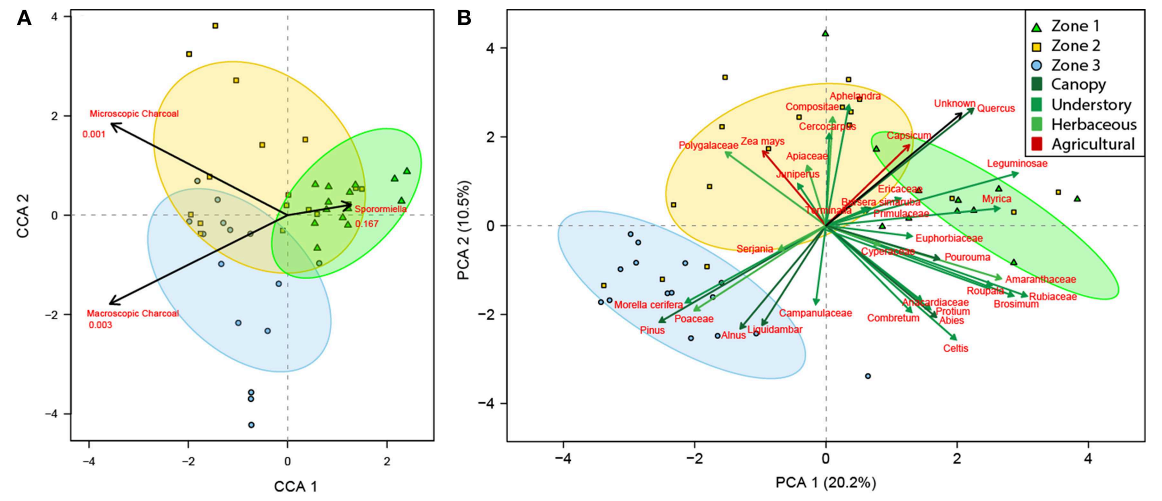

FIGURE 4 | Canonical correspondence analysis of the palaeopalynological data set ordinated against independent environmental indicators of local fire (macroscopic charcoal), regional fire (microscopic charcoal), and herbivory (*Sporormiella*) **(A)**. Principal component analysis of the palaeopalynological data set **(B)**. Zones are derived from the broken stick model and are represented by ellipses at a confidence of 95%. Zone 1 = green triangles; Zone 2 = yellow squares; Zone 3 = blue circles.

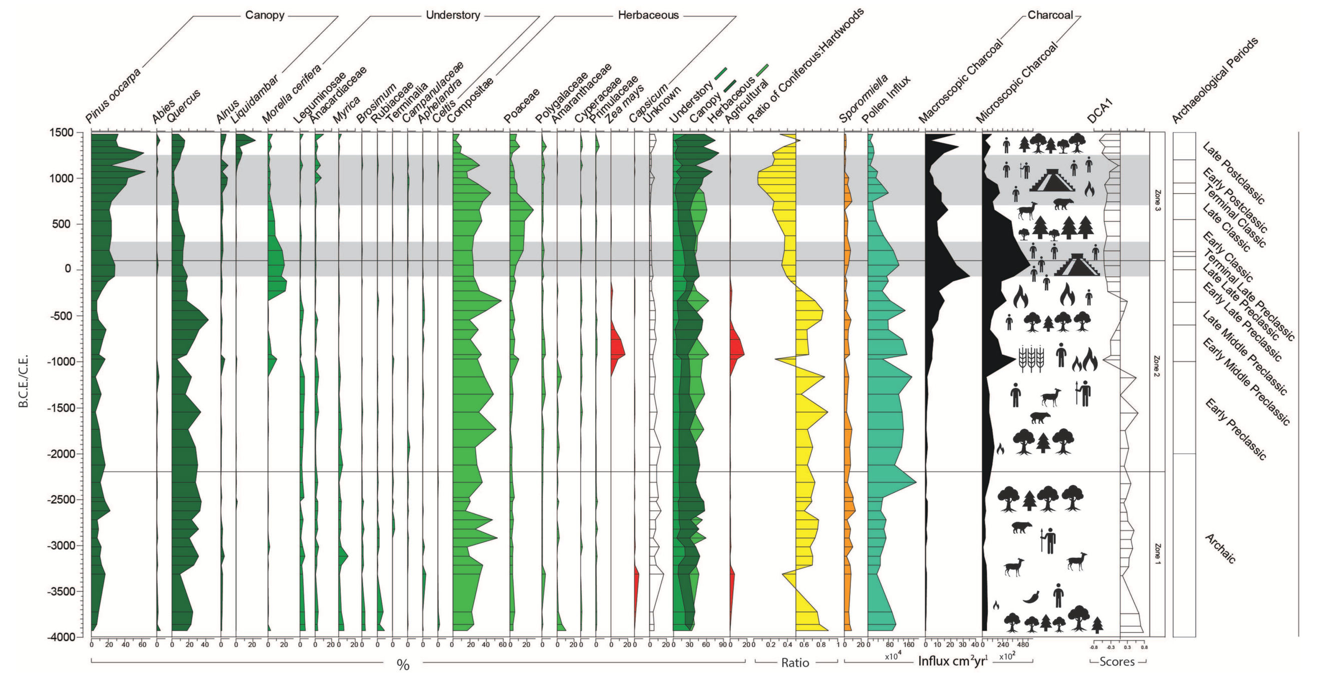

FIGURE 5 | Palynological percentage diagram of taxa appearing in an abundance >2%; forest structure; coniferous to hardwood ratio; pollen influx; macroscopic and microscopic influx; DCA axis 1; and Occupation of Chinkultic (dark bands). The palynological data are expressed as a percentage of total land pollen.

Anacardiaceae (0.3–4.3%), Leguminosae (0–6.3%), *Morella cerifera*, and Rubiaceae (0–9%) are present in low abundance and on average decrease from 4000 to 2200B.C.E. The ratio of coniferous to MHWF is on average 30:70. The coniferous to MHWF ratio changes from 25:75 to 66:34 between 3700 and 3300B.C.E. Compositae abundance increases between 4000 and 3200B.C.E. (17.3–35.3%) and peaks at 2900B.C.E. (53.3%) and 2700B.C.E. (47.3%). Amaranthaceae is present at 10.3% from 4000B.C.E. but subsequently declines leading up to 3700B.C.E. (1.3%). *Capsicum* appears and increases from 3850 to 3300 B.C.E. (0.3–5.3%), and Polygalaceae follows a similar trend, peaking at 3300B.C.E. (4.3%). Poaceae is stable and in low abundance throughout the record (2.3–5.6%). Pollen influx is low, decreasing from 4000 to 3300B.C.E. (965–344 grains x10^3

cm^2 per year) and increasing after 2300B.C.E. (1,919 grains x10^4 cm^2 per year). *Sporomiella* abundance is relatively high and stable (2.6–10.5%), falling below 4% abundance at 3100B.C.E. (2.6%), 2700B.C.E. (2.9%), and 2320B.C.E. (3.8%); there is a sustained high abundance of >10% between 2600 and 2500B.C.E. (10.2–13.3%). Macroscopic and microscopic charcoal are relatively low, decreasing between 4000 and 3000B.C.E. (macroscopic charcoal: 0.44–0.32 particles cm^2 per year; and, microscopic charcoal: 552–86 particles cm^2yr^1) then increasing through to 2300B.C.E (macroscopic: 1.2 particles cm^2 per year; and, microscopic: 770 particles cm^2 per year)."

A correction has also been made to the ***Discussion***, subsection ***Anthropogenic Impacts and Agrarian Practices***, paragraph two:

Archaic populations from the Maya Area combined agriculture (e.g., pepper, beans, maize, squash, and chili) with hunting and gathering from as early as 5200B.C.E. (Pope et al., 2001). Evidence for agriculture from Centote Kail is first indicated by vegetation changes from 4000B.C.E. The observed changes include (i) a decline in canopy and understory taxa; (ii) increases in weedy disturbance taxa; (iii) a very small increase in local and regional burning; (iv) and the presence of cultivated taxa such as *Capsicum* (White, 1999), between *c*.3850 and 3300B.C.E. or *Zea mays*between *c*.970 and 550B.C.E. (**Figure 5**). A mixture of traditional hunter–gather practices combined with limited agriculture is exemplified by the abundance and variety of edible fruits and nuts (e.g., *Brosimum, Myrica*, and Anacardiaceae) and high abundance of fauna as indicated by the influx of *Sporormiella*.

Additionally, a correction has been made to ***Discussion***, subsection ***Forest Structure, Composition and Successional Regeneration***, paragraph one:

"Relatively equal abundances of canopy, understory, and herbaceous taxa from 4000 to 3700B.C.E. indicate a diverse and stratified forest structure comprising at least three vegetative levels. The high diversity of taxa, particularly in the understory (e.g., Leguminosae, Anacardiaceae, *Myrica*, and Rubiaceae), suggests a relatively low and open canopy allowing light to penetrate to the forest floor (Bush, 2000). This structure is typical of middle succession in mixed POF after a large clearance event (Peterson and Reich, 2001)."

Corrections have also been made in ***Figure 4*** and ***Figure 5***. The correct figures appear above.

Lastly, the ***Supplementary Material*** (including Supplementary Tables 1 and 2 and the raw data) has also been updated to reflect the correct taxa.

The authors apologize for this error and state that this does not change the scientific conclusions of the article in any way. The original article has been updated.

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Impacts of Selective Logging and Associated Anthropogenic Disturbance on Intact Forest Landscapes and Apes of Northern Congo

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The tropical forests of Western Equatorial Africa are home to extraordinary biodiversity, including sympatric chimpanzees (*Pan troglodytes troglodytes*) and western lowland gorillas (*Gorilla gorilla gorilla*). The region is also comprised of significant stands of Intact Forest Landscapes (IFL) that are in rapid decline. As part of a regional monitoring effort, we partnered with local government officials, conservation NGOs, and the timber company working in the region to assess ape abundances in relation to habitat characteristics and anthropogenic disturbances and compare IFL and non-IFL areas in the Sangha Trinational landscape, Republic of Congo. We found that chimpanzees and gorillas occur at high densities in IFL, as well as non-IFL. To better understand how selective logging changes floristic factors, we compared herb and tree densities from botanical surveys conducted in IFL and non-IFL. IFL had higher tree stem densities and less terrestrial herbs than logged habitats. However, few ape resources were logged in this extraction cycle and areas with tree stems removed subsequently had higher abundances of terrestrial herbs preferred by apes, which may contribute to the elevated ape abundance estimates. Floristic differences in logged forest were identified to coincide with differences in ape resource use. The chimpanzee tree nesting niche was reduced in non-IFL as night nests were constructed significantly closer to the ground than in IFL. Whereas, gorilla nest height locations did not differ significantly between IFL and non-IFL. To identify other potential anthropogenic impacts, we assessed direct and indirect impacts of road expansion and illegal hunting on wildlife in these remote areas. Increased access to IFL that facilitates illegal hunting raises concern for protecting wildlife across Western Equatorial Africa. We urge that the results of biodiversity assessments and strategic aspects of long-term protection should be taken into account when identifying conservation set-asides and maintaining diverse states of modified forests. Finally, the results of our monitoring efforts are provided as evidence of the value of long-term collaborations among local stakeholders, government officials, conservation agencies, and industrial partners to improve the implementation of certification standards and biodiversity conservation initiatives.

Keywords: gorilla, chimpanzee, certification, biodiversity, Congo Basin

INTRODUCTION

Early efforts to identify the world's remaining "frontier" forests highlighted the substantial abundance of pristine habitats in the tropics (Bryant et al., 1997). Since the identification of such Intact Forest Landscapes (IFL), which are forest/mosaics at least 500 km^2 (50,000 ha) lacking overt anthropogenic disturbance such as infrastructure (Potapov et al., 2008), there has been dramatic decline in such areas (Potapov et al., 2017). The startling loss of IFL is largely due to tropical nations' economies and infrastructural development being rooted in the exploitation of natural resources. Africa contains one of the three large blocks of the world's tropical forests and with the depletion of natural resources in Asia, multi-national companies have sought new outlets in timber-rich nations such as those in Western Equatorial Africa (Angola (Cabinda enclave), Cameroon, Central African Republic, mainland Equatorial Guinea, Gabon, and Republic of Congo). Selective logging is the primary extraction industry responsible for IFL loss in the region (Asner et al., 2010; Potapov et al., 2017) and Republic of Congo has been in the vanguard of this expansion. An accelerated rate of logging road construction has ensued particularly in the north of the country over the last two decades (Laporte et al., 2007; Kleinschroth and Healey, 2017). In the wake of such expansion follows considerable degradation of natural resources and increased human immigration (Geist and Lambin, 2002; Watson et al., 2018). If action is not taken to avert losses, it is estimated that all IFL outside of protected areas in Republic of Congo will have disappeared by 2050 (Potapov et al., 2017) and wildlife populations in the region will be reduced by 80% (Fa et al., 2003). These developments will assuredly have negative consequences on forest and biodiversity within protected areas including those of Natural World Heritage Sites as many are already under elevated levels of human pressure and forest conversion (DeFries et al., 2005; Laurance et al., 2012; Bailey et al., 2016; Lui and Coomes, 2016; Allan et al., 2017).

Identifying important environmental attributes of forest intactness and indicators of change in intactness are key to more informed conservation management. With 77.4% of critically endangered western lowland gorillas and 80.7% of endangered central chimpanzees existing outside of protected areas (Strindberg et al., 2018) there is a great need for management beyond protected areas to conserve these flagship species. Based on recent regional modeling, gorillas and chimpanzees occur at higher densities in IFL compared to non-IFL (Strindberg et al., 2018). The physical structure of these forests has considerable influence on great ape distributions with generally higher ape densities associated with increasing tree canopy height (Strindberg et al., 2018). The emergent and high canopy levels are the result of a few "biomass hyperdominant" tree species (Bastin et al., 2015) in a region overall typified by low tree stem densities (Lewis et al., 2013). Local-scale surveys and remote sensing indicate frequent disruption in canopy continuity even in an intact state (Devos et al., 2008). This is a product of the mixed species forest composition which is comprised of a mosaic of regenerating patches from natural disturbances with canopies varying in height and composition. The dynamic and complex nature of this habitat supports high densities of both chimpanzees and gorillas (Devos et al., 2008).

A key question remains as to how increases in canopy gaps associated with the loss of dominant canopy trees, as occurs in selective logging, affect forest composition and resources important to apes. In South America, highly disturbed forests have been shown to support elevated densities of climbers such as those of the genus *Ficus*, which include species bearing high-quality fruit found to predict populations of primates (Terborgh, 1986; Leighton, 1993; Wrangham et al., 1993; Marshall and Leighton, 2006). Removal of canopy trees also brings elevated light exposure to the lower understory strata which in turn bolsters the growth of non-arboreal pioneer species (Malcolm and Ray, 2000) that are likely of benefit to apes. Members of the families referred to as terrestrial herbaceous vegetation (THV) are important to gorillas and chimpanzees for both foraging and nesting (e.g., Wrangham, 1986; Rogers and Williamson, 1987; Fay, 1997). Chimpanzees are classically referred to as more of a dietary specialist with their resource use focused on fruit-bearing tree species whereas gorillas are typically considered to be more along the lines of a generalist with a diet focused mostly on herbaceous ground vegetation (Bourliere, 1985). This classification has proven to be a useful dichotomy when assessing factors shaping species responses to perturbation, with the former more often negatively impacted by forestry than the latter (Johns and Skorupa, 1987; Sodhi et al., 2010; Burivalova et al., 2014). To date, however, surveys of gorillas and chimpanzees in post-logged forests indicate increases as well as decreases in population numbers, which raises questions regarding the relationship between compositional changes in the environment and ape abundance. Overall, gorilla populations in this region are in decline (Strindberg et al., 2018) and negative impacts of anthropogenic disturbance on chimpanzee behaviors have become increasingly apparent (Kuehl et al., 2019). However, alteration in the structural complexity of IFL may not be the only or principal factor responsible for potential changes in ape abundance in logged habitats of Western Equatorial Africa.

The rise in unsustainable hunting of wildlife for meat (i.e., bushmeat) and body parts is the most severe and rapidly expanding threat facing species today (Ripple et al., 2017). Life-history traits are known to influence species-specific vulnerability to hunting pressure (Reynolds, 2003; Marshall and

Leighton, 2006). Human settlements, consumption practices, and accessibility are also strong determining factors in the persistence or decline of wildlife in an area (Barnes and Lahm, 1997; Fa et al., 2000; Blake, 2002; Jerozolimski and Peres, 2003; Blake et al., 2008). We suggest that a putative pattern of hunting pressure is triggered by increasing access to IFL. Forests distant from human infrastructure have higher abundances of wildlife compared to forests with longer histories of human influence (e.g., Eves and Ruggiero, 2000; Fa et al., 2004; Dupain et al., 2012) and greater accessibility (Yackulic et al., 2011). It follows that larger and highly profitable animals are reportedly originating from more distant and less-accessible areas (Allebone-Webb et al., 2011). There are indications that declines in wildlife associated with opening of IFL are rapid. In a previously intact concession in northern Congo, (Wilkie et al., 1992) estimated that 3,140 km of primary roads, secondary roads, and transects were opened in a single year. This region has subsequently been shown to be a primary source of most ivory reaching markets, substantiated by the staggering 62% decline of forest elephants in the Congo Basin since the early 2000s (Wasser et al., 2004; Maisels et al., 2013). Understanding the temporal-spatial patterning of hunting pressure in relation to the decline of IFL is crucial to preventing species declines both in protected areas and neighboring forests through proactive conservation measures to address such threats.

As part of a regional monitoring effort, we partnered with local government officials, conservation NGOs, and the timber company working in the region to assess ape abundances in relation to habitat characteristics and anthropogenic disturbances and compare IFL and non-IFL in the Sangha Trinational landscape. Baseline estimates of great ape densities in an IFL are compared with post-logging densities to better understand population dynamics in relation to anthropogenic disturbance. We also document floristic differences between IFL and non-IFL and relate floral differences to great ape resource use needs. The study took place in and around the Goualougo Triangle which is located in the southern portion of the Nouabalé-Ndoki National Park. Initial surveys in this region conducted by the Wildlife Conservation Society which led to the creation of the Nouabalé-Ndoki National Park cited the intact nature of the Goualougo Triangle and its conservation as essential for maximizing protection of a key area of core habitat for the region (Fay et al., 1990; Fay, 1992; Blake, 1994). Among all long-term ape research sites in Africa, the Goualougo study area was found to be the least disturbed by anthropogenic disturbances (Wilson et al., 2014). As such, we provide an update on the expansion of timber harvesting in the forest surrounding this protected area and increasing anthropogenic pressures which have reached the most remote areas of the Goualougo Triangle. This provides a rare opportunity to observe the temporal patterning of increased accessibility to remote forests and how this relates to illegal poaching pressures. We use this information to provide recommendations for park management and forest certification policies, as well as to promote the potential for permanent research sites to contribute to conservation initiatives through monitoring and surveillance.

MATERIALS AND METHODS

This study took place in the Nouabalé-Ndoki National Park (NNNP; 2°05′-3°03′ N; 16°51′-16°56′ E) and the adjacent Kabo Forestry Management Unit (FMU) which is an immediately neighboring logging concession in northern Republic of Congo. The National Park was established in 1993 and covers 5,000 km^2 of forest and is part of the Trinational de la Sangha (TNS), a designated UNESCO Natural World Heritage Site (NWHS) which spans the Republic of Congo, Cameroon, and Central African Republic. The landscape is primarily comprised of a vast stretch of lowland Guineo-Congolian forest (White, 1983) with altitudes ranging from 330 to 600 m. The major habitat types in this region include monodominant *Gilbertiodendron* forest, mixed species forest, transitional *Gilbertiodendron* to mixed species forest, and swamp forest. This semi-deciduous mixed species forest has a diverse flora and canopy that is not always continuous. Rainfall is bimodal with a main rainy season from August through November and a short rainy season in May. Annual rainfall averaged 1,728 ± 47 mm between 2010 and 2017.

The Wildlife Conservation Society has the mandate to manage the NNNP and the FMU bordering it. In 1995, the landscape encircling the NNNP was divided into four concessions. The Kabo FMU is comprised of 2,960 km^2 which surrounds the southern sector of the National Park. The western sector of the Kabo FMU was selectively logged between 1971 and 1972 by the Société Nouvelle des Bois de la Sangha (SNBS) and then harvested a second time from 2005 to 2009 by Congolaise Industrielle des Bois (CIB). The Kabo concession was among the first concessions in Western Equatorial Africa to achieve Forest Stewardship Council (FSC) certification in 2006. The majority of the volume extracted consisted of *Entandrophragma* species, *Triplochiton scleroxylon*, and *Milicia excelsa* (CIB 2014). The eastern sector of the Kabo FMU was an IFL until the mid-2000s (**Figure 1**).

The Goualougo Triangle Ape Project (GTAP) was established in 1999 with the aim of conducting applied conservation research on the behavioral ecology of gorillas and chimpanzees in northern Congo. The Goualougo Triangle is an enclave of lowland forest between the Ndoki and Goualougo Rivers, which forms the southernmost section of the NNNP. It is bordered to the south, west, and east by the Kabo FMU (**Figure 1**). The Djeke Triangle is located between the Ndoki National Park in Central African Republic and NNNP in Republic of Congo. The GTAP and Wildlife Conservation Society research teams maintain a year-round field presence in the Goualougo and Djeke Triangles with daily reconnaissance missions to follow great apes that have been habituated to human presence. Both the Goualougo and Djeke Triangles are represented as IFL.

Forest Status

We used the IFL inventory map (Potapov et al., 2008) to define intactness of the NNNP and neighboring Kabo FMU. This map is based on the extent of roads and settlements documented from Landsat images (of 30 m resolution) up to 2013 (Potapov et al., 2017). The IFL regions are forested areas >500 km^2 and >10 km wide that fall outside a 1-km buffer around such infrastructure

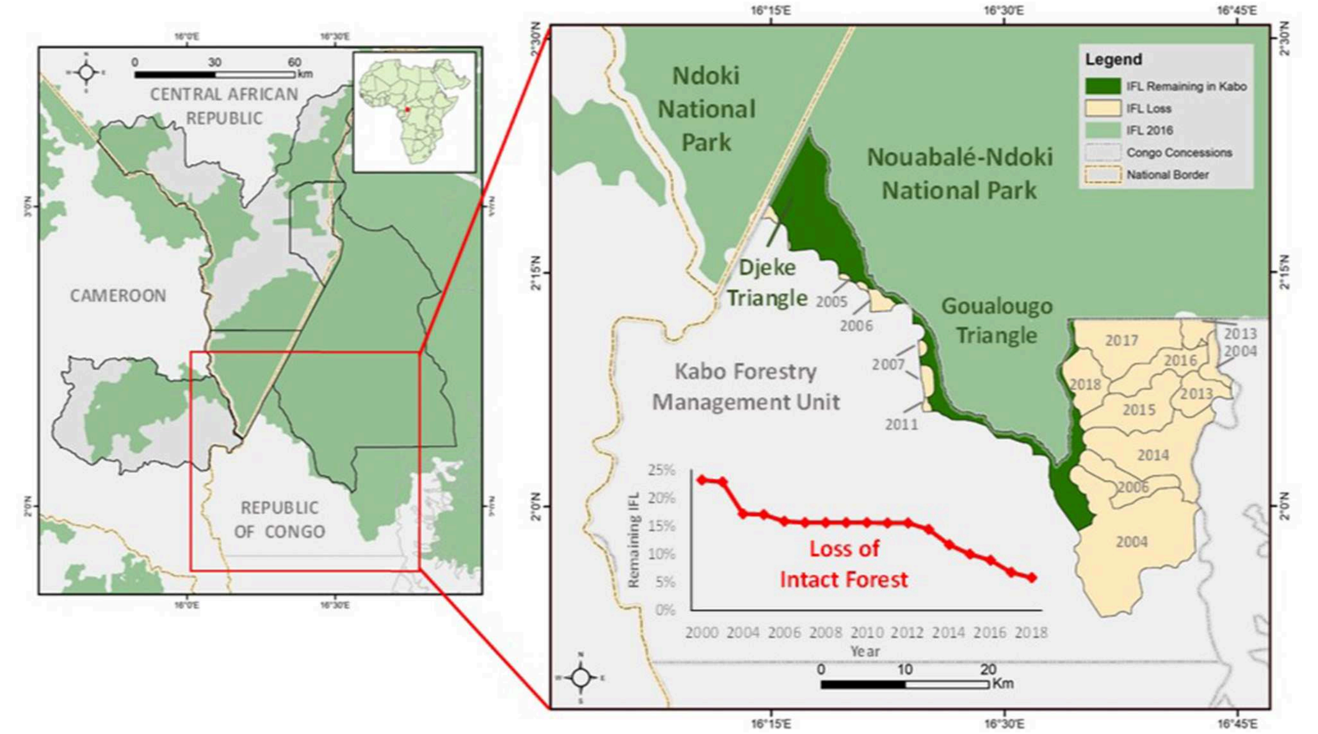

FIGURE 1 | Location of the study area within the Sangha Trinational landscape. Inset shows Goualougo and Djeke Triangle which both consist of IFL in relation to recent declines of IFL within the adjacent Kabo Forestry Management Unit.

(Potapov et al., 2008). Since the 2013 estimate of IFL, new road networks have been established within the concessions surrounding NNNP and within the IFL with updated estimates for the region provided in Morgan et al. (in press). Digital features representing new roads were provided by the local timber operating company and Kleinschroth et al. (2016). We used current Landsat 8 satellite imagery to review road features and verify placement. Duplicated roads in Kleinschroth et al. (2016) and the timber company files were removed. Once completed, the new roads were buffered and used to update the extent of IFL for areas of interest following Potapov et al. (2008). The revised extent of IFL in the Kabo concession was presented and reviewed by the local industrial logging company for verification.

Accessibility

Accessibility was assessed retrospectively based on the progression of roads within the Kabo concession from 1996 to 2018. Peres and Terborgh (1995) proposed a 10-km criterion to set how far hunter incursions into neighboring interior forests are likely to occur from roads. The 10-km criterion differs from the IFL measure that also considers the location of settlements in a given area.

Human Presence

Armed law enforcement teams began foot and vehicle patrols in NNNP and Kabo FMU in 2005. The location of human sign data, as well as other signs (carcasses, spent ammunitions, camps) observed, were recorded by either mobile research teams or patrol teams traversing the study region or on fluvial patrols. In 2015, patrol teams began using the Spatial Monitoring and Reporting Tool (SMART) (Connect version 4.1).

Since the project's inception in 1999, GTAP research teams have documented any human activities detected while following habituated apes or during surveys (ape nest transects, botanical) within or outside of NNNP. Both direct and indirect signs of illegal human activity are reported to law enforcement officials. In 2017, GTAP adopted the SMART data collection method implemented by NNNP patrol teams so as to use our field efforts to contribute to regional surveillance.

Botanical Surveys

Botanical plots (50 × 50 m) were conducted in IFL and a twice selectively logged forest. To enumerate and measure stems of different size classes and growth forms within each plot, we identified and measured all trees with diameter at breast height (DBH) >80 cm with a base falling entirely within 25 m of either side of the midline, and all strangler figs with DBH ≥10 cm whose host trees had a base falling entirely within 25 m of the midline. We identified and measured all trees and free-standing *Ficus* spp. with a DBH 30–80 cm with bases falling entirely within 12.5 m of either side of the midline. All strangler *Ficus* spp. associated with trees in the survey plots were also identified and measured. We recorded all trees with a DBH of 10–30 cm with bases falling entirely within 2.5 m of either side of the midline, as well as every stem or leaf rooted in the ground for all terrestrial herbaceous vegetation. In cases where specimens were not identifiable, vouchers were collected for identification by Dr. David Harris, Royal Botanical Garden of Edinburgh. Overall stem densities were generated by averaging densities across plots within each zone type (intact, logged).

To better understand how herb density is affected by logging, as well as whether the effect is consistent across the floral families present, we used lme4 (Bates et al., 2015) in R (version 3.4.3, R Core Team, 2017) to run a linear mixed effect model with Gaussian error structure. The response variable was the square root-transformed herb density of each floral family in each plot surveyed. The fixed effect predictors were zone (logged and intact), family (Commelinaceae, Marantaceae, and Zingiberaceae), and their interaction. Plot ID was included as a random effect. The model residuals were assessed visually and were normally distributed as well as homogenous. We also assessed model stability by removing data points from each plot ID sequentially and running the model again each time. The results from the models using the reduced datasets were consistent with the results from the original model, suggesting the model was stable. The dataset for this model contained 138 total data points from 46 plots. We first established the combined significance of the fixed effects by comparing the full model, which contained all fixed effects and the random effect, to a null model (Forstmeier and Schielzeth, 2011), which contained only the random effect, using a likelihood ratio test (Dobson, 2002). We then tested the effect of the interaction using a likelihood ratio test (Barr et al., 2013), comparing the full model to a model that did not contain the interaction term.

Ape Abundance

We stratified the southern section of NNNP and Kabo FMU into study zones to systematically evaluate changes in forests and ape abundance and distribution as related to protection status, forestry activities, and other factors. The automated survey design component of the custom Distance software was used to generate systematically-spaced transects with a random start throughout the study area (Thomas et al., 2010). The total line length (and number of transects) in each zone is sufficient to calculate precise densities (and precise estimates of precision) of great apes for each zone individually (see Morgan et al., 2006). Ape nests and human signs were recorded during each survey. See Morgan et al. (2006) for a detailed description of data collection protocols and methods. Ape densities and abundance were calculated using decay rates for gorilla and chimpanzee nests from Morgan et al. (2016) a nest creation rate of 1.09 nests/day (SE = 0.05).

Species Specific Nest Heights in IFL vs. Logged Habitat

All independent gorillas and chimpanzees build one-night nest per day on average. A separate investigation of species-specific nesting heights in IFL vs. non-IFL was conducted using archived ape transect data collected by GTAP research teams in the NNNP and Kabo FMU (see Morgan et al., 2006, 2018). Nests not assigned to a particular species along transects were classified as constructed by either chimpanzee or gorilla following Sanz et al. (2007). A Wilcoxon rank sum test was used to test within species for statistically significant differences in nest heights between IFL and logged forest. This test was chosen since nest height was not normally distributed. We customized the wilcox.test function from R (version 3.4.3, R Core Team, 2017) so that the z-score from the test would be available as an output.

RESULTS

Quantification of IFL

In 2000, 756 km^2 of the Kabo logging concession (2,960 km^2) consisted of IFL. Review of the IFL map from Potapov et al. (2008) revealed 69.7 km^2 of terre firma forest in the Kabo concession was erroneously classified as IFL. This area was selectively logged in the 1970's and so was removed from the IFL estimate. Industrial logging activities in the 1970s focused on timber extraction on the western section of the concession. Over the last two decades 415.38 km^2 of IFL in the concession was spared from timber extraction for conservation purposes. In 2012, a 310 km^2 area known as the Goualougo Triangle was officially annexed to the Nouabalé-Ndoki National Park by presidential decree. In 2005, the 102 km^2 consisting of the Djeke Triangle was designated as a "conservation de serie" or land-set aside to meet environmental standards for certification of the concession.

Over the last two decades the Goualougo Triangle experienced two temporally and spatially distinct periods of logging outside its boundaries. The first was in non-IFL from 2005 through 2009 when a second cycle of industrial logging along the western border of the Goualougo Triangle occurred. Starting in 2014, timber extraction began in neighboring IFL southeast of the Goualougo Triangle and progressed north along the eastern border of the study area through 2018.

From 2000 to 2018, a 68% reduction in the amount of IFL occurred in the Kabo FMU. A notable increase in the yearly percent of IFL loss started in 2013 and continued through 2018 as a result of road expansion and timber removal in the eastern section of the Kabo concession. Since 1985, nearly 1,400 km of timber extraction routes (primary, secondary roads) have been opened in the Kabo concession.

In 2017, the first illegal incursions (three instances of hunting raids) were detected inside the Goualougo Triangle after nearly two decades of surveillance. In 2018, five illegal incursions were recorded. These events coincided with timber removal in the neighboring forest which was previously IFL but being exploited for timber (**Figure 1**). Entry points of poachers into the IFL of the Goualougo Triangle were within 10 km of logging roads.

Botanical Surveys

A total of 28 botanical plots were surveyed within the mixed-species IFL of the Goualougo Triangle. In addition, we surveyed 18 botanical plots within the logged forests of Kabo West. We counted and identified 562 trees and 16,140 herb stems within

TABLE 1 | Comparison of average basal area and density of timber trees in intact vs. logged forests.

Species	Avg basal area (m^2)		Small tree density 10–30cm (stems/km^2)		Medium tree density 80–30cm DBH (stems/km^2)		Large tree density >80cm DBH (stems/km^2)	
	Intact	**Logged**	**Intact**	**Logged**	**Intact**	**Logged**	**Intact**	**Logged**
Entandrophragma angolense	0.074	0.000	0.000	0.000	0.286	0.000	0.286	0.000
Entandrophragma candollei	0.065	0.000	0.000	0.000	0.000	0.000	0.286	0.000
Entandrophragma cylindricum	0.251	0.248	4.286	0.000	0.857	0.444	0.857	0.667
Entandrophragma utile	0.023	0.000	0.000	0.000	0.000	0.000	0.143	0.000
Milicia excelsa	0.000	0.036	0.000	0.000	0.000	0.000	0.000	0.222
Nauclea diderrichii	0.007	0.000	0.000	0.000	0.286	0.000	0.000	0.000
Pterocarpus soyauxii	0.100	0.124	1.429	4.444	1.143	1.333	0.286	0.444
Pterygota bequaertii	0.012	0.000	0.000	0.000	0.286	0.000	0.000	0.000
Triplochiton scleroxylon	0.110	0.102	0.000	0.000	0.000	0.000	0.286	0.444
Total	0.642	0.510	5.715	4.444	2.858	1.777	2.144	1.777

Medium and Large tree average diameter at breast height (DBH) measurements provided.

TABLE 2 | Comparison of herb densities between intact and logged forests.

Family, Species	Intact forest				Logged forest			
	Mean ± 95%CI	**SD**	**Range**	**% Plots**	**Mean ± 95%CI**	**SD**	**Range**	**% Plots**
Commelinaceae								
Palisota ambigua	0.14 ± 0.04	0.12	0.0–0.5	100	0.36 ± 0.14	0.30	0.0–1.2	100
Palisota brachythyrsa	0.42 ± 0.10	0.28	0.1–1.1	100	0.40 ± 0.16	0.35	0.0–1.5	100
Palisota spp.	0.02 ± 0.03	0.07	0.0–0.4	35.7	0.01 ± 0.01	0.02	0.0–0.1	27.8
Marantaceae								
Haumania danckelmaniana	0.45 ± 0.05	0.14	0.2–0.7	100	0.49 ± 0.13	0.29	0.1–1.0	100
Hypselodelphys scandens	0.00 ± 0.00	0.00	0.0–0.0	0	0.03 ± 0.05	0.11	0.0–0.5	11.1
Marantochloa spp.	0.44 ± 0.16	0.42	0.0–1.9	96.4	0.63 ± 0.37	0.81	0.0–3.0	100
Megaphrynium macrostachyum	0.16 ± 0.11	0.30	0.0–1.2	39.3	0.10 ± 0.18	0.38	0.0–1.6	22.2
Sarcophrynium schweinfurthianum	0.63 ± 0.18	0.48	0.0–2.5	100	0.72 ± 0.30	0.65	0.1–2.4	100
Trachyphrynium braunianum	0.00 ± 0.00	0.00	0.0–0.0	3.6	0.02 ± 0.05	0.10	0.0–0.4	5.6
Zingiberaceae								
Aframomum spp.	0.05 ± 0.03	0.08	0–0.30	53.6	0.41 ± 0.31	0.68	0–2.70	83.3

IFL. A total of 313 trees and 14,314 herb stems were surveyed within the logged forest.

Average density of trees and figs was 389.86 stems/ha in IFL, with 38 families and 143 species represented. We documented an average density of 354.89 stems/ha in the logged forests, representing 34 families and 110 species. The average basal area for trees in IFL (4.35 m^2) was higher than in logged forest (3.17 m^2 per plot). As shown in **Table 1**, this was also the case for the subset of timber tree species. Total densities of trees across large, medium, and small size classes were lower in logged forest vs. IFL.

The average herb density in the intact zone, 2.31 stems/m^2, was lower than the average herb density in the logged zone which was 3.18 stems/m^2. Mean herbaceous stem densities ranged considerably between families and forest status (**Table 2**). The combined fixed effects from the linear mixed model were found to be significant (likelihood ratio test: $X^2 = 156.470$, $df = 5$, $p < 0.001$). Specifically, the interaction between forest status (intact vs. logged) and herb family exhibited a trend (likelihood ratio test: $X^2 = 4.826$, $df = 2$, $p = 0.090$). The nature of the interaction can be seen in **Figure 2**. The density by family is always larger in the logged zone, with the difference between intact and logged areas appearing largest for the Zingiberaceae family and more moderate for the Commelinaceae and Marantaceae families. These THV density estimates are placed in context of botanical surveys conducted across African ape field sites (**Table 3**).

Ape Density Estimation

As reported in **Table 4**, line transect surveys of great ape nests were conducted in both intact and logged forests of northern Congo. A total of 272 ape nests were surveyed along 26 transects (34 km of total effort) in the Djeke Triangle which comprises the last block of IFL in the Kabo FMU.

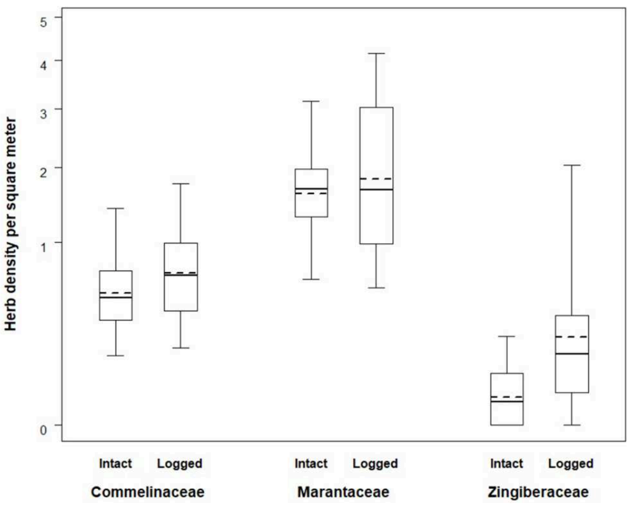

FIGURE 2 | Herb densities across intact and logged forest. Boxes span the 25th to 75th percentile and whiskers extend to the 2.5th and 97.5th percentiles. Medians are shown as bold lines while expected values produced by the model are shown as dashed lines.

TABLE 3 | Comparison of THV densities between sites.

Study site	Ape(s) present	THV density (stems/m^2)	References
Seringbara, Guinea	*P.t.v.*	4.2	Koops et al., 2013
Odzala, RoC	*P.t.t., G.g.*	20.0	Brugière et al., 2000
Lopé, Gabon	*P.t.t., G.g.*	7.7	Rogers and Williamson, 1987
Kabo FMU, RoC	*P.t.t., G.g.*	3.2	This study
Dja, Cameroon	*P.t.t., G.g.*	3.0	Willie et al., 2013
Goualougo, RoC	*P.t.t., G.g.*	2.3	This study
Ndoki, RoC	*P.t.t., G.g.*	2.3	Malenky et al., 1994
Bai Hokou, CAR	*P.t.t., G.g.*	0.8	Carroll, 1988
Petit Loango, Gabon	*P.t.t., G.g.*	0.5	Morgan, 2000
Ngotto, CAR	*P.t.t., G.g.*	0.3	Brugiere and Sakom, 2001
Kahuzi, DRC	*P.t.s., G.b.g.*	1.0	Basabose, 2002
Kalinzu, Uganda	*P.t.s.*	0.1-2.1	Furuichi et al., 2001
Kibale, Uganda	*P.t.s.*	0.9	Malenky and Wrangham, 1994
Virungas, DRC	*G.b.b.*	8.8	Watts, 1984
Lomako, DRC	*P. paniscus*	2.0	Malenky and Wrangham, 1994

We surveyed another 332 ape nests along 10 transects (54 km of effort) in the Goualougo Triangle which comprises the southernmost section of NNNP. Surveys within logged forest were conducted within the once-logged forests located to the east of the Goualougo Triangle (henceforth referred to as Kabo East) and within forests that have been harvested twice that are immediately west of the Goualougo Triangle (henceforth referred to as Kabo West). A total of 471 ape nests were surveyed along 29 transects (107 km of effort) in Kabo East, and a total of 647 nests along 14 transects (88 km of effort) in Kabo West.

Transect surveys within IFL yielded overall density estimates of 1.43 apes/km^2 within the Goualougo Triangle and 1.47 apes/km^2 within the Djeke Triangle (see **Table 4**). In the logged forests, we documented 1.05 apes/km^2 in once-logged forests located to the east of the Goualougo Triangle and 2.10 apes/km^2 in the forests west of the Goualougo Triangle which have been subjected to a second cycle of timber exploitation.

Species Specific Nest Heights in IFL vs. Logged Habitat

A total of 3,902 nests representing 1,447 nest sites were identified as either built by chimpanzee or gorilla. In IFL we recorded the heights (m above ground) of 359 chimpanzee and 267 gorilla nests included within 141 and 94 nest sites, respectively. Whereas, in twice logged forests we documented 1,794 chimpanzee and 1,482 gorilla nests within 682 and 530 nest sites, respectively. This allowed nest height comparisons between these two different environmental conditions. Chimpanzee nests were built significantly closer to the ground in logged forests than IFL ($Z = 13.89$, $p < 0.001$; 95% CI, 5.0–6.0) (see **Figure 3**). While gorilla nest heights were also lower in logged forests than IFL, the difference was non-significant ($Z = 0.36$, $p = 0.72$) (see **Figure 4**).

DISCUSSION

Once considered a stronghold of pristine habitat, IFL loss in Western Equatorial Africa is occurring at an alarming rate. Comparisons between intact vs. disturbed habitats in the Kabo FMU confirmed that overall tree stem density and total basal area were lower in non-IFL than IFL forests. While ape food resources still persist in these forests, as selectively logged habitats contain fruit-bearing tree species and canopy gaps promote growth of high abundances of terrestrial herbs, the long-term ecological consequences of timber extraction on ape populations are not yet known. For example in this study, we documented species-specific changes in resource use in nesting between IFL and twice logged habitat. Chimpanzees nested significantly closer to the ground in logged forests suggesting that changes in forest structure associated with logging may impact resource use. In addition, nearly two decades of antipoaching surveillance in the region indicate concerning trends between proximity of new roads in IFL and increasing vulnerability of wildlife to illegal hunting in neighboring IFL including protected areas. Together, such biodiversity assessments and strategic aspects of long-term protection should be taken into account when identifying conservation set asides. For example, the majority of the remaining IFL in the Kabo concession is

TABLE 4 | Ape density estimates in IFL and non-IFL with percent coefficient of variation (%CV) and 95% confidence intervals (95% CI) for each survey stratum and for the landscape.

Status	Protection	Area	Effort (km)	Ape Density	% CV	Upper 95%CI	Lower 95%CI
Intact	National Park	Goualougo	54	1.43	15.29	1.03	1.98
	Conservation de serie	Djeke	26	1.47	16.46	1.06	2.04
Logged	Kabo FMU	Kabo East	107	1.05	17.58	0.74	1.49
	Kabo FMU	Kabo West	88	2.10	15.67	1.52	2.91

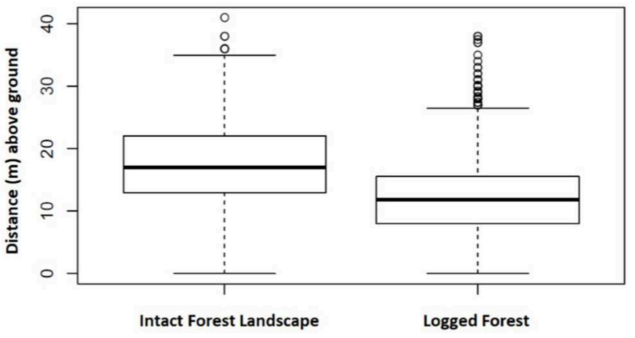

FIGURE 3 | Chimpanzee nest height in IFL and logged differed significantly. Boxes span the 25th to 75th percentile and whiskers extend to the 2.5th and 97.5th percentiles. Medians are shown as bold lines. In IFL chimpanzee nests were constructed higher in the forest canopy compared to those documented in twice logged habitat.

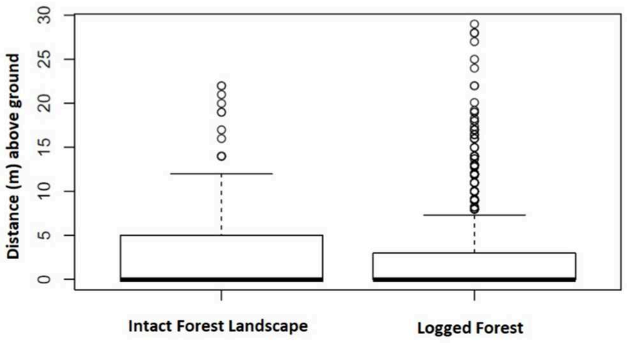

FIGURE 4 | Gorilla nest height locations in IFL and logged forest were not significantly different. Boxes span the 25th to 75th percentile and whiskers extend to the 2.5th and 97.5th percentiles. Medians are shown as bold lines.

within the Djeke Triangle which is contiguous with the Ndoki National Park in Central African Republic and the Nouabalé-Ndoki National Park in Republic of Congo. Thus, this area is a strategic location for curbing future poaching incursions into both protected areas. It also comprises the home ranges of gorillas habituated to human presence for scientific study and tourism development. This information could be used to advocate for the formal protection of the Djeke Triangle, not only as remaining IFL but for its conservation value and role in serving as a buffer to neighboring protected areas. However, such initiatives will only be successful through collaboration of local stakeholders, government officials, conservation agencies, and industrial partners.

It has been previously asserted that chimpanzees prefer primary forest (Tutin and Fernandez, 1984; Furuichi et al., 1997), whereas primary lowland forests were thought to be insufficient in terrestrial herbaceous vegetation to support high gorilla numbers (Schaller, 1963; Groves, 1971). The intact Ndoki forest can be considered a climax forest with a high vertical canopy structure created by light-demanding pioneer species such as mahogany (*Entandrophragma* spp.) which were established centuries ago (Fay, 1997). Such large trees play critical ecological roles in forest dynamics (Lindenmayer and Laurance, 2017) and also influence neighboring floral communities. Natural canopy disturbance is consequential in terms of THV recruitment and can resemble structural changes similar to selectively logged forest. The impact is reflected in our botanical surveys, showing relatively high densities of THV in intact as well as logged forests. In sum, the diversity of tree species and variation in canopy coverage of IFL in northern Congo provide adequate resources to support relatively large numbers of both chimpanzees and gorillas.

Overall dietary flexibility and degree of folivory have been cited in primate species' abilities to cope with environmental disturbances (Johns, 1997; Meijaard and Sheil, 2008) and could explain high ape densities documented in non-IFL. However, it is also possible that these forests historically differed in their inherent suitability to support great apes which was not taken into account in this investigation. We found lower stem densities and total basal areas of larger trees in logged forest which has implications on carbon storage potentials and elevating environmental risks. Forest stand change was also accompanied by a successional shift to more numerous trees in the small and medium size classes. These findings are in accord with other studies on the effects of selective logging on forest composition and growth dynamics in semi-deciduous forests in Western Equatorial Africa (Gourlet-Fleury et al., 2013a,b) and support findings that logged tropical forests transition to shorter and more broken canopy stands (Felton et al., 2003). Evidence for changes in forest structure influencing ape resource use was provided by species-specific nest height selection. We found that chimpanzees preferentially nested in the middle and upper story tree stratums in IFL. Whereas, chimpanzees nested at significantly lower heights in logged forests than in IFL. Nesting options located higher in the canopy may have diminished with the loss of the large timber species. These findings are similar to reports that orangutans shift their nest locations lower in logged environments (Felton et al., 2003). Gorilla nests heights did not significantly differ between IFL and logged habitat. There was however notable variability in gorilla nest height location in logged vs. intact forests which may indicate this species is opportunistically responding to increased nesting options. Increased diversity in nest construction patterns of gorillas may be a result of the elevated availability of THV documented and associated growth in pioneer species in the exploitation zone.

Industrial logging is projected to continue at 30-year rotation cycles in most of Western Equatorial Africa and so the fate of many tree species is unknown. Repeated removal of timber even at low intensity levels can degrade the quality of habitat over time (Lindenmayer and Franklin, 2002), and could have negative consequences for apes as shown in the degraded forests of Asia (Rao and van Schaik, 1997; Felton et al., 2003; Wich et al., 2004; Husson et al., 2009). Structural changes in the logged forests in this study indicate some implications for floral climbers and epiphytes. Compared to the diverse representation of *Ficus* in the IFL, few figs were found in non-IFL which raises important questions about host specificity of strangler figs in relation to logging species and potential consequences to the frugivore community reliant on these resources. *Ficus* spp. are a critical component of the overall chimpanzee diet in IFL (Morgan and Sanz, 2006). Monitoring the direct impacts of logging on large fruit-bearing tree species preferred by chimpanzees and gorillas in future exploitation cycles will be important as such resources can influence reproduction and fitness in wild apes (Emery Thompson et al., 2007). Future studies of nesting resource use and distribution could also be informative for conservation planning, as the difference observed in chimpanzee nesting in IFL vs. logged habitat could be the result of indirect rather than direct disturbances associated with logging. Low intensity logging was practiced in the concession with off-take ranging between 0.5 and 3.0 trees/ha. Importantly, the top three marketable tree species exploited in the study area were rarely used for nest construction by chimpanzees or gorillas. Such insights on shifting resource use by apes should be considered in identification of High Conservation Value Forests (HCVF) which is an important environmental criterion of FSC certification.

Compared to IFL, apes in non-IFL are also at increased risk of synergistic interactions with other threats such as edge effects and emerging diseases. For example, areas of high disturbance and elevated undergrowth as documented in this study are likely to be more fire prone. Logging routes and their margins transform the local forest with elevated levels of disturbance (Brandt et al., 2016) which is followed by rapid growth of high densities of Marantaceae and Zingiberaceae families in the abandoned tracks and edges (Malcolm and Ray, 2000; Kleinschroth et al., 2015). Increased rates of tree mortality, leaf litter accumulation, and damage (Ferreira and Laurance, 1997; Laurance et al., 1998) likely combine with changes in microclimate conditions and combustibility of flora, elevating risks of severe fire (Leighton and Wirawan, 1986; Campbell, 1992; Dennis and Colfer, 2006). The recent fire that raged across IFL and non-IFL bordering the main national road accessing the north of Republic of Congo provides evidence that wildfire is now an agent of disturbance in this region (Potapov et al., 2017). Another threat that is exacerbated by reduction of IFL is considerable spatial overlap between apes and humans occurring in proximity to roads that may elevate risk for cross-species transmission of pathogens through handling of shared resources or even direct contact. Finally, dramatic reductions of great ape numbers in some regions of northern Congo have been attributed to excessive hunting levels (Bermejo et al., 2006).

Poaching remains the greatest threat to wildlife in this region, and the spatial-temporal relationship between expanding road networks and increased illegal hunting pressure within NNNP is both pervasive and instructive. Since the Park's creation, effective management of poaching pressure in the surrounding logging concessions has been a priority to protect the integrity of the core area (Elkan et al., 2006). Law enforcement patrols can lower threat levels to protected areas (Stokes et al., 2010; Tranquilli et al., 2014), but increased support for these activities is critical as expanding road networks are providing unprecedented access to previously remote areas. We documented the first instances of poacher incursions in Goualougo Triangle region of NNNP that coincided spatially and temporally with the arrival of roads and active logging in adjacent forest. The spatiotemporal patterning of high-value natural resource extraction in Africa has expanded across a gradient from high to low sourced areas (Ahrends et al., 2010). Currently, the NNNP is in the midst of experiencing the first wave of hunting pressure targeted at ivory. This supports assumptions that poachers preferentially target IFL. It is likely part of a larger spatial pattern that has typified hunting in Western Equatorial Africa since the onset of selective logging in the early 1970s, but is only now reaching the previously inaccessible forests which form the core protected areas of the Sangha Trinational NWHS. At the time of this study, the poaching profitability perimeter for ivory hunters remained spatially close to logging roads. Entry points of illegal raids into the southeastern sector of the NNNP were typically within 10 km of the nearest road which supports broader assumptions of distances traveled by hunters (Peres and Terborgh, 1995). We strongly urge research assessing whether the profitability of hunting diminishes with closure of logging roads. The arrival and sudden intensification of poaching in the Goualougo Triangle is particularly concerning given the incessant poaching pressure over the last decade in the IFL of the Dja Faunal Reserve NWHS which is another important landscape for great ape conservation (IUCN, 2014). Long-term studies in Malaysia also suggest survival prospects for species such as orangutans in production forests are mainly determined by hunting (Ancrenaz et al., 2004). If properly coordinated with regional antipoaching efforts, we assert that research outposts and field teams can serve as sentinels of such poaching pressure in remote areas and act as force multipliers in maintaining surveillance. In addition to improving coordination of ecological and behavioral data collection across research sites, technologically-enhanced monitoring with SMART has the potential to expedite reporting of regional antipoaching efforts. More importantly, this increased monitoring and collaboration can lead to the arrest of poachers, which proves that the relationship between law enforcement and research efforts can be mutually beneficial in safeguarding wildlife.

Beyond implementation of best practice guidelines in and outside production forests, the most effective way to protect the outstanding flora and fauna attributes of IFL is through policies that formally set aside such forests (Watson et al., 2016). Successful mandates to attain increased protected status require collaborative and holistic approaches (Peres, 2005; Haurez et al., 2017; Chazdon, 2018) such as those that led to the annexation of the Goualougo Triangle to the NNNP (Morgan et al., 2012). In these cases, increases in formal protected status were the result of coordination among local stakeholders, government officials, conservation agencies, and industry partners. Over the last several years the debate regarding the fate of IFL, particularly in certified logging concessions, has become a central focus of global conservation. In 2016, the IUCN World Conservation Congress adopted a motion (https://portals.iucn.org/congress/motion/048) encouraging the monitoring and sparing of IFL from degradation and loss. FSC has integrated the protection of IFL into their International Standards, urging governments and concessionaires to decrease the rate of IFL loss. The Djeke Triangle comprises the majority of remaining IFL in the Kabo concession, and is also the location of the longest-running gorilla research and tourism site in Western Equatorial Africa, which employs a large number of local people. Given its location along the international borders of two National Parks, increased protected status through annexation to the NNNP would further strengthen efforts to maintain the ecological integrity of the Sangha Trinational.

CONCLUSION

Our ground-based efforts to identify and verify IFL resulted in a more accurate depiction of both the amount and location of remaining intact forest in the Kabo FMU. We found that 69.7 km^2 of the terre firma forest in the concession had previously been erroneously classified as lacking anthropogenic disturbance, when it had actually been logged. Botanical surveys conducted in IFL revealed higher densities of trees across all size classes, relative to non-IFL. Non-IFL forests were composed of reduced numbers of trees, but elevated herb densities. Results from our longterm studies of chimpanzees and gorillas show that ape resource use may be affected by logging, as nesting patterns differed between intact and logged forests. The height of chimpanzee nests was significantly lower in non-IFL compared to IFL, indicating that nesting niche options may be reduced in modified habitats. In contrast, there is indication that the gorilla niche may have expanded in logged habitat as a result of greater nesting material options associated with secondary growth in logged habitats. Along with the ecological changes in logged forest, we also documented that road expansion was associated with increased poaching pressure in nearby IFL. Real time indicators of forest change and associated data on resource use by endangered species are critical to promoting long-term preservation of biodiversity across different landscapes. However, such opportunities to study and protect IFL areas are quickly vanishing. As of 2013, it was estimated that only 8% of forests within Central Africa remained intact (Potapov et al., 2017).

AUTHOR CONTRIBUTIONS

DM, SS, and CMS: designed the study and oversaw data collection. WW, WM, and FI: compiled data for this study. SS, WW, CRS, CT, and CMS: analyzed the data. CMS and DM: wrote the manuscript with input from all co-authors. DM, CA, CMS, SN, WM, DK, and FI: collected data in the field. DM, CA, and CMS provided logistical support and infrastructure for data collection.

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Protecting Forests From Conversion: The Essential Role of Supply-Side National Laws

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The growing demand in global markets for commodities like palm oil, soy and cocoa has a disastrous impact on forests, carbon emissions, as well as the lands and livelihoods of forest-dependent people. Governments, private sector, civil society and forest-dependent people have, separately or jointly, committed to voluntary actions to protect forests (e.g., pledges, zero deforestation commitments, certification standards). However, recent research shows that these voluntary commitments and standards have neither halted nor slowed deforestation. This demonstrates that they cannot stand alone. Alongside voluntary action, national legal frameworks that regulate forest conversion are crucial. This research explores the importance of national laws for reducing deforestation from forest-risk commodities and the legal options available to national law-makers to address competing demands for forested lands.

Keywords: forest conversion, law, supply chain, deforestation, land, voluntary commitments, forest risk commodity

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INTRODUCTION

Global demand for commodities like soy, cocoa, palm oil, beef, and minerals drives global tropical deforestation (FAO, 2016). Forests are being cleared and permanently converted to other land uses, predominantly agriculture but also mining and urbanization (Kissinger et al., 2012)—a process referred to in this paper as forest conversion. Forest conversion is the largest cause of global deforestation (Curtis et al., 2018) and intact forest landscapes[1] are not spared from land use change (Potapov et al., 2017).

Demand for forest-risk commodities[2] comes from both domestic and international markets (FAO, 2016). Therefore, policy measures to reduce forest conversion should come from both commodity-producing countries (supply-side) and commodity-consuming countries (demand-side) (Walker et al., 2013). On the demand side, the European Union (EU) is one of the major global importers of meat, soy and palm oil, and it is exploring ways to tackle its impact on deforestation (COWI A/S, 2018). However, the EU has yet to establish a binding regulation targeting forest-risk commodities.

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[1] An intact forest landscape (IFL) is a seamless mosaic of forest and naturally treeless ecosystems with no remotely detected signs of human activity and a minimum area of 500 km^2 (Potapov et al., 2017).

[2] Forest-risk commodities are "globally traded goods and raw materials that originate from tropical forest ecosystems, either directly from forest areas, or from areas previously under forest cover whose extraction or production contributes significantly to global tropical deforestation and degradation" (Rautner et al., 2013).

In the current absence of international binding regulatory measures that directly address forest conversion, many actors on both the demand and supply side have adopted voluntary measures (COWI A/S, 2018). They include international policy declarations—such as Goal 15 of the Sustainable Development Goals and the 2014 New York Declaration on Forests; private-sector zero-deforestation commitments—such as the Consumer Goods Forum resolution to achieve zero net deforestation; public-private initiatives—such as the Tropical Forest Alliance 2020; and private certification standards—such as the Roundtable on Sustainable Palm Oil. Voluntary measures rely mostly on sustainability criteria, encompassing economic, social, and environmental requirements.

Voluntary measures have not yet proven effective in reducing deforestation [Donofrio et al., 2017; Food and Agriculture Organization of the United Nations (FAO), 2018; Haupt et al., 2018; Jopke and Schoneveld, 2018]. On their own, they have been found insufficient due to *inter alia* (i) the selective adoption of commitments and (ii) leakage. First, not all companies have adopted voluntary measures; some question the business need and others the costs of complying with sustainability criteria (Lambin et al., 2018). Small companies and farmers, in particular, face unmanageably high costs and administrative burdens. They are, therefore, not signing up to voluntary commitments, which can exclude them from profitable international markets (Jopke and Schoneveld, 2018; Lambin et al., 2018). Second, leakage is the displacement of deforestation from one location to another or from certain actors to others, due to measures that restrict deforestation within a limited geographic or production scope or among a limited group of actors (Delacote et al., 2016). Leakage is likely to occur when demand for forest-risk commodities is not reduced (Lambin et al., 2018).

Despite the limits of voluntary measures, they have a role to play. Voluntary measures fit within a policy mix that also includes demand-side regulations and national supply-side laws (see **Table 1**). Nonetheless, as demand-side regulations have been slow to materialize and voluntary measures are not yet achieving their aims, this article analyses opportunities presented by national supply-side laws to protect forests from conversion. National laws can particularly address the abovementioned failings of voluntary measures. First, national laws set a (minimum[3]) standard that all actors within a jurisdiction must adhere to, thereby preventing selective adoption (Brack and Wolosin, 2018). Focusing on national laws also grants producer countries the ability to set standards based on national context (COWI A/S, 2018). Setting this minimum standard also avoids leakage between actors. If designed to encompass all conversion activities, national laws can also minimize leakage between commodities. Nevertheless, stringent regulations in one country are a significant factor in leakage to others with less stringent standards (Gan and McCarl, 2007). This is because, depending on the rules established, national laws can either set up a framework to reduce or halt forest conversion, or encourage it (FAO, 2016).

ClientEarth's research analyzed national legal frameworks governing forest conversion in nine tropical countries, which all have a significant rate of deforestation: Brazil, Cameroon, Cote d'Ivoire, Gabon, Ghana, Liberia, Peru, Republic of Congo, and Vietnam. The research identified areas of legal weakness, including ambiguities, overlaps, and gaps that create risks for national forests. It found that supply-side legal frameworks involve laws of several different sectors, such as land, forest, agriculture, environment, mining and investment. This opens up the potential for laws to be unclear, incomplete or contradictory, which means forest conversion is ineffectively regulated (ClientEarth, 2018).

While recognizing differences between countries, and complexities of creating a unique set of rules, ClientEarth identified several key legal areas that require specific attention in all countries in order to achieve a comprehensive and clear national framework that regulates forest conversion and protects forests (ClientEarth, 2018). Section 2 describes ClientEarth's research findings on three of these areas: laws governing land allocation, forest clearance and protection of the environment. However, laws on paper are only the beginning. Therefore, we also identify complementary policy processes that enable supply-side laws to function. Section 3 draws out actionable recommendations for supply-side law reform to strengthen national laws for forest conversion.

POLICY OPTIONS AND IMPLICATIONS: NATIONAL SUPPLY-SIDE LAWS FOR REDUCING DEFORESTATION

Achieving a cohesive supply-side legal framework governing forest conversion across all sectors is challenging (Hewitt, 2013). Through a process of legal reform, national law-makers and other actors can undertake an exercise of balancing economic growth, food security, protection of forests and climate change mitigation. Acknowledging the importance of natural resources for development in many forested countries but considering the need to protect intact forests, this review concentrates on legal options for forest protection and their implications.

Allocation of Land—The Need for Clarity

Before implementing a project that includes forest conversion, all nine countries analyzed require a developer to have a right to use the land. When the government grants a land title for a project, the land may include forests. ClientEarth's legal analysis found that before allocating land, it is essential that the relevant authority has a clear understanding of whether the land under consideration contains forest, and if so, which areas of forested land cannot be allocated to land-use change and which can be converted, and under what conditions.

One legal instrument which can assist countries to map the forested land in their territory is land-use planning (de Wasseige et al., 2010). A land-use plan is a national document that provides information on the most appropriate use(s) of land [UN Economic Commission for Europe (UNECE), 2008]. The zoning of forested land is particularly important because it has to balance economic, sustainable development, food security, as well as environmental interests and equity considerations. It should be acknowledged that achieving this balance in practice

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[3] See e.g., the discussion in Brack and Wolosin, 2018 of how a legality approach can "act as a stepping-stone" to sustainability.

TABLE 1 | Complementarity of policy options for deforestation.

Policy measures and their roles	Binding nature	Select challenges	How can voluntary measures address the selected challenges?	How can national supply-side laws address the selected challenges?	How can demand-side laws address the selected challenges?
Voluntary measures Role: Frontrunner actors make a commitment to zero deforestation from their supply chains.	Voluntary	Selective adoption of commitments by countries and companies. Leakage, where deforestation from one region/area, commodity or actor is displaced to another.		Set a standard for forest conversion to which all actors within a jurisdiction must adhere. A single standard aligns requirements across different sectors, minimizing leakage.	Set a standard to which all companies wishing to sell products to that country or region must adhere. If covering all/most deforestation-risk commodities, aligns requirements, minimizing leakage between sectors.
National supply-side laws Role: set a nationally-determined standard to which all actors involved in forest conversion must adhere.	Mandatory	If national laws are not ambitious, clear nor comprehensive, there may be no reduction in forest conversion. Weak enforcement limits impact of laws. Leakage, where companies move production to countries with weaker laws and/or enforcement.	Voluntary measures that are more stringent than national laws can build the ambition of national actors to strengthen laws.		Incentive to strengthen national laws if countries wish to remain competitive in markets applying demand-side standards. If covering all/most deforestation-risk commodities, aligns requirements, minimizing leakage between sectors.
Demand-side laws Role: Reduce demand for products associated with deforestation, ensuring trade is used as a means of reducing deforestation in supply chains.	Mandatory	Slow to materialize (French law on the corporate duty of vigilance one of the few) Leakage, where companies sell commodities at risk of deforestation to regions and countries with weaker standards.	Voluntary measures that are more stringent than demand-side laws can build the ambition of demand-side actors.	Frontrunner supply-side countries reduce deforestation from their supply chains. Strong legal frameworks supply-side countries may increase the ambition of demand-side standards.	

has proven a challenge for many tropical forested countries (Nana Inkoom et al., 2017).

In the absence of, or in addition to land-use planning, sectoral laws on forestry, land, agriculture and mining may address land allocation; however, these laws are often contradictory and open to conflicting interpretations (Sartoretto et al., 2017). For instance, forest laws may clearly specify which forested lands should remain permanently forested. In Liberia, the Protected Forest Areas Network Law prohibits prospecting, mining and farming in national parks, nature reserves, communal forests and cultural sites (Republic of Liberia, 2003). However, in other countries, such as Gabon, the forest legislation does not provide for any permit to convert forests, which makes it more difficult to know whether particular forests can or cannot be converted (Sartoretto et al., 2017).

Even where forest laws provide protection from conversion to certain categories of forests, laws from other land-use sectors may contradict them. In Ghana, laws and policies across sectors give contradictory information on whether mining is permitted in forest reserves. The National Land Policy bans mining outright in forest reserves (Ghana Ministry of Lands and Forestry, 1999). The Forest and Wildlife Policy implies that mining is permitted in forest reserves, within limits (Ghana Ministry of Lands and Natural Resources, 2012). The Minerals and Mining Act limits the land available for mineral rights, however, these limits do not include a restriction on mining in forest reserves (Republic of Ghana, 2006). This legal confusion has meant some mining exploration has already begun. We, therefore, suggest it is essential that forest land banned from being allocated to conversion projects under forest law is also recognized in other sectoral laws.

Coherent laws that clearly specify which forests may not be converted offer an opportunity to protect intact forests or forests with biologically important ecosystems. Research has demonstrated that the loss of intact forests were lower in protected areas where enforcement was strong, than outside protected areas (Potapov et al., 2017). Where strong enforcement is lacking, land may be granted to conversion projects even in designated protected areas and national parks, as has been seen in Gabon (Gabonese Republic, 2012).

Clearing Forested Land—The Need for a Permit

A clearance permit provides the right to deforest in order to use forested land for another purpose (Hewitt, 2013). ClientEarth's research found that a clearance permit can represent a crucial step in the forest-conversion process if it requires due consideration of whether it is appropriate to clear an area of forest for another use.

ClientEarth's legal analysis found that it is important for the law to establish clear rules about where, when, how and by whom clearance can take place – but that this has been challenging in practice. Without clarity, state authorities can operate under different mandates and according to different rules. In Liberia, for example, the Minerals and Mining Law gives authority to the Minister for Mines to authorize clearing trees and shrubs "necessary for the mineral rights holder's activities outside the boundaries of his license or licenses" (Republic of Liberia, 2000). This is incoherent with the forest law, which designates the forestry administration as the representative of Government in any matter concerning the use of forest (Republic of Liberia, 2006).

ClientEarth's research also found that clearance permits may be inappropriately used for the sole aim of selling the timber, particularly if they are easier or quicker to obtain than a selective logging permit. This is undesirable as clear-cutting a forest for timber is more environmentally destructive than selective logging (Edwards et al., 2014). For example, in the Republic of Congo, a conversion project can access rights to clear timber more easily than a logging concessionaire (Sartoretto et al., 2017), and may freely dispose of the timber stemming from forest clearance (Republic of Congo, 2000). According to the country's Independent Monitor[4], five companies obtained a forest clearance permit and have been found to use this permit simply to commercialize high-value timber, seemingly without the intention to undertake the planned agricultural activities (Independent Monitor of the FLEGT-VPA in the Independent Monitor of the FLEGT-VPA in the Republic of Congo, 2017). In order to avoid this, clearance permits can include a requirement to develop the land within a certain timeframe. Companies in violation of this requirement may face a penalty.

Environmental Protection—The Need for Consideration

Environmental protections can be established in law to reduce forest loss, and anticipate and mitigate environmental impacts of agricultural, mining or infrastructure projects. While many environmental legal tools may impact upon forests, two are of interest here.

The first is the environmental (and social) impact assessment (ESIA) that grants an opportunity 1) to assess a conversion project in its proposed form before decisions are made to commit to that project, and 2) to investigate mitigating measures to reduce environmental issues identified in that assessment (Morgan, 2012; FAO, 2016). ESIA laws should also establish clear grounds on which to refuse an environmental permit. However, to be effective, the practical details of how the ESIA process should proceed and what it should include must be explicit in the law itself. In Gabon, by contrast, details of the ESIA process are established in the Manual of Procedures for ESIAs and in the Guidance on Implementation of the Manual of Procedures, neither of which are legally binding (Biotope, 2015; Gabonese Republic, 2015). This can make it harder to enforce implementation.

While not traditionally considered environmental law, our research found that access to environmental information can support protection of forests. Legal rights to access environmental information, such as final decisions and documentation on land allocation, clearance permits and ESIA approvals can empower citizens and NGOs to monitor and seek government enforcement of companies' obligations (Gouldson, 2004). For example, in Liberia, the law establishing the Liberia Extractive Industries Transparency Initiative requires a national depository of mining, oil, logging, agriculture and forestry concessions, as well as the right to audit the process by which each concession, contract, license, and other right is granted (Republic of Liberia, 2009; Liberia Extractive Industries Transparency Initiative (LEITI), 2013).

Complementary Policy Options to National Supply-Side Laws

National laws in supply-side countries cannot work alone. This section considers two complementary policy options that enable laws to function: participatory law reform and enforcement.

Firstly, to achieve a comprehensive legal framework that mitigates environmental and social damage from forest conversion, countries may need to undertake a legal reform process. Research has shown that legal reform involving a participatory approach, including civil society, local communities, and indigenous peoples in decision-making processes can better achieve environmental aims (Newig and Fritsch, 2009). The EU's Voluntary Partnership Agreement negotiations with forested countries are one example of how this participatory approach has been applied to the forest sector, with encouraging results for improved forest governance and clearer laws (Overdevest and Zeitlin, 2018).

Secondly, strong enforcement is a necessary complement to strong laws, in order to regulate and reduce deforestation (FAO, 2016). When laws are implemented consistently and when authorities detect and penalize violations, the law on paper is more likely to translate into results on the ground (Downs, 2013). Even so, law enforcement can exacerbate socio-economic inequalities, as informal activities (often by the poorest people) become criminalized (Colchester et al., 2006).

In many of the tropical forested countries analyzed, there is a complex enforcement environment, with overlapping mandates across different government agencies, which weakens the governance system (Hoare, 2015). Moreover, many forestry and environmental agencies are under-resourced and therefore struggle to operate effectively (ClientEarth, 2017). ClientEarth's research found that it is necessary for national governments and judiciaries to have the appropriate financial and human capacity as a first step toward strong law enforcement.

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[4] The Independent Monitor is a component of the Forest Law Enforcement Governance and Trade (FLEGT) Voluntary Partnership Agreements with timber-producing countries. It is independent of a country's forest sector regulatory bodies and aims to provide credibility to the FLEGT licensing scheme by checking that all relevant aspects of a country's forest laws are operating as intended [European Commission (EC), 2007].

ACTIONABLE RECOMMENDATIONS

Tropical countries may need to undertake review or reform of national laws to ensure that the legal framework facilitates balancing of competing demands for land. As an initial step in the legal reform process, all relevant laws and institutional mandates across different sectors should be assessed for consistency and harmonized as necessary (Blaser, 2010; ClientEarth, 2018). The following recommendations offer guidance to legal reform:

- Land-use plans that identify which forested land is allowed or prohibited from clearance can assist land-use agencies to grant appropriate areas of land for projects at risk of conversion.
- Coherence of prohibitions on clearing certain areas of forest land across sectoral laws, particularly those that give a mandate for land allocation, can help to streamline forest protection.
- In order to ensure that clearance permits are not used as a loophole to clear the land for the sole aim of selling the timber, clearance permits can include a requirement to develop the land into the planned agricultural, mining or infrastructure project within a certain timeframe.
- Making the practical details of how environmental assessments proceed and what they should include explicit in the law itself can strengthen the effectiveness and enforceability of ESIAs.
- Strong enforcement of laws is important to translate the law on paper into forest protection on the ground, but requires clear enforcement mandates and appropriate financial and human capacity.

CONCLUSION

The risk to forests from the global demand for agricultural is firmly understood (Heino et al., 2015; Potapov et al., 2017) and is driven by a global demand for forest-risk commodities (Hosonuma et al., 2012; Curtis et al., 2018). To address this risk, policy solutions need to match the scale of the issue: they need to encompass the demand side, as well as the supply side. The nature of the policy measures—voluntary or binding—also has to match the need for an effective framework that is able to lead to behavioral change.

The current situation remains far from this goal. Many voluntary measures have emerged over the past decades, but have not achieved the aim of reduced deforestation, and demand-side regulations have been slow to materialize. National supply-side regulations offer an opportunity for forested countries to establish a framework to reduce deforestation taking into account each national context. However, ClientEarth's research has shown that supply-side regulations are still often unclear, contradictory and incomplete.

ClientEarth's research has identified the details of what a supply-side national framework should include, in order to regulate forest conversion. Clear, complete, and comprehensive legal frameworks involve coordination across a complex array of sectoral laws and institutional mandates to create a set of rules to be followed by those involved in forest conversion. If well-developed, these rules determine (i) what will be authorized, (ii) what is forbidden, and (iii) what conditions need to be followed for rights to access forested land and clear it for another use to be granted.

We acknowledge that laws on paper are not enough. Laws must be implemented and enforced (FAO, 2016). Moreover, laws must be accepted by the citizens of a country, and a participatory process of law reform can be crucial to reaching this acceptance (Newig and Fritsch, 2009).

AUTHOR CONTRIBUTIONS

CaH and ClH contributed to the design and implementation of the research, to the analysis of the results and to the writing of the manuscript.

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Fire in the Swamp Forest: Palaeoecological Insights Into Natural and Human-Induced Burning in Intact Tropical Peatlands

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Tropical peat swamp forests are invaluable for their role in storing atmospheric carbon, notably in their unique below-ground reservoirs. Differing from *terra firme* forests, the peat-forming function of tropical swamps relies on the integrity of discrete hydrological units, in turn intricately linked to the above-ground woody, and herbaceous vegetation. Contemporary changes at a local, e.g., fire, to global level, e.g., climatic change, are impacting the integrity, and functioning of these ecosystems. In order to determine the level of impact and predict their likely future response, it is essential to understand past ecosystem disturbance, and resilience. Here, we explore the impact of burning on tropical peat swamp forests. Fires within degraded tropical peatlands are now commonplace; whilst fires within intact peat swamp forests are thought to be rare events. Yet little is known about their long-term natural fire regime. Using fossil pollen and charcoal data from three peat cores collected from Sarawak, Malaysian Borneo, we looked at the incidence and impact of local and regional fire on coastal peat swamp forests over the last 7,000 years. Palaeoecological results demonstrate that burning has occurred in these wetland ecosystems throughout their history, with peaks corresponding to periods of strengthened ENSO. However, prior to the Colonial era *c*. 1839 when human presence in the coastal swamp forests was relatively minimal, neither local nor regional burning significantly impacted the forest vegetation. After the mid-nineteenth century, at the onset of intensified land-use change, fire incidence elevated significantly within the peatlands. Although fire does not correlate with past vegetation changes, the long-term data reveal that it likely does correlate with the clearance of forest by humans. Our results suggest that human activity may be strongly influencing and acting synergistically with fire in the recent past, leading to the enhanced degradation of these peatland ecosystems. However, intact tropical peat swamp forests can, and did recover from local fire events. These findings support present-day concerns about the increase in fire incidence and combined impacts of fire, human disturbance and El Niño on peat swamp forests, with serious implications for biodiversity, human health and global climate change.

Keywords: disturbance, fire, human impact, palaeoecology, peat swamp forests, resilience, tropical peatlands, vegetation change

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INTRODUCTION

Tropical peatlands constitute one of the most effective mediums through which we can mitigate the ongoing global rise in carbon emissions (Page et al., 2011; Lawson et al., 2015). This is only the case however, if these peatlands are in an intact state (Dommain et al., 2014). The peat swamp forests of Southeast Asia, covering an area of 25 million ha (Page et al., 2011), hold *c.* 12%, some 69 Giga tons, of the total carbon stored in the world's peatlands (Page et al., 2011). The performance of these peat swamps as a carbon sink relies on a tight interrelationship between the landscape, vegetation, and hydrological conditions (Page et al., 1999; Dommain et al., 2010; Posa et al., 2011), making the forest component of this ecosystem vital for its maintenance.

Tropical peat swamp forests are formed in environments where water-logged conditions develop, coupled with high humidity (Liong and Siong, 1979; Andriesse, 1988; Dommain et al., 2014). Waterlogging creates an anaerobic environment, in which limited decomposition can occur, resulting in an accumulation of layers of leaves, and woody matter from the resident vegetation. Though not restricted to low-lying areas, coastal peat domes are common across Southeast Asia (Dommain et al., 2011). Their development is thought to have started *c.* 7000 Cal. year BP (Dommain et al., 2014), after the mid-Holocene sea-level highstand, prior to sea-level fall and coastal progradation (Dommain et al., 2011).

These coastal peat swamp forests provide multiple ecosystem services to many different communities. At a global level, they are hugely important for their carbon storage and sequestration potential (Dommain et al., 2014); the peat swamp forests of Malaysia store 9.1 Giga tons of carbon, *c.* 2% of the volume globally stored in peat despite comprising <1% of the global area (Page et al., 2011), and have been sequestering it for thousands of years (Dommain et al., 2011, 2014). With much of the region's lowland forest habitat of mineral soils having already been converted into agriculture or other uses (Miettinen et al., 2016), the peat swamp forests also act as a refuge for a vast array of flora and fauna (Yule, 2010), and a primary habitat for specially-adapted species, such as blackwater fish (Thornton et al., 2018).

Despite this, peat swamp forests are being lost at a rapid pace: in Southeast Asia between 2000 and 2010, 56% were converted to plantations (Miettinen et al., 2012b), in addition to the area lost through logging and other development (Koh et al., 2011). In particular, fire is considered one of the most important drivers of land-use change and vast areas of these tropical peat swamps burn every year (Razali et al., 2010; Phua et al., 2012; Gaveau et al., 2014), especially on the island of Borneo (Langner and Siegert, 2009; Hoscilo et al., 2011; Miettinen et al., 2016).

Burning has increasingly affected the peat swamp forests of Southeast Asia in the last 2 to 3 decades (Taylor, 2010) and is now claimed to be one of the most profound threats to peatland habitats (Lee, 2000; Razali et al., 2010), as well as to all rainforest ecosystems (Laurance, 2003). However, natural fires, predominantly caused by lightning strikes, have constituted an important part of the ecosystem dynamics in these tropical peat swamps (Taylor et al., 2001) by creating gaps in which succession can occur. A study on peat swamp forests in Western Kalimantan suggests that fire has been a component of the landscape for at least the last 30,000 years (Anshari et al., 2001), and in Singapore, for the last 23,000 years (Taylor et al., 2001).

Small-scale forest burning by humans, largely as part of shifting cultivation practices (Haberle et al., 2001), has been recorded in forests in Sarawak from the early Holocene (Hunt and Premathilake, 2012). More recently however, fires are reported to have increased in frequency, magnitude, and impact in peat swamp forests in eastern Kalimantan (Hope et al., 2005), in Australasia over the last few centuries (Mooney et al., 2011), and across other areas of Southeast Asia in the last 2 or 3 decades (Taylor, 2010). How much recent fire frequency has increased relative to historical levels, and what impact it has had in shaping ecosystem dynamics in the peat swamp forests of Sarawak, is still poorly understood. These constitute important knowledge gaps for the ongoing management of fire within these peatland ecosystems, as has been proven elsewhere (Marrs et al., 2018).

This study aimed to investigate the patterns of fire, both local and regional in scale, in Sarawak's coastal peat swamp forests, using a long-term ecological approach. Three sediment sequences were extracted from peatlands on the coast of northern Borneo, where peat swamp forests dominated in the past (Cole et al., 2015), replaced now by degraded peatlands. Cole et al. (2015) demonstrated that peat swamp forest plant communities persisted for thousands of years in these locales, showing resilience through periods of climatic variability and other forms of disturbance; but that these communities have become more unstable in the recent past, coinciding with increases in indicators of human presence in the landscape. The overall objective of this paper is to explore more closely the presence, dimensions and impact of fire in these forests over the Late Holocene: to determine the change in frequency and magnitude of past burning in these (previously) intact ecosystems, infer the likely causes of any changes and examine if/how fire has influenced forest composition. Through reconstructing past burning regimes and vegetation change from these three fossil records, this work addresses three key research questions: (i) What is the natural fire regime in these swamps, and how has it changed through time?; (ii) What caused such patterns of fire in the landscape?; and (iii) How do the changing fire regimes impact the peat swamp forest vegetation? Results provide insights into past fire regimes, and their drivers, across three coastal peatland ecosystems, demonstrating the differing impacts of burning on the forest communities over time.

MATERIALS AND METHODS

Data Collection

The State of Sarawak, in northern Borneo, contains the greatest proportion of Malaysia's peat swamp forests, covering an area of approximately 3,000 km^2 or 2% of the State (Miettinen et al., 2012a), and its deforested peatlands, which extend over an additional 11% (FAO, 2012). Until recently, the peat swamp forests of Sarawak were denounced as "marginal wastelands" (Sawal, 2003), of little use except in the absence of alternative land. As such, large-scale conversion has occurred (Miettinen

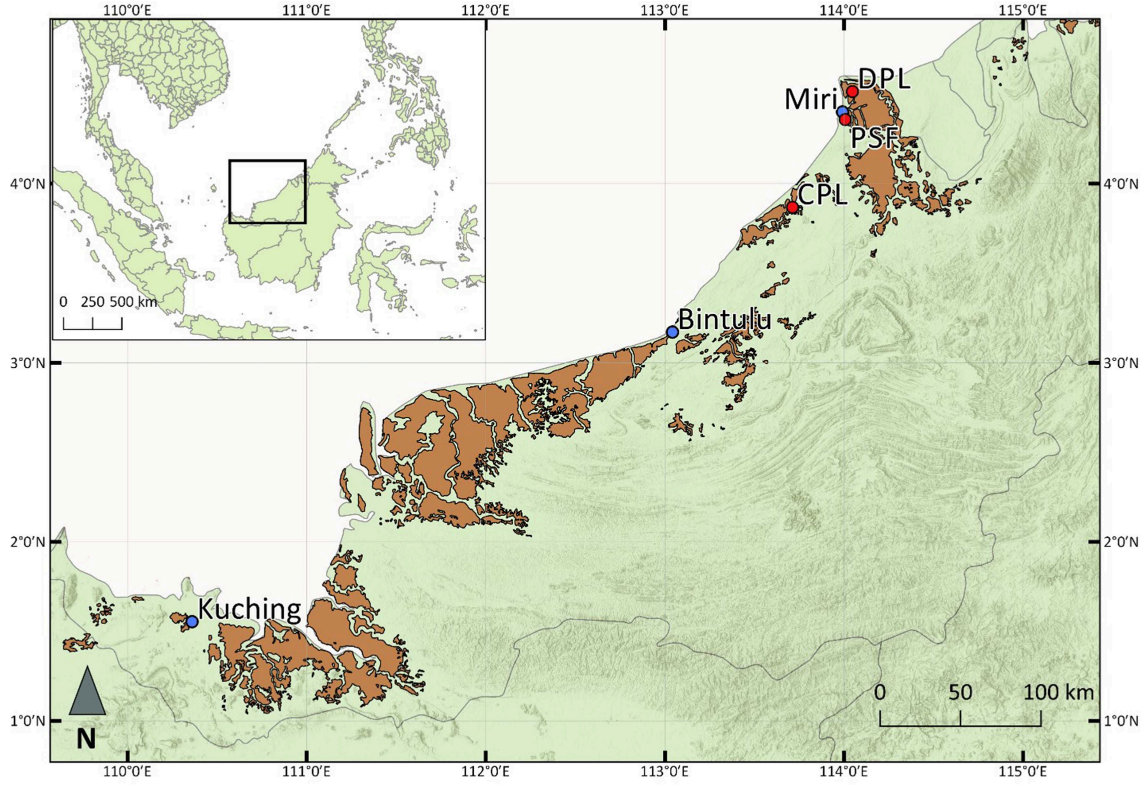


FIGURE 1 | Map showing the geographical location of Sarawak, Malaysian Borneo (inner box), within Southeast Asia, annotated with the main settlements (blue circles), and three peat swamp sites (red circles) from which cores were extracted: DPL (Deforested Peatland), PSF (Peat Swamp Fragment), and CPL (Converted Peatland). Sarawak State Boundary is demarked by a gray line; peatland areas by brown shading [courtesy of Wetlands International: "Malaysia peat lands," accessed through Global Forest Watch (www.globalforestwatch.org) (17/04/2019)].

et al., 2012b), predominantly for agricultural production (Koh et al., 2011), where fire is commonly used to clear the forest vegetation (Wooster et al., 2012).

Sedimentary cores were extracted using a hand-held coring device, from three peatlands across the Miri and Batu Niah Districts of north-east Sarawak: Deforested Peatland from Senadin, Kuala Baram (04°30′47″N, 114°2′47″E), an area of degraded peatland covering >50 km^2; Peat Swamp Fragment from Sungai Dua Forest Reserve (04°21′24″N, 114°0′21″E), a *c.* 2 km^2 fragment of secondary peat swamp forest; and Converted Peatland from Sungai Niah (03°52′4″N, 113°42′43″E), an agriculture-forest matrix of *c.* 1 km^2 (**Figures 1**, **2**). Though these three sampled sites cover a relatively narrow geographical range of 80 km along the coast of northern Borneo, since there is limited variation in climate, geology and land-use across the region, they are sufficiently representative of the coastal peat swamp ecosystems of Sarawak, and potentially those at a greater distance within insular Southeast Asia.

Using standard palaeoecological techniques (Bennett and Willis, 2001), the sediment cores were analyzed at set intervals for fossil pollen, microfossil, and macrofossil charcoal, and mineral magnetic material (magnetic susceptibility) (see **Supporting Material** for more information on the methods used in sediment and pollen preparation and analysis).

Chronology

To determine the age-depth relationship of the three sedimentary profiles, samples containing bulk organic material, were extracted from each peat core, prepared for ^{14}C dating and analyzed with AMS radiocarbon dating techniques, at the ^{14}Chrono Center in the Archaeology and Palaeoecology Department, Queen's University Belfast, and the SUERC AMS Laboratory, NERC Radiocarbon Facility. (See Wust et al., 2008, for a critique of sampling techniques of tropical peat cores for radiocarbon dating). The coding package *Clam* (Blaauw, 2010) in R Core Team (2012), with a Northern Hemisphere correction, i.e., the IntCal04 curve, was used to calibrate the conventional radiocarbon dates, and construct the best-fitting age-depth models (see **Figure S1**).

Reconstructing Past Burning Regimes

A size-class analysis of fossil charcoal, i.e., differentiating between macrofossil and microfossil charcoal, was performed to investigate changes in local and regional fire regimes, respectively, in each site through time (Whitlock and Larsen, 2002). Macrofossil charcoal particles, henceforth macrocharcoal, were isolated from each 1 cm^3 sample extracted for pollen analysis, by passing the sample through a 150 µm sieve. This process divides the macro- and microfossil components of the sediment. The resulting macrofossil isolates were then observed

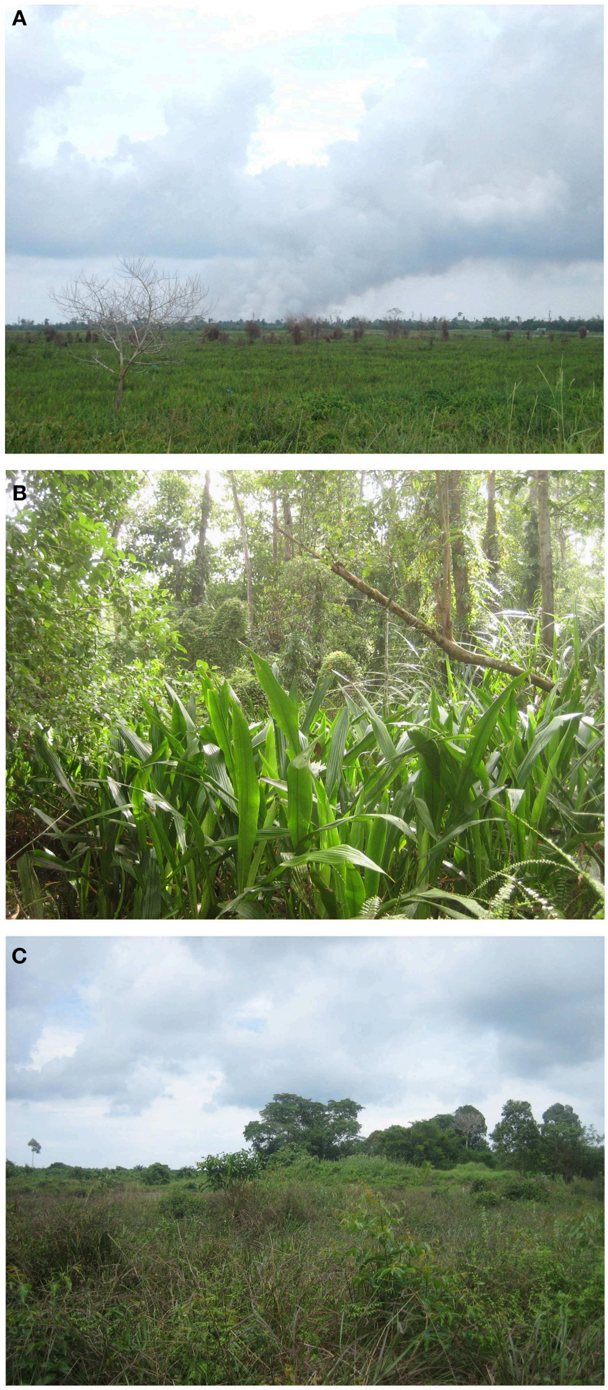


FIGURE 2 | Photographs of each study site: **(A)** Deforested Peatland, an area of degraded peatland covering >50 km^2 (with a fire burning in the distance when this photograph was taken); **(B)** Peat Swamp Fragment, a *c.* 2 km^2 fragment of secondary peat swamp forest; and **(C)** Converted Peatland, an agriculture-forest matrix of *c.* 1 km^2 (Photographs taken by L.E.S.C).

under a light microscope and the complete macrocharcoal content counted to give a measure of the number of particles per cm^3 at simultaneous intervals with fossil pollen counts. Fossil charcoal particles are identifiable as black, opaque, block-shaped, and angular (Clark, 1988). The microfossil charcoal concentration, henceforth microcharcoal, was counted at the same intervals. Since microcharcoal particles are both small, i.e., $<150\,\mu$m, causing them to separate out with the pollen component during the sieving of samples, and resistant to the processing performed to isolate fossil pollen grains and spores, they can be counted on the same slides prepared for pollen analysis. Clark's point count method (Clark, 1982), which converts standardized count data into concentration values, measured in cm^2/cm^3, was used to quantify the microcharcoal concentration in thin section. Macrofossil charcoal is used to broadly reconstruct local fire events, since the larger charcoal particles produced during fires, i.e., those $>150\,\mu$m, will be heavier and less easily transported by wind or other vectors away from the burning focus, and thus concentrate around it. Whereas, microcharcoal, comprising smaller and therefore lighter charred particles, can be transported over large distances from the site of burning, and therefore signal regional fire events (Clark, 1988).

Reconstructing Vegetation Change Over Time

Due to the diversity of species in the peat swamp flora and differing levels of pollen production, and to allow for an interpretation of the palaeo-plant communities (for example Muller, 1963), taxa identified in the fossil pollen record were allocated to ecological groups (see **Table S2**, Supporting Material) using various publications from the region (Anderson, 1964, 1980; Stuijts, 1993; Coode et al., 1996; Anshari et al., 2001, 2004). A pollen sum was then calculated and used to estimate the relative abundance of each taxa and each ecological group through time, giving a percentage score, e.g., PSF%. The different ecological groups are defined as follows: total PSF (TotPSF), which encompasses all peat swamp forest (PSF) associated taxa; the mature PSF community (PSF); the pioneer PSF community (PSF+) (indicative of transient canopy openings within a closed peat swamp forest); taxa of degraded peatlands (DP) (signaling spatially and temporally greater forest discontinuities on peat); taxa of other forests not occupying peat substrates (OF); coastal vegetation (CV) (e.g., mangroves); and *Open vegetation*, comprising taxa which dominate highly disturbed, open-canopied areas, for example Poaceae, Cyperaceae, and ferns (both of monolete and trilete morphologies). This latter ecological group is used as an indicator of human impact: Poaceae can be associated with human presence in forested palaeo-environments (Bush, 2002), and Cyperaceae and ferns are documented as characteristic of unmanaged degraded peatlands (Miettinen and Liew, 2010). These taxa can also produce unusually large volumes of pollen per plant, which can bias the interpretation of the vegetation composition of the landscape in palaeo studies (Bush, 2002). For this reason, and for their utility as anthropogenic indicators, *Open vegetation* was not included within the pollen sum but reported as a separate response variable.

Significant pollen assemblage zones were constructed using an optimal splitting by information content technique on all pollen data, after assessing the number of zones that were significant via a broken stick modeling approach across multiple analyses (Bennett, 1996). *Psimpoll* version 4.26 (Bennett, 1994) was used to display all pollen, spore, and charcoal records (**Figure 3**, and **Figures S2, S3**).

Data-Handling Techniques

In order to explore the fire regime of each core and specifically when/if peaks in fire activity have occurred through time, the macrocharcoal and microcharcoal data (C), recorded as cm^2/cm^3 and particles/cm^3, respectively, were transformed to isolate such peaks from background noise. Firstly, background burning levels were assessed, and secondly, peaks in fire activity isolated from these. Prior to the transformation, both sets of data were divided by the sediment accumulation rate calculated in *Clam*, to produce a rate of macrocharcoal and microcharcoal accumulation through time, measured in cm^2/year and particles/year, respectively. This reduced the chances of fossil charcoal peaks in the sedimentary records being an artifact of sediment accumulation variability rather than real elevations in fire activity through time (Higuera et al., 2012). Both sets of fossil charcoal data were then resampled in the first step of the transformation, using a natural logarithm to stabilize the variance in the datasets and isolate the background fire activity, C_{back}, i.e., the baseline fire activity recorded in each sediment profile, using the following equation:

$$C_{back} = \log(C + 1)$$

The second step then involved subtracting this background trend from the macrocharcoal and microcharcoal data, to create a series of residuals, i.e., peaks:

$$C_{peak} = C - \ C_{back}$$

This transformation thus provides a record of fossil charcoal fluctuation, C_{peak}, through time for all three sites (see **Figure S2**, Supporting Material), in which unusually intense burning incidences are highlighted. Although the true rate of fire events cannot be estimated due to unequal sampling intervals, episodes of increased burning frequency can be inferred where there are a greater number of elevated peaks within a period of time.

To investigate the relationship between fire and peat swamp forest vegetation through time, multivariate analyses were carried out. Principal Components Analysis (henceforth PCA) was performed in CANOCO (ter Braak and Smilauer, 2002) to explore and graphically represent the nature of the relationships between all recorded environmental variables and both internal and external peat swamp forest dynamics. Data were square-root transformed and species scores were divided by standard deviations and scaled according to inter-species correlations. Internal dynamics are represented by changes in PSF% and PSF+%, and external dynamics by the four key ecological groups in the landscape, i.e., TotPSF, DP, OF, and CV%. To analyse the strength of the correlation between firstly fire, and secondly all environmental variables, Monte Carlo Permutation Tests were performed, using 999 restricted permutations by sample, to account for the time-series nature of the data.

RESULTS

(i) What Is the Natural Fire Regime in These Coastal Peat Swamps? How Has It Changed Toward the Present Day?

Fire has been present in all three sites through time (**Figure 3**, and **Figure S2**). Fluctuations in macrocharcoal and microcharcoal levels vary within and between cores, though there are several distinct phases of elevated magnitude and frequency of burning as follows.

2,800–1,800 Cal. year BP

Within the Peat Swamp Fragment and Converted Peatland sites, there is a coincident increase in size, i.e., magnitude, of macrocharcoal peaks, and microcharcoal for the latter site, between approximately 2,800–1,800 Cal. year BP. These magnitudes do not exceed those seen in the last 200 years however. In the Converted Peatland site the magnitude and frequency of macrocharcoal peaks and frequency of microcharcoal peaks appear to be greater prior to *c.* 5,000 Cal. year BP, coinciding with the local presence of a mangrove ecosystem (**Figure 3**). After this period, levels of macrocharcoal, and microcharcoal demonstrate very low magnitudes in all three sites until the next period of elevated burning, from *c.* 200 Cal. year BP.

200 Cal. year BP to Present

Over the last 200 years, macrocharcoal and microcharcoal levels indicate an increase in both magnitude and frequency of local and regional burning, respectively, in all three sites. These results further suggest that levels of burning exceed those seen throughout the fossil charcoal records of all cores. Microcharcoal levels in the Deforested Peatland and Peat Swamp Fragment sites, especially, greatly exceed those recorded in the past. The exception to these historically-novel elevations of fossil charcoal is in the Converted Peatland site, though not associated with a peat swamp vegetation community (**Figure 3**).

(iii) How Do the Changing Fire Regimes Impact the Peat Swamp Forest Vegetation?

Peat swamp forest is considered the baseline vegetation at all three sites over the Late Holocene period, given that this ecosystem type has dominated the vegetation profiles since its development in each location. Each sediment core records a different peat development history, with Deforested Peatland having the most recently accumulated peat soils, starting from approximately 1,500 Cal. year BP; in Converted Peatland, organic matter started to accumulate in the substrate of an estuarine mangrove ecosystem several thousand years prior, though the forest associated with peat swamps did not develop until *c.* 2,800 Cal. year BP; and in Peat Swamp Fragment the onset of peat development arose *c.* 3,500 Cal. year BP (See **Figure S3**, for summary pollen diagrams).

Since the inferred onset of peat swamp development, the percentage of pollen from the total PSF ecological group (aggregate dark and light green components on the pollen sum diagram, **Figure 3**) has been relatively constant in each site

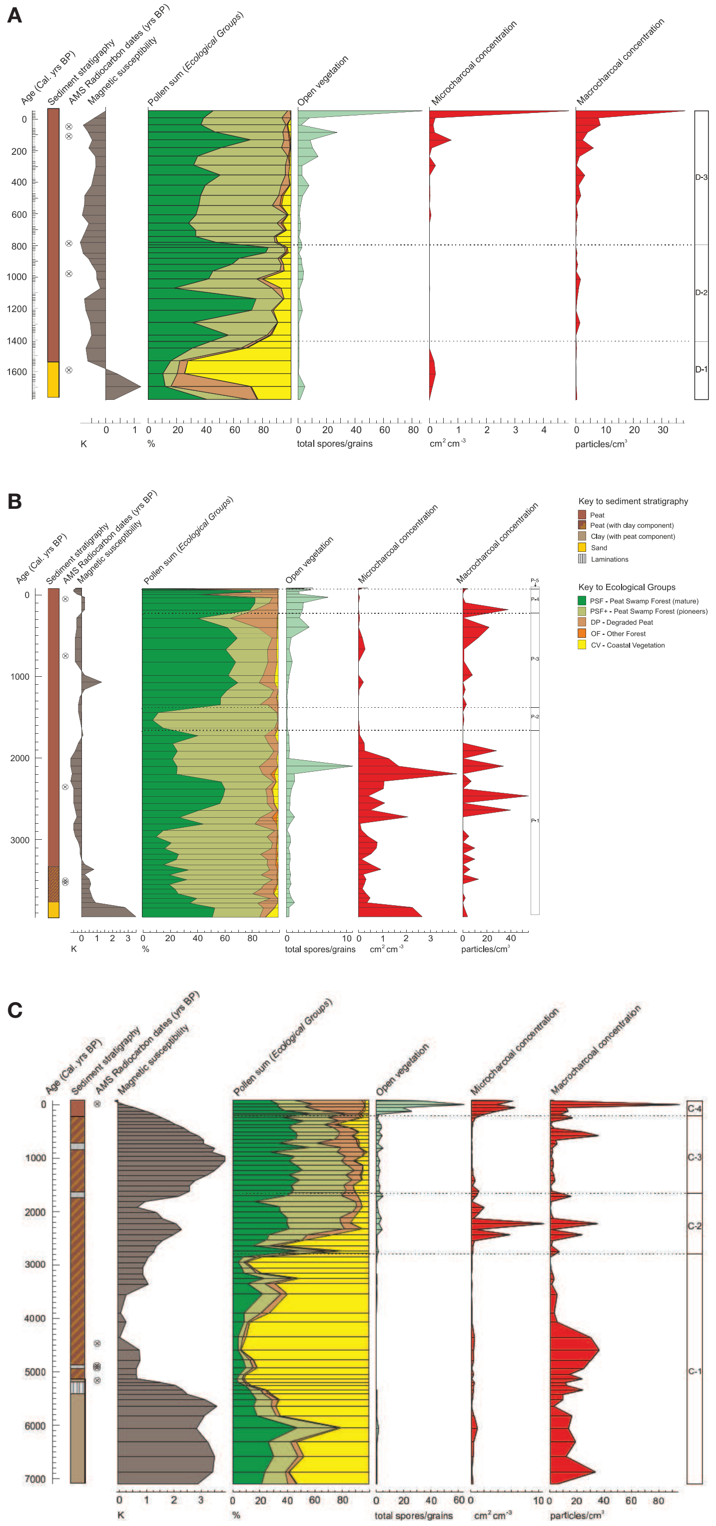


FIGURE 3 | Pollen summary diagrams for each site: **(A)** Deforested Peatland; **(B)** Peat Swamp Fragment; and **(C)** Converted Peatland, showing the sediment stratigraphy, magnetic susceptibility, five different ecological groups (represented by the following colors: PSF dark green, PSF+ light green, DP brown, OF orange and CV yellow), open vegetation (light gray), and macrocharcoal and microcharcoal (red). Significant pollen zones are shown for each (labeled D-, P-, and C-, respectively). TotPSF% comprises the sum of PSF% and PSF+%, and is represented by the division between PSF+% and DP%.

TABLE 1 | Monte Carlo Permutation Test results, performed to analyse the strength of the relationship between changes in the vegetation in each site and (a) microcharcoal and macrocharcoal, and (b) all recorded environmental variables, i.e., macrocharcoal, microcharcoal, magnetic susceptibility and open vegetation (only the strongest relationship is displayed).

	Site	Environmental variable	*F*-statistic	*p*-value	Degrees of freedom†
DEFORESTED PEATLAND					
(a)	Internal	Microcharcoal	0.14	0.892	61
		Macrocharcoal	0.82	0.553	61
	External	Microcharcoal	0.57	0.476	125
		Macrocharcoal	1.77	0.180	125
(b)	Internal	Magnetic Susceptibility	6.28	0.078	61
	External	Magnetic Susceptibility	12.75	0.094	125
PEAT SWAMP FRAGMENT					
(a)	Internal	Microcharcoal	1.75	0.482	99
		Macrocharcoal	0.74	0.477	99
	External	Microcharcoal	3.51	0.142	101
		Macrocharcoal	0.55	0.527	101
(b)	Internal	Open vegetation	4.21	0.155	99
	External	Microcharcoal	3.51	0.142	101
CONVERTED PEATLAND					
(a)	Internal	Microcharcoal	2.04	0.097	117
		Macrocharcoal	1.66	0.685	117
	External	Microcharcoal	6.08*	0.014	237
		Macrocharcoal	0.84	0.723	237
(b)	Internal	Magnetic Susceptibility	15.59	0.262	117
	External	Open vegetation	9.55*	0.015	237

**Significant relationship at $p < 0.05$ level.*

†Number of sampled sediment levels per core: Deforested peatland, 33; Peat swamp fragment, 52: Converted Peatland, 61.

*The vegetation is split into **internal** PSF dynamics, i.e., the most significant recorded factors associated with PSF% and PSF+% dynamics, and **external** landscape dynamics, i.e., factors most strongly linked with changes in all ecological groups in the landscape (TotPSF, DP, OF, and CV%). [999 restricted permutations by sample (allowing a time-series analysis) were used to calculate F-statistics and p-values].*

through time, fluctuating *c.* 80%. However, in the Peat Swamp Fragment and Converted Peatland sites, the total PSF proportion declines in the last *c.* 500 years. The indicator group for turnover within the peat swamp forest, *PSF+*, does not appear to follow a pattern within or across sites, thus demonstrating internal dynamism throughout the past. Open vegetation levels in all sites remain low until *c.* 200 Cal. year BP, with the exception of an anomalous peak in the Peat Swamp Fragment prior to 2,000 Cal. year BP. This notable increase in open vegetation taxa suggests that there was a higher incidence of open-canopied areas in the vicinity of these sites in the last several 100 years.

Both internal peat swamp forest dynamics and external landscape change do not appear to correlate with fire, whether local or regional in scale (**Table 1**). The exception is the relationship between microcharcoal and external ecological change in the Converted Peatland site. Here, regional burning is correlated with vegetation fluctuations in the wider landscape (*F*-statistic = 6.08, *p*-value = 0.014): as microcharcoal levels increase, the degraded peat ecological group (*DP*), and to an extent non-PSF-related forest taxa (*OF*), increase (**Figure 4C**). In terms of other environmental variables, the peat swamp forest and landscape vegetation within the Deforested Peatland site appears to correlate most with magnetic susceptibility changes, and in the Peat Swamp Fragment with changes in open vegetation and regional fire, albeit all non-significantly. In the Converted Peatland site, PSF dynamics had the strongest association with magnetic susceptibility, and landscape dynamics were significantly correlated with changes in open vegetation (*F*-statistic = 9.55, *p*-value = 0.015).

Despite each core exhibiting different ecological patterns, one key trend is visible from the ordination diagrams: increases in open vegetation are correlated in all three sites with the pollen samples counted within the last *c.* 200 years (see circled clusters, **Figure 4**). In the Converted Peatland and Peat Swamp Fragment cores, the degraded peat ecological group is also associated with this recent landscape trend, and across all sites, *Trema* (Cannabaceae), increases during this period (see **Figure S3**, Supporting Material).

DISCUSSION

This investigation has provided novel insights into the local to regional patterns of past burning across three peatland sites over the Late Holocene, the potential drivers of this pattern and its influence on the peat swamp forest vegetation. Fossil charcoal analysis found there to be no consistent fire regime across the three studied peat swamp forest ecosystems on the coast of Sarawak over the last 2,000–7,000 years. Palaeoecological results also demonstrate that fire has not had a significant impact

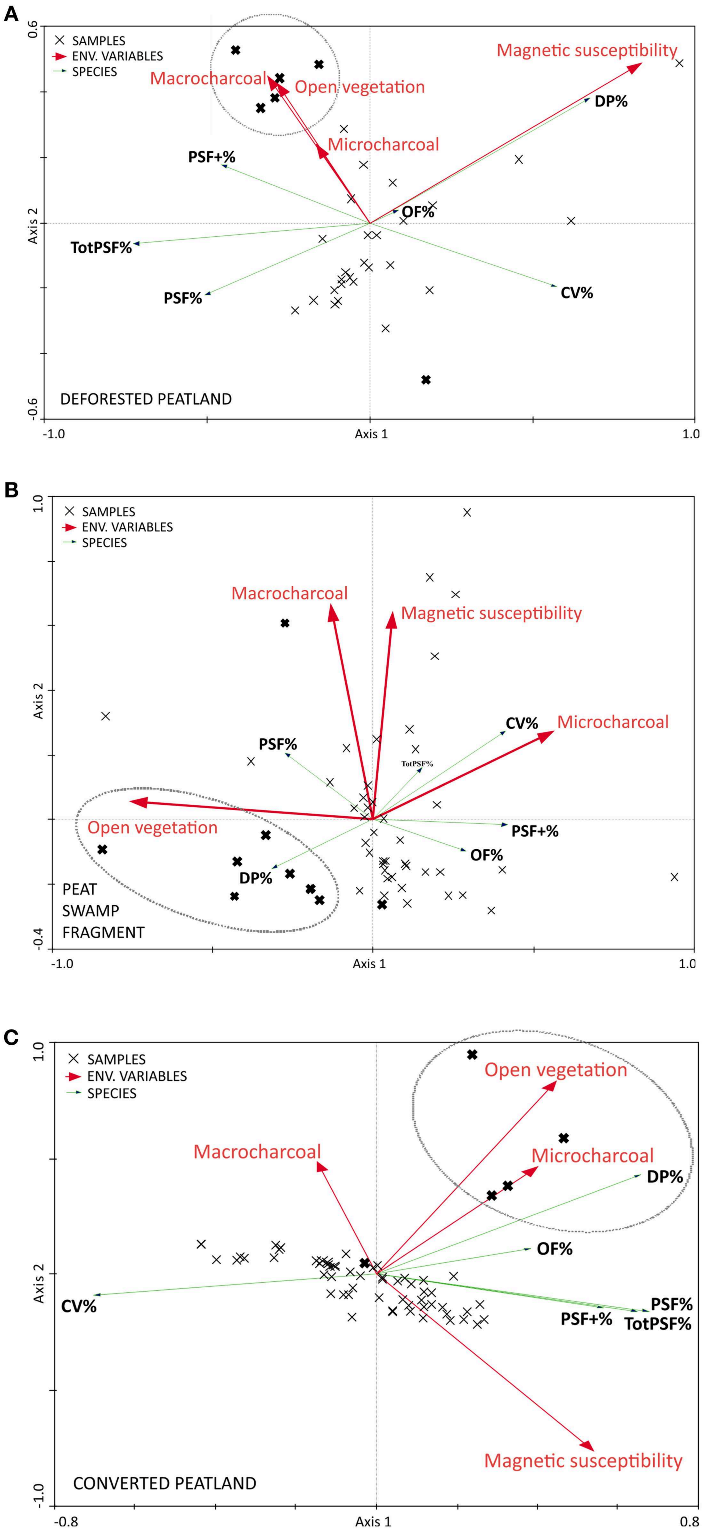


FIGURE 4 | PCA Ordination diagrams for coring sites **(A)** Deforested Peatland, **(B)** Peat Swamp Fragment, and **(C)** Converted Peatland, showing the relationships between the recorded environmental variables (i.e., macrocharcoal, microcharcoal, magnetic susceptibility, and open vegetation), and temporal changes in (i) internal PSF dynamics: mature (PSF%), and pioneer PSF taxa (PSF+%), and (ii) external landscape dynamics: the ecological groups comprising total PSF (TotPSF%), degraded peat (DP%), other forest (OF%), and coastal vegetation (CV%). In **(A)**, the 1st axis of the ordination explains 33.3% of the variance in the distribution of the ecological groups and the 2nd axis, 4.4%; with the inclusion of environmental variables, this percentage variance accounted for by the 1st and 2nd axes becomes

(Continued)

FIGURE 4 | 87.1 and 11.4%, respectively. In **(B)**, 11.3% variance is attributed to the 1st axis and 2.2% to the 2nd axis, with the explained variance increasing to 79.5 and 15.4%, respectively, when environmental variables are accounted for in the assessment of directional distribution of taxa. In **(C)**, 43.9 and 3.1% are due to the 1st and 2nd axes, and 93.1 and 6.6%, respectively, when environmental variables are included. As **Table 1** demonstrates, only microcharcoal and open vegetation are significantly correlated with external landscape dynamics in the Converted Peatland site. All samples dated within the last 200 Cal. year BP have been highlighted (represented by a thicker cross), and encircled where they have a notable association with environmental variables, i.e., predominantly open vegetation.

on either internal peat swamp forest vegetation communities or ecological change within the wider landscape through time. Rather, patterns of burning appear to be predominantly idiosyncratic and drivers of vegetation change predominantly anthropogenic, influenced by changes in the political, social, and economic environment of the region in the last two millenia.

(i) What Is the Natural Fire Regime in These Coastal Peat Swamps? How Has It Changed Toward the Present Day?

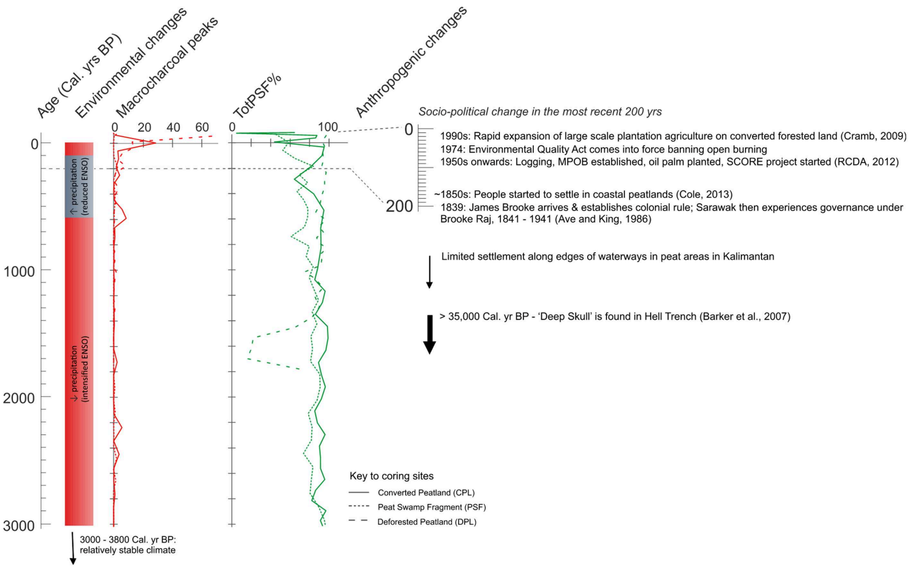
Results from this study demonstrate the presence of fire, to some degree, throughout the past within these coastal peat swamp forests, in accordance with findings from elsewhere in the region (Anshari et al., 2001; Taylor et al., 2001). However, there is no apparent "natural" or predictable baseline for the local or regional burning regime. Instead, evidence suggests that there were two notable episodes of increased fire across sites, overlaying a background of heterogeneity. In line with other studies, there are lengthy periods, for example between *c.* 1,800–500 Cal. year BP, where fire frequency and magnitude appear to be low. Hope et al. (2005) found that fire was a rare occurrence in peat swamp forest at a distance from rivers before 3,000 years ago, and from contemporary work, Miettinen et al. (2012c), and Cattau et al. (2016) report the near absence of burning in intact peat swamp forests in Sumatra and Kalimantan, respectively. The large elevation in local and, to an extent, regional burning in the Converted Peatland site prior to 5,000 Cal. year BP can likely be explained by the existence of an estuarine ecosystem during that period. It is probable that charcoal from extra-local fires was washed in with tidal currents and accumulated in the mangrove muds (a process enabling both micro- and macro-sized particles to travel and become deposited), since past mangrove ecosystem dynamics are not strongly associated with fire (e.g., Alongi, 2008). Thus, these earlier elevated levels of burning are likely associated with tidally-influenced mangrove communities, rather than peat swamp forests.

Two episodes where considerable coherence and elevation in the fossil charcoal records do occur across sites, suggestive of increased regional burning, or pervasive landscape change, are as follows: the first between approximately 2,800–1,800 Cal. year BP, and the second, within the last 200 years. In order to explore the factors that could have influenced these fire patterns over the Late Holocene, records of regional climate and information on local anthropogenic land-use change were sourced.

(ii) What Caused Such Patterns of Fire in This Landscape?

In general, climate did not appear to have a significant impact on the burning regime in any of the three sites through time. However, the first simultaneous episode of elevated local and regional burning observed between *c.* 2,800–1,800 Cal. year BP, coincides with a period of climatic drying in the Tropics that is reported to occur in the interval 2,000–3,000 Cal. year BP (Woodroffe et al., 2003; Selvaraj et al., 2007) (**Figure 5**). Anshari et al. (2001) report a similar increase in microfossil charcoal particles during this period, in a peat core extracted from West Kalimantan, and suggest that increased ENSO-related climatic variability may have been one reason for such an increase, predominantly through causing stress to previously stable ecosystems. They also refer to human disturbance as a potential driving force for greatly elevated charcoal to pollen ratios recorded from *c.* 1,400 year BP (Anshari et al., 2001).

In order to assess the probable anthropogenic influence on burning regimes in the coastal peat swamp forests studied here, there is a complex history of human-environment interactions (**Figure 5**) that warrants consideration. Evidence for the first human presence in northern Borneo comes from a "Deep Skull" found in the Niah Caves in northeast Sarawak, which has been dated to over 35,000 Cal. year BP (Barker et al., 2007). Other work suggests that people have been living in this area for even longer (Hunt and Premathilake, 2012), and using fire to clear forest vegetation (Hunt and Rushworth, 2005). During the late Pleistocene and much of the Holocene, low-density human communities in Borneo would have had limited impact on their densely-forested environment, and their activities, predominantly as hunter-gatherers and shifting cultivators, are unlikely to have extended far beyond the edges of peat domes, or from river-based transport networks (Hope et al., 2005). Large-scale landscape modification started to happen with the establishment of Colonial rule. Captain James Brooke, the first Viceroy of Sarawak, landed on Borneo's shores in 1839, and proceeded to organize her politics and landscape. Captain Brooke's goals were to improve levels of peace amongst the resident communities and to increase the productivity of the land (MacDonald, 1956). Fire would have played an important role in this strategic landscape conversion. At this time, people searched for land on which to farm and secure rights, in some cases turning to the relatively under-exploited peat swamps. Interview data suggests that people began living in these areas from *c.* 1850, but the majority settled in peatlands much later, i.e., the early 1970s (Cole, 2013). Approximately 100 years after the first settlement, mechanization had drastically increased, along with the wealth and population of the State; developing this waterlogged "wasteland" on a large scale became both more feasible and more financially rewarding. Selective logging in the coastal peat swamps started in the early 1950s and constituted a key income for the State for 20 years. It continues today, although with declining extraction rates due to the much-depleted tree stocks. Prior to the Environmental Quality Act of 1974 (Dolmat,



1990s: Rapid expansion of large scale plantation agriculture on converted forested land (Cramb, 2009)
1974: Environmental Quality Act comes into force banning open burning
1950s onwards: Logging, MPOB established, oil palm planted, SCORE project started (RCDA, 2012)
~1850s: People started to settle in coastal peatlands (Cole, 2013)
1839: James Brooke arrives & establishes colonial rule; Sarawak then experiences governance under Brooke Raj, 1841 - 1941 (Ave and King, 1986)
Limited settlement along edges of waterways in peat areas in Kalimantan
> 35,000 Cal. yr BP - 'Deep Skull' is found in Hell Trench (Barker et al., 2007)
3000 - 3800 Cal. yr BP: relatively stable climate

FIGURE 5 | Composite diagram illustrating the environmental, anthropogenic, and peat swamp forest ecological changes occurring within the study region over the last 3,000 years, from the first distinct phase of elevated burning across two sites (CPL and PSF, **Figure 3**). Historical and climatic drivers of past fire incidence within Sarawak's coastal peatlands have been identified through a literature search and interviews (Cole, 2013), with the most recent 200 years hosting a period of significant socio-political change. Variability in macrocharcoal peaks (C_{peak}, measured in peak component charcoal accumulation rate (cm^3/yr), see **Figure 2**, Supporting Material) and TotPSF% (percentage of pollen sum) across all cores are represented on separate axes, aligning with one chronological scale. (For more information on: ENSO variability, see **Table S3**, Supporting Material; and the history of political development in Sarawak, see (Cramb et al., 2009) and references therein).

2005), open burning to clear peat swamp forest was legal, and thus would have been used extensively by smallholder and plantation farmers. After this time, only small controlled burns were permitted by the Department of the Environment, and clearance fires were replaced by large machinery that also drained, compressed and piled peat in preparation for the establishment of oil palm and pulpwood plantations, amongst other land uses. Such modification of the land, in particular the drying caused by drainage, makes peatlands more vulnerable to fire (Page et al., 2002; Hoscilo et al., 2011; Taufik et al., 2018), whether ignited by natural or anthropogenic sources (Cattau et al., 2016).

Until several 100 years ago, local fires (those within peat swamp forest) would predominantly have been driven by natural disturbances such as lightning strikes, especially during dry climatic periods, i.e., El Niño years (Hope et al., 2005). Human disturbance would have been minimal (Sawal, 2003), restricted to activities such as subsistence sago cultivation: a crop that grows well on marginal lands (Donner, 1987). Within the last 200 years however, the coincidence of data showing dramatic increases in the magnitude and frequency of local and regional fire (and open areas), with the reporting and documenting of increased human interaction with Sarawak's coastal peat swamp forests, suggests that humans were responsible for these elevations in burning. Significant landscape exploitation by people is likely to have started after Colonial Rule was established in Sarawak approximately 170 years ago. The following quote, attributed to the Second Raj of Sarawak, Charles Brooke, in 1867, illustrates the attitude toward "idle" forested land that would have driven large-scale landscape conversion: *"[We want] to see the jungle falling left and right and people settled over what are now lonely wastes and turning them into cultivated land."* The dramatic recent increase in burning peatlands has also been recorded in Sumatra (Miettinen et al., 2012c) and across Southeast Asia (Van Eijk et al., 2009; Dohong et al., 2017).

(iii) How Do the Changing Fire Regimes Impact the Peat Swamp Forest Vegetation?

Results from this study suggest that fire has not caused significant disturbance to these three coastal peat swamp forests through time. Even during episodes of elevated burning in the past, for example during the inferred dry phase between *c.* 2,800–1,800 Cal. year BP, there is no decline in the peat swamp forest or apparent impact on the vegetation within these ecosystems. In terms of internal peat swamp forest dynamics through time, the fluctuation between mature and pioneer taxa does not correlate with fire incidence, again suggesting that, in general, burning has not played a significant role in the regeneration of these ecosystems. Since anthropogenic burning is hypothesized to have only started in the last two centuries, it appears that the natural burning regimes in each site, which have been predominantly idiosyncratic, have not had a significant negative impact on these peat swamp forests. An exception to this appears in the results of the Converted Peatland site, where regional fire appears to have a significant impact on peat swamp forest ecosystem abundance within the wider landscape. Further sampling is required to decipher reasons for this unusual finding in the Converted Peatland site.

In contrast to the long-term burning and peat swamp forest vegetation dynamics, as levels of local and regional fire elevate to historically-novel levels in the most recent past, declines in peat swamp forest within the landscape and an apparent lack of regeneration within the forests, suggests fire is now impacting on these ecosystems. However, the most influential drivers of peat swamp forest change across sites appear to be disturbances associated with anthropogenic activity: open vegetation, signifying forest clearance, and magnetic susceptibility, indicating disturbance and/or drying in the peat substrate. These relationships are strongest in the recent past (**Figure 4**), coinciding with and, most probably, driving the large elevations in local and regional fire, as suggested by other studies in this region (Lee, 2000; Langner and Siegert, 2009; Van Eijk et al., 2009). Despite these associations between peat swamp forest and environmental variables, it is important to note that the only significant relationship observed in this study occurs between open vegetation and external landscape change, i.e., a decline in peat swamp forest, in the Converted Peatland site. Further evidence for the predominantly anthropogenic origin of fire within peat swamp forest in the last 200 years, is the coincident increase in ferns, Poaceae and other non-woody taxa of open areas (Hoscilo et al., 2011), such as *Trema* (Cannabaceae). This plant has been associated with the creation of gaps within the peat swamp forest greater than those resulting from local disturbances (Flenley and Butler, 2001), such as wind-throw (Anderson, 1964).

In conjunction, the results from the three studied sediment cores strongly suggest that fire has been present in tropical peat swamp forests for thousands of years and that it is *not* the most prominent driver of long-term or recent changes in coastal peat swamp forest vegetation, contrary to the common concern expressed in the literature on the sustainable management of tropical peat swamp forests today (for example Razali et al., 2010; Miettinen et al., 2012c). Instead, human impact has had the most influence on internal peat swamp forest dynamics and peat swamp forest decline: with this disturbance manifesting only in the last *c.* 200 years and at unprecedented levels when compared to the last 7,000 years. In reality, it is likely that various forms of human disturbance, notably forest clearance, drainage and fire, occur simultaneously and act synergistically in these landscapes, exacerbating impacts, reducing forest regeneration potential and thus jeopardizing the resilience of these peat swamp forests.

To explore the relationship between fire, its drivers and vegetation change at a higher temporal resolution, further sampling, and the use of additional proxies, would be required. Though individual fire events can be identified from fossil charcoal records extracted from peat deposits, palaeoecological data is best suited to identifying historical trends in fire regimes (Remy et al., 2018). Observing a true response of the vegetation to an incidence of burning, or another form of disturbance, can also be challenged by differing rates of pollen production amongst species and varying distances over which pollen grains are transported, in turn affected by the changing characteristics of the canopy around the coring site, amongst other constraints (Davies et al., 2018). Signals of regional burning can, in particular, be affected by canopy cover, since microcharcoal particles can be caught in the vegetation overlying the forest floor; this can reduce the volume of microcharcoal that is found in sediment profiles causing potential under-estimations of fire incidence and intensity at a regional scale. However, this potential under-estimation is not considered a significant obstacle in this and other palaeo-environmental reconstructions in tropical peatland ecosystems (e.g., Hope et al., 2005). Due to these various factors, interpretations of the data reported in this study have been limited to broad trends, and thus give an impression of ecosystem level sensitivity to burning during the Late Holocene.

Despite the limitations of long-term ecological studies, the insights gained through these data greatly extend our ability to understand the ecological functioning of ecosystems (Willis et al., 2010; Cole et al., 2015), particularly in response to fire. The findings can be used to infer how the intact peat swamp forests, and degraded peatlands, may respond to future disturbances and thus develop informed management strategies (Davies et al., 2014). In contemporary ecosystems that now exist predominantly in a degraded state (as is increasingly the case for Southeast Asia's peat swamp forests (Murdiyarso et al., 2009), long-term ecological data also enable us to define the parameters, and resilience, of their intact condition.

Management Implications

The causes of fire are complex, and include underlying cultural, political and socio-economic conditions, not simply environmental factors (Stolle et al., 2003; Langner and Siegert, 2009; Carlson et al., 2012; Shimin Sze et al., 2018). However, when considering peat swamp forest management, it is important to note that degraded, in comparison to relatively intact peatlands, are more susceptible and fundamentally less resilient to fire (for example Page et al., 2002; Van der Werf et al., 2008; Wösten et al., 2008; Hoscilo et al., 2011). The interaction between different drivers of disturbance requires further investigation when considering management interventions. This study has demonstrated however, that recent forms of anthropogenic disturbance, likely driving elevated incidences of burning, are unprecedented in the ecological history of these ecosystems.

Draining and/or forest clearing, which accompanies the majority of peat swamp forest land-use change, leads to highly flammable conditions, and inevitably subsidence (Hooijer et al., 2011) and ongoing carbon emissions (Wijedasa et al., 2018). This often results in peatlands becoming "unmanaged wastelands" or entirely converted to agriculture (Miettinen et al., 2012b). Restoration of such areas is being attempted in peatlands in Central Kalimantan (Page et al., 2009) and across Indonesia (BRG, 2018), but unless these areas are protected against fire, notably through re-wetting (Dommain et al., 2010), restoration may prove impossible (Van Eijk et al., 2009).

Contemporary studies have shown that the impacts of local fire within peat swamp forests can be severe: once the substrate has been ignited, fires can burn both above and, devastatingly, below-ground for many months (Goldammer and Seibert, 1989; Goldammer, 1992; Saharjo and Nurhayati, 2006; Posa et al., 2011), destroying meters of peat. In addition to destroying the current understory vegetation, these fires can hinder regeneration post-fire (Saharjo and Nurhayati, 2006; Cole, 2013), and thus reduce the possibility of future recovery, especially if soil seed banks are disturbed (Posa et al., 2011).

Unusually intense and frequent fires can also disturb natural regeneration cycles, such as those that have burnt in Indonesia's inland peat swamps during the recent extreme drought events of strong El Niño years, exemplified by the 1997–1998 episode (Page et al., 2009). Biomass burning during this period released vast amounts of carbon (between 0.81 and 2.57 Gt) into the atmosphere (Page et al., 2002). In addition, these fires caused a host of serious health and environmental problems in the region (Marlier et al., 2013), as well as disrupting economic activity (Varma, 2003; Aiken, 2004). Although the coastal peatlands of Southeast Asia appear to have been less impacted by these climatic events in the past (Dommain et al., 2011), managing for increased fire risk during dry El Niño years [(Pan et al., 2018) and indeed non-El Niño years, with recent land-use change causing an elevation in burning uncoupled with ENSO (Gaveau et al., 2014)], may help to prevent a recurrence of these disastrous effects in the future (Phua et al., 2007, 2012). Fire risk mapping, looking at impacts of infrastructure, for example roads and settlement, may also help (Razali et al., 2010; Shimin Sze et al., 2018), since historical fire incidence in peatlands in Kalimantan has been associated with accessibility (Hope et al., 2005). Furthermore, if the international mechanisms being developed to encourage countries to reduce their carbon emissions through forest conservation, such as the Reducing Emissions from Deforestation and Degradation (REDD+) scheme (FAO, 2012), are to include tropical peat swamp forests, the huge volumes of carbon gases released from peat fires will need to be abated (Murdiyarso et al., 2010).

At present, large scale burning of tropical peat is largely confined to Indonesia, but tropical peatlands are not only found in Southeast Asia: vast areas have recently been mapped in the Peruvian Amazon (Draper et al., 2014) and the central Congo Basin (Dargie et al., 2017). Currently, these ecosystems are largely intact and as such of huge global significance (Watson et al., 2018); but this could change if they are not protected from the multiple threats to which they could soon be exposed (Roucoux et al., 2017; Dargie et al., 2018), including the more pervasive threat of climate change (Wang et al., 2018).

If recent elevated trends in burning can be prevented, predominantly through halting forest clearance and drainage, this and other studies (e.g., Hope et al., 2005; Hapsari et al., 2018) provide evidence that peat swamp forests can recover. However, in the face of current conversion rates and future land-use planning in the region (Miettinen et al., 2012b, 2016; Gaveau et al., 2016; Wijedasa et al., 2017), potential disturbance by fire must be a central consideration in the more responsible management of these carbon-rich ecosystems.

AUTHOR CONTRIBUTIONS

LC performed data collection and analysis, designed, wrote and revised the manuscript, KW assisted with manuscript structure. KW and SB contributed to manuscript revisions.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2019.00048/full#supplementary-material

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Climate Benefits of Intact Amazon Forests and the Biophysical Consequences of Disturbance

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Tropical forests have an important regulating influence on local and regional climate, through modulating the exchange of moisture and energy between the land and the atmosphere. Deforestation disrupts this exchange, though the climatic consequences of progressive, patch-scale deforestation of formerly intact forested landscapes have not previously been assessed. Remote sensing datasets of land surface and atmospheric variables were used to compare the climate responses of Amazon forests that lost their intact status between 2000 and 2013. Clear gradients in environmental change with increasing disturbance were observed. Leaf area index (LAI) showed progressively stronger reductions as forest loss increased, with evapotranspiration (ET) showing a comparative decline. These changes in LAI and ET were related to changes in temperature (T), with increased warming as deforestation increased. Severe deforestation of intact Amazon forest, defined as areas where canopy cover was reduced below 70%, was shown to have increased daytime land surface T by 0.44°C over the study period. Differences between intact and disturbed forests were most pronounced during the dry season, with severely deforested areas warming as much as 1.5°C. Maintenance of canopy cover was identified as an important factor in minimizing the impacts of disturbance. Overall, the results highlight the climate benefits provided by intact tropical forests, providing further evidence that protecting intact forests is of utmost importance.

Keywords: intact forest landscapes, deforestation, leaf area index, evapotranspiration, temperature, precipitation

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INTRODUCTION

Tropical rainforests moderate the flux of energy and water between the land and the atmosphere, and affect atmospheric chemistry through the exchange of trace gases (Silva Dias et al., 2002). Tall rainforest trees provide a physical connection between deep soil layers and heights up to 40 m above the Earth's surface (Simard et al., 2011). In the Amazon, tropical forest has an important and complex role governing local and regional climate (see Marengo et al., 2018 and references therein). At the local scale, evaporating moisture affects the partitioning of radiation between sensible and latent heat (the Bowen ratio), leading to a cooling and moistening of the boundary layer (Da Rocha et al., 2004; Bonan, 2008). At larger spatial scales, the "cascade" of water vapor propagating across the basin drives regional rainfall and provides a buffer against the damaging effects of drought, with forests in the southern Amazon a particularly important source of re-evaporated water for sustaining forest biomes further downwind (Zemp et al., 2014; Staal et al., 2018).

Almost 1 million km^2 of Amazon forest has already been deforested, representing nearly a fifth of its original extent (Davidson et al., 2012; Nobre et al., 2016). Most of the deforestation has occurred along the southern margins of the basin, in the so-called "arc of deforestation" (Malhi et al., 2008). The implementation of a satellite monitoring program in Brazil [Projeto de Monitoramento do Desmatamento na Amazônia Legal por Satélite (PRODES)], saw a marked reduction in annual deforestation rates over the Brazilian legal Amazon from 2004 to 2012, since which time the clearance rate has remained comparatively stable, though evidence suggests that it has begun to rise again in recent years (INPE, 2019). However, a new study has shown that PRODES, which only considers primary forest removal and excludes small-scale ($<$6.25 ha) patches from its definition of deforestation, may have been underestimating recent deforestation by as much as a factor of two. Kalamandeen et al. (2018) showed that small-scale forest loss accounted for approximately 40% of deforestation across the entire Amazon from 2001 to 2014, and had a strong positive trend over this period. This rise in low-density forest loss just as large-scale forest clearance events appeared to be coming under control, illustrates the growing threat of small-scale deforestation to Amazon ecosystems.

In addition to perturbing the global carbon balance (Pan et al., 2011; Baccini et al., 2012), removal of tropical forest has consequences for local and regional climate, and can even drive temperature and precipitation changes outside of the tropics (see D'almeida et al., 2007; Davidson et al., 2012; Lawrence and Vandecar, 2014). Much understanding has come from experiments with regional or general circulation models, with simulations revealing the climate consequences of forest clearance in the model world (D'almeida et al., 2007; Sampaio et al., 2007; Costa and Pires, 2010; Medvigy et al., 2011, 2013; Swann et al., 2015). A meta-analysis of 44 modeling studies found a negative linear relationship between Amazon deforestation extent and basin-wide rainfall (Spracklen et al., 2015), though many of the studies analyzed had highly idealized deforestation scenarios, such as 100% forest removal. Trajectory-based analyses have also shown that deforestation is likely to exacerbate the effects of droughts in the Amazon, through a reduction in atmospheric moisture transport from deforested areas to regions downwind (Spracklen et al., 2012; Bagley et al., 2014).

Site-level studies have provided valuable data on the impacts of Amazon forest clearance on the local microclimate. Net surface radiation is lower over cleared areas, due to a combination of higher albedo, and greater outgoing longwave radiation compared with forests (Bastable et al., 1993; Gash and Nobre, 1997). However, despite a lower energy balance, station data show deforested sites may be up to 2°C warmer than adjacent forested areas, and show higher diurnal and seasonal temperature variability (Von Randow et al., 2004; Dubreuil et al., 2012). This is due to differences in evapotranspiration (ET): eddy covariance flux tower measurements from pasture and forest sites in the southern Amazon revealed lower ET and higher sensible heating over the pasture site throughout the year (Von Randow et al., 2004). Differences were greatest during the dry season (June–August) as forests were able to access and transpire deep groundwater, unlike short-rooted pasture vegetation.

Remote sensing techniques have made it possible to analyse the environmental impacts of deforestation over larger spatial scales. Studies using satellite ET observations to evaluate the effects of deforestation in the Brazilian Cerrado (Spera et al., 2016), and the Brazilian Amazon (Lathuillière et al., 2012; Silvério et al., 2015), all found strong hydrological responses to land cover change. High ET fluxes over continuous forest in the Xingu Indigenous Park of southern Amazonia resulted in it being 1.9°C cooler than the surrounding patchwork agricultural landscape (Silvério et al., 2015). At the pantropical scale, Alkama and Cescatti (2016) used satellite temperature retrievals to show that, in line with ground-based measurements, diurnal temperature variability increased by approximately 2°C following clearance of tropical forest. The authors also showed land surface temperature to be more sensitive to forest cover loss than air temperature, which showed approximately two thirds of the sensitivity. Impacts on rainfall may depend on the scale of deforestation. Some remote sensing studies have observed increased rainfall over patches of forest loss (Negri et al., 2004; Chagnon and Bras, 2005; Funatsu et al., 2012), particularly within a few kilometers of forest edges (Knox et al., 2010), though larger-scale deforestation reduces moisture recycling and thus has a negative effect on rainfall (see Spracklen et al., 2018 and references therein).

Over the past decade, researchers and conservationists have used satellite data to map intact forests across the globe (Potapov et al., 2008, 2017). Intact forests were defined as forests with no remotely-detectable signs of anthropogenic disturbance, with forests assumed to be intact unless evidence to the contrary was found. One caveat of this approach is that selective logging and small-scale disturbances, which are difficult to observe remotely, could be overlooked, causing a possible overestimation of "intact" status (Potapov et al., 2008). In a recent review, Watson et al. (2018) summarized the myriad benefits and services that intact forest ecosystems provide, including regulating weather on local and regional scales, mitigating climate change, contributing to the conservation of biodiversity, improving air quality, and helping to preserve indigenous cultures. In the tropics, only 20% of all forested areas are classified as intact, a fraction that is diminishing as humans continue to encroach further into pristine ecosystems (Potapov et al., 2017). Protected areas can help prevent deforestation in the Amazon (Soares-Filho et al., 2010; Spracklen et al., 2015), but face a variety of legal threats (Nogueira et al., 2018). Together with the rise in small-scale disturbances in the region documented by Kalamandeen et al. (2018), this shows that there is a growing need to evaluate the climate impacts of deforesting intact forests in the Amazon.

This study seeks to quantify the climatic value of intact tropical forests in the Amazon, and evaluate the biophysical changes that occur during progressive, patch-scale deforestation of larger forested landscapes. Forest change datasets were used in conjunction with remote sensing observations of the land surface and the atmosphere to identify local environmental changes over areas that were differentially impacted by anthropogenic disturbance between 2000 and 2013.

MATERIALS AND METHODS

Classification of Forest Disturbance Categories

To evaluate the biophysical consequences of deforesting intact Amazon forest between 2001 and 2013, forest pixels were classified into four categories that were designed to represent increasing levels of anthropogenic disturbance. This approach utilized two global forest datasets: the Intact Forest Landscapes (IFL) product, which maps forests that have no remotely-detectable signs of human impact (Potapov et al., 2017), and the Global Forest Change (GFC) version 1.6 product, which records forest cover change over time (Hansen et al., 2013). The IFL shapefiles for 2000 and 2013 were used in this study (IFL_2000 and IFL_2013), along with the following GFC layers: tree canopy cover for year 2000 (treecover2000) and year of forest cover loss (loss year).

The 2000 and 2013 IFL shapefiles were rasterised to 0.05° spatial resolution in order to match the grids of the climate data used in the analysis. This was performed using the Geospatial Data Abstraction software Library Python package (GDAL/OGR contributors, 2018). Pixels were classified as "intact" if the center of the pixel fell within the IFL polygon and non-intact if the pixel center fell outside the polygon. Pixels that were classified as intact but had tree cover changes $>5\%$ were excluded from the analysis ($<2\%$ of IF pixels), as it is likely these were misclassified as a result of the rasterization process.

The GFC datasets were first used at their original resolution (approximately 30 × 30 m at the Equator) to calculate a tree cover dataset for the year 2013 (treecover2013). For this, the treeCover2000 dataset was masked to remove pixels where deforestation had occurred up to and including the year 2013 (determined using the loss year dataset). The GFC data layers treecover2000 and treecover2013 were then resampled to 0.05° by finding the mean tree cover across all 30 m-resolution pixels within each 0.05° grid cell.

Next, the GFC datasets were used to derive forest masks for use in the classification procedure. A 70% tree-cover threshold was chosen to distinguish between land areas classified as forest and non-forest. The treecover2000 and treecover2013 datasets (each at 0.05°) were then used to create forest masks for 2000 and 2013 by selecting all pixels where tree cover exceeded 70% in those years (forestcover2000 and forestcover2013). Our results were found to be robust across a gradient of other canopy cover thresholds (**Figure S1**).

Amazon forest pixels were divided into four categories representing a gradient in the extent of disturbance that occurred between 2000 and 2013 (**Table 1**). The analysis was constrained to the Amazon evergreen broadleaf forest biome, as defined by the Collection 5 (C5) Moderate Resolution Imaging Spectroradiometer (MODIS) land cover classification product (MCD12C1) for the year 2001 (Friedl et al., 2010). Boolean logic was applied to identify pixels in each category. First, intact forest (IF) pixels were identified using the 2013 IFL dataset. IF pixels represent undisturbed or pristine forests that did not experience any remotely-detectable disturbance over the period analyzed and were thus considered the control group. The other three categories represent the "disturbance categories," and include forests that have lost their intact status, either prior to, or over the course of, the analysis period. The non-intact forest (NIF) category contained pixels that were not classified as intact in 2000, but had $>70\%$ tree canopy cover in 2000 and were still forests ($>70\%$ tree cover) in 2013. The third and fourth categories were forests that lost their intact status between 2000 and 2013. If tree cover was $\geq 70\%$ in 2013 then pixels were classified as having experienced "moderate," patch-scale deforestation, while pixels where tree cover fell below the 70% threshold were categorized as having experienced "severe" deforestation. For pixels in both of these categories, landscapes of intact forest with high canopy cover in 2000 were transformed to a patchwork of forested and deforested areas by 2013, with categories differing only in the size and extent of the deforested patches.

The spatial distributions of intact forest, non-intact forest, and previously intact forest areas that experienced either "moderate" or "severe" deforestation between 2000 and 2013, are shown in **Figure 1A**. Non-intact forests are fairly widely distributed across the Amazon, but tend to follow the contours of rivers and other water courses. This is related to the IFL mapping approach, which excludes forests within 1 km of navigable rivers, as these are more accessible to humans and thus more likely to have experienced disturbance than inaccessible inland forests (Potapov et al., 2017). Most of the forests that lost their intact status over the analysis period (orange and magenta areas in **Figure 1**) are in the southern Amazon, with a few patches of moderate deforestation over the Guiana Shield in the northeast. Deforestation primarily occurred along the margins of non-intact forest areas, indicating an expansion of human-impacted forest landscapes along disturbance frontiers.

Remote Sensing Datasets

The environmental impact of intact forest disturbance was assessed using remote sensing datasets of the land surface and the atmosphere (**Table 2**). Leaf area index (LAI), evapotranspiration (ET), land surface temperature (T) and precipitation (P) datasets were analyzed over the period 2001–2013.

LAI data were retrieved from the monthly GLASS01B01 0.05° product, which is based on MODIS reflectance from 2001–2014 (Liang et al., 2014). For ET, we used the Level 3, gap-filled 0.05° C5 MOD16 MODIS product provided by the Numerical Terradynamic Simulation Group (NTSG) at the University of Montana (Mu et al., 2007, 2011), regridded from 8-day to monthly resolution. Since previous work has highlighted differences in remote sensing ET products over the Amazon, and warned against using any one data product in isolation (Miralles et al., 2016), monthly ET estimates were additionally obtained from the 8-km Global Land Surface Evapotranspiration (GLS-ET) product (Zhang et al., 2010), also distributed by NTSG, and the 0.25° × 0.25° Global Land Evaporation Amsterdam Model (GLEAM) version 3.2a dataset (Miralles et al., 2011; Martens et al., 2017). The MODIS ET and GLS-ET products were derived using variations of the Penman-Monteith equation (Monteith, 1965), although the remote sensing and reanalysis input datasets for the two products are different. Meanwhile, the GLEAM ET estimates are founded on the Priestley-Taylor approach for

TABLE 1 | Forest disturbance categories used in this study.

Category	Definition	Tree cover in year 2000 (%)	Tree cover in year 2013 (%)	Tree cover change (%)
Intact forest (IF)	Forest pixels classified as intact in 2013 (no anthropogenic degradation)	97.79	97.62	−0.18
Non-intact forest (NIF)	>70% tree cover in 2000 but not within IFL, still >70% tree cover in 2013	93.49	89.73	−4.04
Moderate deforestation	Forest pixels that were intact in 2000 but not in 2013, still >70% tree cover in 2013	97.80	93.54	−4.37
Severe deforestation	Forest pixels that were intact in 2000 but not in 2013, with <70% tree cover 2013	91.56	53.98	−39.81

Mean tree cover values for 2000 and 2013 are shown for each category, and the mean change in fractional tree cover as a percentage of the original coverage.

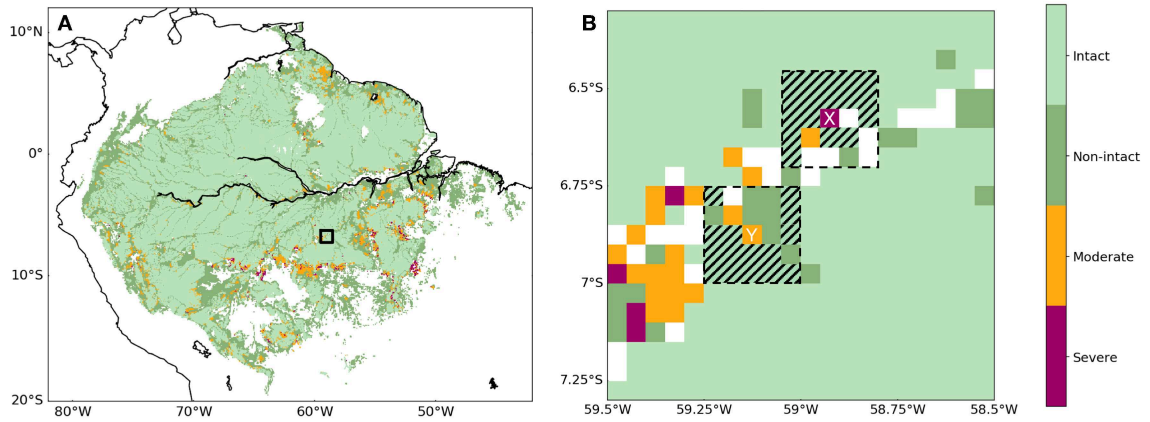

FIGURE 1 | (A) Map showing the distribution of intact forest (pale green), non-intact forest (sage green), moderately deforested (orange), and severely deforested (magenta) pixels across the Amazon evergreen broadleaf forest biome at 0.05° × 0.05° resolution. The black box indicates the region shown in **(B)**. **(B)** Illustration of the moving-window analysis used in this study. Each pixel in each disturbance category (non-intact, moderate, and severe) was placed at the center of a 5 × 5-pixel grid box. For the biophysical variable of interest, change over the central pixel (e.g., the "severe deforestation" pixel marked "X," or the "moderate deforestation" pixel marked "Y"), was compared with the mean change over surrounding intact forest (hatched pixels).

estimating ET (Priestley and Taylor, 1972). GLS-ET and GLEAM were analysed at 0.25° resolution and results are shown in the Supplementary Material (**Figures S2** and **S3**).

T data were taken from the monthly 0.05° × 0.05° C6 Terra MODIS (MOD11) land surface T product (Wan, 2014). The Terra satellite has a local daytime overpass time of 10:30 a.m. We used the MOD11 Terra product because of the longer time record compared to the MYD11 Aqua satellite product (data available from 2000 vs. 2002 for Terra and Aqua, respectively). Repeating the analysis using the Aqua product yielded similar results (**Figure S4**). The 0.05°-resolution Climate Hazards Group InfraRed Precipitation with Station data (CHIRPS) dataset, which merges spaceborne and ground-based measurements to estimate P (Funk et al., 2015), was also downloaded. CHIRPS is based on the Tropical Rainfall Measuring Mission (TRMM) Multi-Satellite Precipitation Analysis (TMPA) version 7 product (Huffman et al., 2007), which was used to calibrate a longer timeseries of thermal infrared observations of cold cloud duration to estimate P from 1981–present. In addition to CHIRPS, 3-h TRMM P data were retrieved from the 3B42 version 7 product, in order to test the diurnal P response to deforestation. High-resolution LAI, ET, T, and P data were regridded to 0.25° using an area-weighted regridding scheme (Python package Iris: https://scitools.org.uk/iris/docs/latest/index.html) to test the influence of spatial scale on our results. Finally, topography data from the Global Land One-km Base Elevation Project (GLOBE) (Hastings and Dunbar, 1998) were resampled to 0.05° to match the climate datasets.

Statistical Analysis

For each biophysical variable (LAI, ET, T, and P), multi-year composites were created by finding the annual mean across the first three years of the analysis period (2001–2003) and across the last three years (2011–2013). Change (Δ) in each variable was then determined by differencing the 2001–2003 composite from the 2011–2013 composite. This approach removed some of the influence of interannual climate variability from the datasets and was therefore expected to make the Δ estimates more robust. Maps showing the mean annual change (Δ_{annual}) over the Amazon for each variable are presented in the Supplementary Material (**Figure S5**). In addition, deforestation responses were

TABLE 2 | Details of the remote sensing observations used in this study.

Variable	Product	Original resolution (°)	References
Leaf area index (LAI)	MODIS GLASS01B01	0.05	Liang et al., 2014
Evapotranspiration (ET)	MODIS MOD16	0.05	Mu et al., 2007 Mu et al., 2011
	Global Land Surface ET	*0.08*	Zhang et al., 2010
	GLEAM v3.2a	*0.25*	Miralles et al., 2011 Martens et al., 2017
Land surface temperature (T)	MODIS MOD11	0.05	Wan, 2014
	MODIS MYD11	*0.05*	Wan, 2014
Precipitation (P)	CHIRPS	0.05	Funk et al., 2015
	TRMM 3B42	*0.25*	Huffman et al., 2007

Results from datasets in italics are presented in the supplementary information.

evaluated at the monthly timescale by differencing the seasonal climatologies for 2011–2013 and 2001–2003. For P data only, the annual and monthly-scale analyses were repeated using data from the southern (5–20°S) and northern (5°S—10°N) regions of the Amazon separately, to account for spatial variation in precipitation seasonality. Changes in the mean diurnal P cycle were also computed, using the same multi-year composites, also analyzing data from the south and north Amazon separately. Finally, to compare the climate impacts of deforestation between the wet and dry seasons, annual mean Δ values for all variables were determined using the three wettest and three driest months in each year, calculated on a per pixel basis using seasonal P data from CHIRPS (Δ_{wet} and Δ_{dry}).

As can be seen in **Figure 1A**, forests that lost their "intact" classification between 2001 and 2013 are not randomly distributed in space, but show spatial clustering, particularly along the southern margins of the Amazon. This tendency for nearby pixels to have more similar characteristics than distant pixels is known as positive spatial autocorrelation (SAC). In order to relate the biophysical changes detectable from remote sensing to changes in forest cover in a robust way, SAC must be taken into consideration. To remove the influence of SAC, we used a moving-window analysis to compare environmental changes over pixels in each of the disturbance categories with changes observed over nearby IF. For each of the categories (**Table 1**), a 5 × 5-pixel grid box was centered on each pixel in turn, and the change value for that pixel was compared with the mean change over all IF pixels within the grid box (**Figure 1B**). For the 0.05°-resolution analysis, this meant comparing against IF pixels within a radius of approximately 10 km (2 × 0.05° grid cells), while for the 0.25° resolution analysis it meant comparing IF pixels within approximately 50 km (2 × 0.25° grid cells). This meant that pixels in each disturbance group were matched with a set of neighboring IF pixels, ensuring that all comparisons were made between geographically-close impacted and non-impacted forests (see **Table S1** for the number of pixels included in each group). Pixels that had no IF within the grid box to compare against were excluded from the analysis. Mean Δ values of the paired datasets were compared using a Student's *t*-test, to test the statistical significance of any observed differences.

Finally, Δ values for each environmental variable were related to reductions in canopy cover following loss of intact status. For this, the treecover2000 and treecover2013 datasets were used to calculate the fractional tree cover change over the analysis period [(Δtree_cover = (treecover2013–treecover2000)/treecover2000]. For all formerly intact forest pixels that experienced deforestation over the analysis period (i.e., pixels in the "moderate" and "severe" disturbance categories combined), ΔLAI, ΔET, ΔT and ΔP values were binned by Δtree_cover, using a bin width of 2.5%, and discarding bins with fewer than five data points. The analysis was applied to Δ_{annual}, Δ_{wet} and Δ_{dry} values to compare responses across different climatic conditions.

RESULTS

Differences between intact and human-impacted forests were found for three out of the four land-surface and atmospheric variables examined. Annual mean ΔLAI, ΔET, and ΔT showed significant differences from the changes observed over intact forests for all disturbance categories (**Figure 2**), while ΔP showed no significant responses (**Figure 2D**, **Figure S6**). The strongest differences in ΔLAI, ΔET, and ΔT were evident over pixels that saw the most extensive land-cover changes from 2001 to 2013 – those in the "severe" category, where deforestation reduced tree cover to below 70%. Forests that lost their intact status but maintained at least 70% tree cover, and forests that had lost their intact status prior to 2000 (NIF pixels), also showed stronger changes in LAI, ET, and T compared with forests that remained intact. Biophysical responses across pixels in these two categories were of a similar magnitude, consistent with tree cover reductions of approximately 5% in each case (**Table 1**).

LAI, ET, and T showed clear response gradients with increasing forest disturbance (**Figures 2**, **3**). Forest pixels in all categories showed absolute declines in LAI, including forests classified as intact in 2013 (**Figure 2A**). Relative ΔLAI values were all negative, and reduced progressively with increasing forest disturbance (**Figure 2B**). The observed pattern of LAI reductions was consistent with our independently-defined disturbance categories (**Table 1**), providing verification that they represented a true impact gradient. NIF pixels showed the

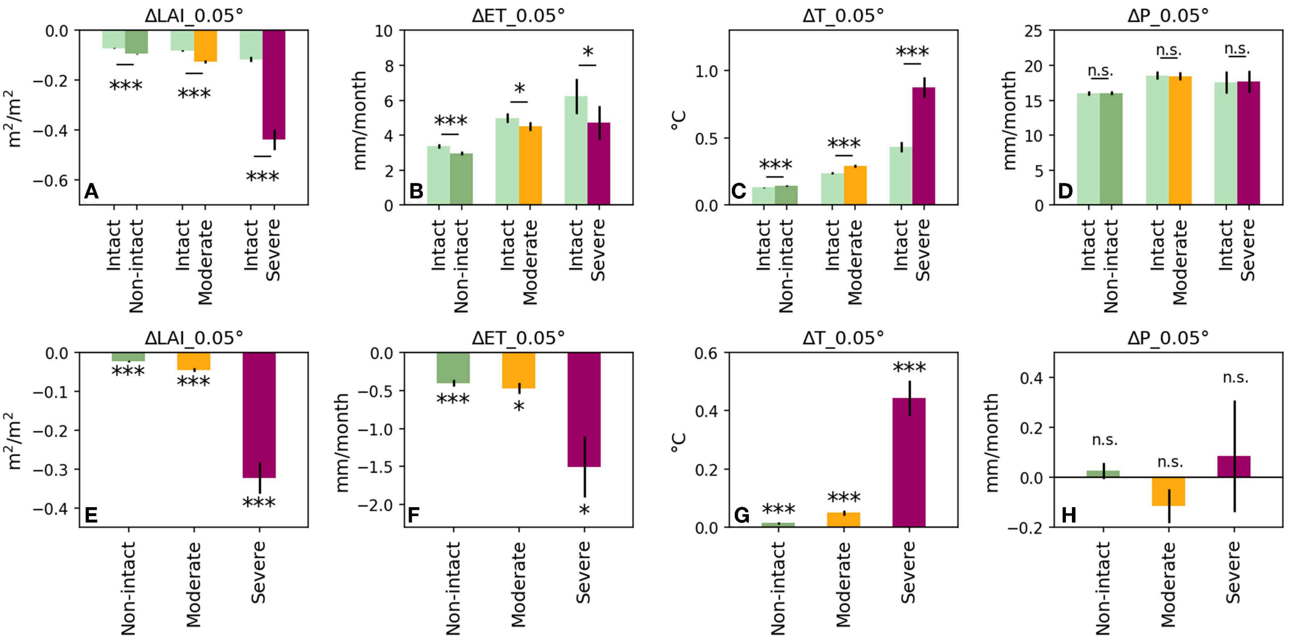

FIGURE 2 | (A–D) Absolute changes in annual mean 0.05° remotely-sensed leaf area index **(A)**, evapotranspiration **(B)**, daytime land surface temperature **(C)**, and precipitation **(D)**, averaged over pixels in each disturbance category and the corresponding neighboring intact forest (see **Figure 1B**), for the period 2001–2013. **(E–H)** As in **A–E**, but with values expressed relative to the changes observed over nearby intact forest. Error bars show the 95% confidence intervals. Asterisks indicate the significance of the differences, calculated using the Student's *t*-test (**p* < 0.05, ****p* < 0.001, n.s. = not significant).

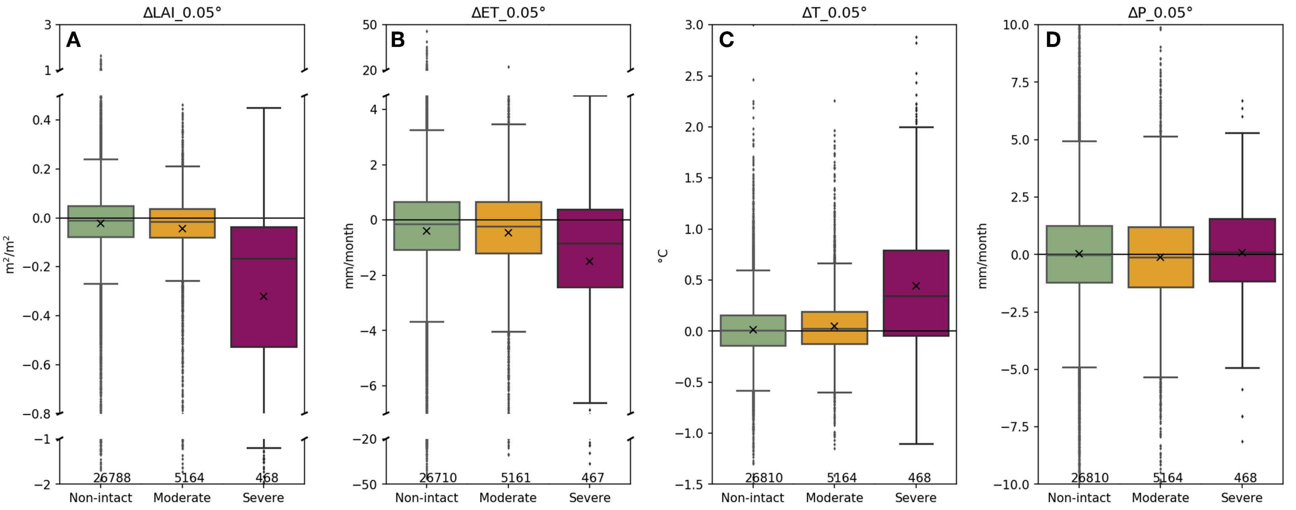

FIGURE 3 | Changes in annual mean 0.05° remotely-sensed leaf area index **(A)**, evapotranspiration **(B)**, daytime land surface temperature **(C)** and precipitation **(D)**, averaged over pixels in each disturbance category, and expressed relative to the changes observed over neighboring intact forest, for the period 2001–2013. The boxes in each panel represent the quartiles of each dataset, mean values are marked with an "x," and values along the lower axis indicate the number of data points.

smallest LAI response as these areas were degraded from intact to non-intact forest prior to the analysis period, whereas pixels in the other two categories lost their intact classification between 2001 and 2013. Even over "severe" deforestation pixels, the size of the LAI response is still relatively modest, with a mean reduction of 0.44 ± 0.04 m^2m^{-2} (mean ± 95% confidence interval [CI]). However, the variance within each category is large, as can be seen in **Figure 3**. It must also be noted that satellite LAI tends to saturate over dense broadleaf canopies (Myneni et al., 2002), and thus reductions in LAI above the saturation threshold may not be detected, which could partly explain the small magnitude of the mean response.

ΔET becomes more negative as forests become more heavily deforested, following the same trend as ΔLAI. The MODIS ET dataset is computed using MODIS LAI as an input, so the two variables cannot be considered fully independent. However, since absolute changes in LAI and ET showed opposite signs (**Figures 2A,B**), we do not think our results were strongly biased by the relationship between the datasets. The maximum relative change in mean annual ET was over intact forests that saw "severe" deforestation (-1.5 ± 0.4 mm month^{-1}, **Figure 2F**). Similar trends were found for all three of the remote sensing ET products analyzed, though not all responses were significant for the lower resolution datasets (**Figure S2**). Nonetheless, the consistency in trends provides a good indication that the relationship between ET and tropical forest disturbance is robust. Absolute change values varied slightly between ET products, with MODIS, and GLS-ET showing ET increases across all forest change categories, while GLEAM showed declines (**Figure 2**, **Figures S2a,b**). These differences highlight the necessity of comparing results across multiple satellite ET products.

Most of the Amazon basin showed a warming trend over the analysis timeframe (**Figure S5c**), though disturbed forests warmed significantly more than neighboring intact forests (**Figures 2C,G**). As with LAI and ET, the magnitude of the ΔT response increased with increasing disturbance. Non-intact forests and forests affected by "moderate" or "severe" deforestation respectively warmed 0.014 ± 0.003, 0.050 ± 0.008, and 0.44 ± 0.06°C more between 2001 and 2013 than nearby forests that remained intact. For regions in the "severe" category, warming was double that observed over surrounding intact forests (**Figure 2C**). The mean elevation of pixels in each degradation category was calculated to test for potential biases that might influence the ΔT results. Pixels in the "non-intact" and "moderate" categories were found to be at significantly lower elevation than IF pixels (NIF $= -33.3 \pm 1.8$ m, $p < 0.001$, and "moderate" $= \pm 3.3$ m, $p < 0.01$). Since warming rates generally increase with altitude (Vuille et al., 2003; Bradley et al., 2006), stronger warming over the lower elevation forests could mean that elevational differences are masking some of the effect of disturbance on ΔT in these two categories. Although, since the differences that were observed were <50 m, and no significant differences were observed for "severe" deforestation areas, elevation is unlikely to have had a substantial impact on the findings presented here.

We tested the sensitivity of our analysis to the spatial resolution and to satellite overpass time. Repeating our analysis at a coarser resolution of 0.25° yielded similar results (**Figure S7**), with disturbed forests warming significantly more than respective nearby intact forests ($p < 0.001$). Relative change values were higher, since the 5×5 grid box used to pair degraded and intact forest pixels covered a larger area (approximately 125×125 km), and thus T values were compared across larger distances. The reductions in LAI and ET with increasing disturbance showed similar trends to those observed at 0.05° (**Figures S7a,b**), though for the 0.25° ET analysis responses were not statistically significant. Mean annual P showed no response to forest disturbance at either resolution (**Figure 2D**, **Figure S7d**).

We repeated our analysis with MYD11 T data from Aqua, which has a local daytime crossing time of 1:30 p.m. compared to 10:30 a.m. for Terra. Consistently, we found more warming over pixels in all disturbance categories compared to IF (**Figure S4**), with the strongest mean T response over "severe" deforestation pixels (0.55 ± 0.05°C). This Δ value is higher than that for MOD11 (0.44 ± 0.06°C), despite a slightly shorter data record for Aqua (MYD11 Δ values were calculated from 2003 to 2013), suggesting the midday warming response is stronger than that in the morning. Variation in the diurnal T response to deforestation was also tested using night-time T data from the Terra and Aqua satellites, which have local evening overpass times of 10:30 p.m. and 1:30 a.m. respectively. Both datasets showed a modest night-time cooling response over regions where intact forest was severely deforested (-0.1 ± 0.03°C for MOD11 and -0.07 ± 0.03°C for MYD11, **Figure S8**).

Seasonal variations in environmental response to disturbance were evaluated. ΔLAI, ΔET, and ΔT showed a clear seasonal signal in relative differences between intact and disturbed forests (**Figure 4**). Seasonality increased with increasing forest disturbance, with "severe" deforestation pixels showing the highest intra-annual variability. Differences were greatest toward the end of the Amazon dry season and lower during the wetter months. In August and September, heavily disturbed forests warmed by as much as 0.75 ± 0.1°C more than nearby intact forests (**Figure 4C**). Meanwhile, P responses to deforestation, which were evaluated over the northern and southern Amazon separately due to spatial differences in P seasonality, showed limited monthly variability (**Figure S9**). Furthermore, the differences between the forest disturbance categories were much less distinct for ΔP than for the other variables analyzed. Changes in the diurnal P cycle were also examined, though no clear responses to forest degradation were detected (**Figures S10, S11**).

Finally, climate responses following loss of intact status were related to fractional canopy-cover loss. ΔLAI, ΔET, and ΔT were roughly proportional to the reduction in tree cover, while ΔP showed no relationship with colocalized canopy cover reductions (**Figure 5**). LAI, ET, and T showed small responses to disturbance where canopy-cover changes were small, and progressively larger responses with increasing canopy loss. Stronger responses were observed during dry months and weaker responses during wet months, in line with the monthly-scale analysis (**Figure 4**). Pixels where tree cover declined by more than 60% showed up to 1.5°C more warming in the driest three months of the year (**Figure 5c**). This result highlights the need to limit canopy destruction for tropical forests to be able to buffer the impacts of climate change.

DISCUSSION

The aim of this research was to quantify the climatic value of intact tropical forest in the Amazon. Following several recent studies that used satellite data to examine the biophysical impacts of deforestation (e.g., Alkama and Cescatti, 2016; Li et al.,

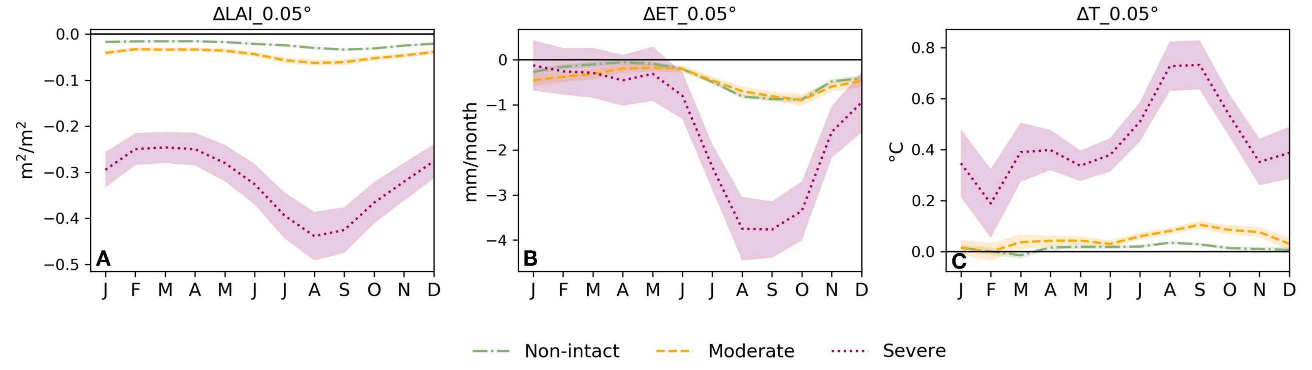

FIGURE 4 | Monthly changes in 0.05° remotely-sensed leaf area index **(A)**, evapotranspiration **(B)**, and daytime land surface temperature **(C)**, averaged over pixels in each disturbance category, and expressed relative to the changes observed over neighboring intact forest, for the period 2001–2013. Shading shows the 95% confidence intervals.

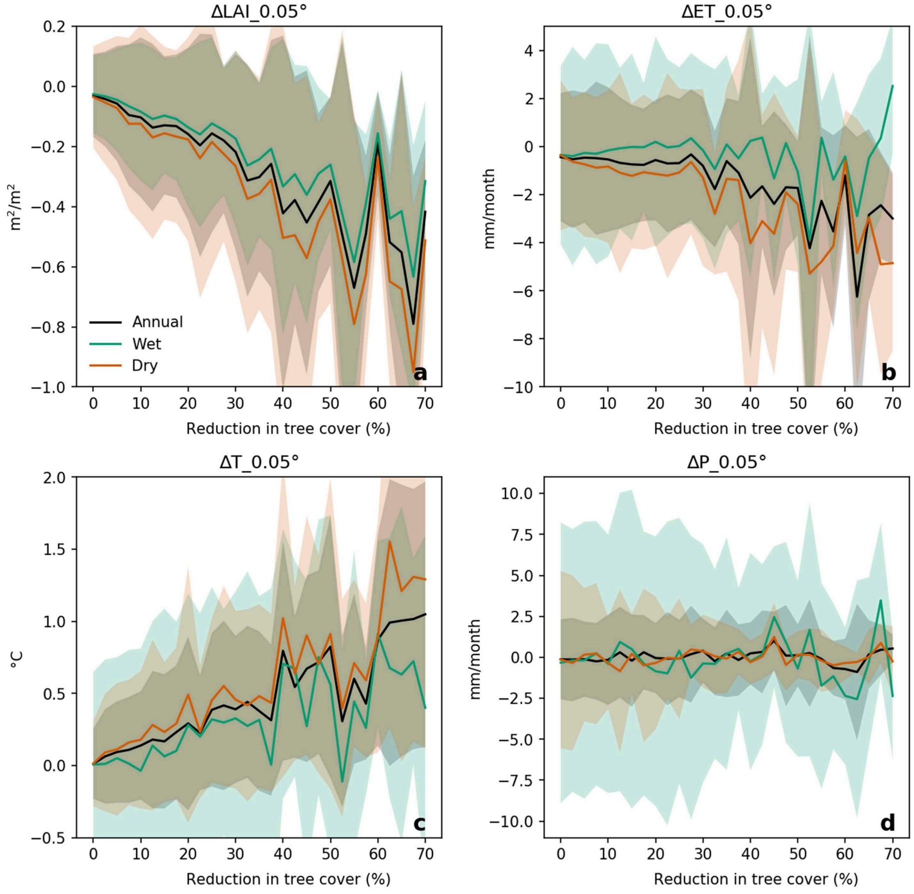

FIGURE 5 | Changes in annual mean, wet season (data from wettest 3 months, calculated per pixel) and dry season (driest 3 months, calculated per pixel) 0.05° remotely-sensed leaf area index **(a)**, evapotranspiration **(b)**, daytime land surface temperature **(c)**, and precipitation **(d)**, in response to reduction in tree cover. Data come from all forest pixels that lost their intact status between 2000 and 2013. Values are expressed relative to the changes observed over neighboring intact forest, for the period 2001–2013.

2016; Schultz et al., 2017), our analysis focused on detecting the subtler changes that occur when tropical forest transitions from an intact state to a non-intact state. To achieve this, we used remote sensing observations to evaluate the environmental consequences of progressive forest disturbance over a large spatial scale.

The IFL product classifies intact forests as areas with no remotely-detectable signs of human activity (Potapov et al., 2017). This definition could mean areas of forest with selective logging or sub-canopy disturbance could potentially be misclassified as intact. In comparisons between intact and disturbed forest, overestimation of intactness may have led to a slight underestimation in the biophysical responses to disturbance shown here (**Figures 2**, **3**). However, given that climate impacts were small when declines in tree cover were close to zero (**Figure 5**), potential overestimation of IFLs is unlikely to have substantially influenced our results. Meanwhile, where canopy loss did occur, such as the small ($<5\%$) decreases over the non-intact and "moderate" disturbance categories (**Table 1**), ET and T showed significant responses relative to nearby intact forest (**Figure 2**). This is consistent with work showing that relatively subtle disturbance rates (5–10% canopy reduction) can result in remotely detectable changes in Amazon forest functioning (Koltunov et al., 2009). Another study, based on flux tower measurements, reported reductions in carbon, water and energy exchange that were directly proportional to canopy loss following reduced-impact logging of an old-growth Amazon forest, though these effects were found to be only transient (Miller et al., 2011). Overall, the results presented here demonstrate that the climate benefits provided by intact tropical forests are inherently related to the intactness of canopy cover, suggesting the IFL methodology provides an adequate method of classifying intactness from a climate perspective.

Our results revealed distinct gradients in environmental change with increasing forest disturbance. As deforestation increased, LAI and ET both showed declines relative to neighboring intact forest (**Figures 2**, **3**, **Table 1**). These results are consistent with each other, since ecosystem ET has previously been shown to scale with LAI (Zhang et al., 2016), and there were no significant P responses that might have modulated the ET response (**Figures 2D,H**). Tropical broadleaf forests have some of the highest LAI of all land cover types (Bruijnzeel et al., 2011), with values up to five times higher than measured over crops or pastures (Gash and Nobre, 1997; Zhu et al., 2013; Yan et al., 2016). The fall in LAI accompanying loss of intact status reduces the efficiency of ET, since there is a smaller surface area for transpiration, or for rainfall interception and subsequent evaporation (Spracklen et al., 2018). In addition, the removal of deep-rooted forest trees stems the flow of deep soil water to the atmosphere, further contributing to ET reductions (Von Randow et al., 2004; Davin and De Noblet-Ducoudré, 2010). Indeed, declines in average root depth and thus ET were thought to explain why even low levels of selective logging resulted in seasonal reductions in greenness over forests in Brazil (Koltunov et al., 2009). The results presented here confirm that even relatively minor disturbance can impact forest hydrological functioning.

The increase in surface ΔT with increasing disturbance is consistent with the declines in ΔLAI and ΔET (**Figure 2**). Both modeling (Davin and De Noblet-Ducoudré, 2010), and observational (Zhang et al., 2014; Silvério et al., 2015; Alkama and Cescatti, 2016; Li et al., 2016) studies agree that although the T response to deforestation varies with latitude due to variable influences on the surface energy budget (Duveiller et al., 2018), in the tropics deforestation leads to a net daytime warming. This is due to a combination of reduced ET efficiency and lower surface roughness. Lower ET reduces latent heat fluxes, while a smoother surface inhibits the turbulent transfer of energy from the land to the atmosphere, both of which result in stronger warming at the land surface (Davin and De Noblet-Ducoudré, 2010; Li et al., 2016). This contrasts with the T response to deforestation at higher latitudes, where the increase in albedo following forest clearance leads to a net cooling effect (Li et al., 2016; Schultz et al., 2017). Our estimate of the surface warming due to Amazon deforestation (0.44°C from 2001 to 2013, which equates to $0.34^{\circ}\mathrm{C}$ decade^{-1}) is based on simple differencing of multi-year T composites, but is comparable with that estimated by Li et al. (2016), who used a regression approach to calculate pantropical T trends over a similar timeframe ($0.28^{\circ}\mathrm{C}$ decade^{-1} for 2003–2013). The weak night-time cooling also observed over deforested areas in this study (e.g., $-0.1 \pm 0.03^{\circ}\mathrm{C}$ for MOD11, **Figure S8**) is consistent with previous work showing deforestation causes a small negative night-time T response in the tropics, and a stronger negative night-time T response at higher latitudes (Schultz et al., 2017). The cooling is due to a reduction in forest-generated turbulence, which brings warmer air to the surface at night, and the lower thermal storage capacity of open areas compared with forests. Finally, this study only considered local surface warming, though a recent modeling study showed that the non-local cooling impacts of deforestation caused by changes in albedo and large-scale circulation could dominate the T response at the global scale (Winckler et al., 2019).

Previous work has highlighted the climatic resilience of intact forest (Huete et al., 2006; Malhi et al., 2008), and the results presented here provide further evidence of this. Non-intact forests warmed 11% more than neighboring intact forest (0.014°C from 2001 to 2003; **Figure 2G**), which could have implications for drought-sensitive species at the limit of their biogeographic range (Esquivel-Muelbert et al., 2017). The climate impacts of deforestation could be particularly consequential during periods of prolonged drying, such as occur during an El Niño. It should be noted that land surface T, as used in this study, may be up to 50% more sensitive to changes in forest cover than air T (Alkama and Cescatti, 2016). Therefore, perceived T changes in response to disturbance may be slightly lower than those shown in **Figure 2**. Radiometric surface T can be measured remotely by satellites, while air T products are based on ground-based station measurements that may not be available over some regions of remote tropical forest (e.g., Heft-Neal et al., 2017), and are thus unlikely to co-locate with areas of forest loss. In a recent study, Winckler et al. (2019) reviewed the differing responses of these two T metrics to deforestation in climate models. They concluded that surface T is particularly important for understanding surface energy budgets and thus land-atmosphere interactions, while 2–m air temperature might have greater ecological relevance. Overall, the results shown here emphasize that non-intact forests warm more, and thus might be less able to buffer the effects of climate change, compared to forests that have been unimpacted by anthropogenic disturbance.

In this study, we identified forests as areas within the MODIS evergreen broadleaf forest classification with tree canopy cover above a threshold of 70%. Following this, we distinguished between areas of "moderate" deforestation, which experienced tree losses and LAI declines but where canopy cover remained above 70%, and areas of "severe" deforestation, where tree removal resulted in canopy cover declining below 70%. Much lower canopy thresholds have been used to define forests, such as the much-criticized United Nations Framework Convention on Climate Change definition, which specified a tree cover threshold of just 10–30% (UNFCCC, 2002; Sasaki and Putz, 2009; Putz and Redford, 2010), or the Food and Agricultural Organization threshold of 40% tree cover for closed canopy forests (FAO, 2001). However, the Amazon intact forest pixels in this study had a mean tree cover of more than 97% (**Table 1**), thus a higher canopy threshold was deemed appropriate. Lowering (raising) the threshold effectively raises (lowers) the amount of deforestation required before a pixel is considered "deforested," thus giving a stronger (weaker) warming response. However, in general our results were shown to be robust to threshold variation (**Figure S1**).

We found conversion of intact forest and increasing forest loss had no discernible impact on annual mean P at the local scale across Amazonia (**Figures 2–4**), and little effect on seasonal or diurnal P cycles over the northern or southern Amazon (**Figures S9–S11**). Previous studies, focusing on deforestation in Rondônia in the southern Amazon, found forest removal resulted in local increases in rainfall and a possible shift toward more afternoon convection (Negri et al., 2004), or a redistribution of rainfall in space (Khanna et al., 2017). Deforestation may reduce downwind rainfall through reductions in ET and reduced atmospheric moisture transport (Spracklen et al., 2012). Modeling studies also suggest that regional-scale land-use change will reduce rainfall at the regional scale (Spracklen and Garcia-Carreras, 2015; Alves et al., 2017). However, such remote impacts are not easily evaluated through an examination of co-located land-use and climate changes, and any spatial offset in the P impacts of deforestation wouldn't be detected through the methodology applied here. Further work should focus on evaluating P responses to disturbance at different spatial scales, and comparing impacts across the tropics.

Finally, seasonal variations in ΔLAI, ΔET, and ΔT were shown to increase along the degradation gradient (**Figure 4**), with the most pronounced differences at the end of the dry season. Responses to canopy cover change were also enhanced during the driest part of the year, with deforestation causing warming of up to 1.5°C over areas with high tree cover loss (**Figure 5c**). Only the deepest-rooted trees can maintain ET during the dry season, as they can access deep soil water that remains unavailable to shorter-rooted pasture vegetation (Von Randow et al., 2004; Davin and De Noblet-Ducoudré, 2010). It follows, therefore, that removal of trees causes the strongest changes at the end of the dry season, when soil water would be at its most depleted. It has been suggested that ET fluxes at the end of the dry season may play a role in triggering the onset of the wet season, through increasing the humidity and buoyancy of air, and thus making conditions more favorable for atmospheric convection (Fu and Li, 2004; Myneni et al., 2007; Wright et al., 2017). Deforestation disrupts this process, with reduction in dry season ET possibly contributing to an observed lengthening of the Amazon dry season over recent decades, as has been suggested from observational (Fu et al., 2013) and modeling (Alves et al., 2017) studies. Increased temperatures have also been linked to greater fire occurrence in the Amazon (Aragão et al., 2018; Lima et al., 2018), making degraded forests more susceptible to dry season burning. Altogether, the results presented here indicate that deforestation disrupts normal forest functioning, particularly during the dry season when vegetation is already at its most vulnerable.

SUMMARY

In this study, we used forest change datasets and remote sensing observations to evaluate the climatic consequences of disturbing intact Amazon forests. We found a clear signal of stronger T increases over more disturbed forests, corresponding to reductions in LAI and ET, while mean annual P showed no significant response to deforestation at the scale of our analysis. Deforestation of intact forests to below 70% tree cover was shown to have caused 0.44°C of annual warming between 2001 and 2013. Differences between intact and disturbed forests were most pronounced during the driest part of the year, when T increases of up to 1.5°C were observed. The climatic stability of intact tropical forests was closely related to preservation of tree coverage, highlighting the importance of minimizing canopy loss to limit changes in forest-climate interactions. Overall, our results illustrate the climate benefits provided by intact forests, strengthening the argument that intact forests are a vital component of the Amazon climate system and should be a conservation priority.

AUTHOR CONTRIBUTIONS

JB and DS were involved in designing the study, shaping the research, and discussing and interpreting results. JB performed the analysis and wrote the manuscript with input from DS.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2019.00047/full#supplementary-material

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Combining Contemporary and Paleoecological Perspectives for Estimating Forest Resilience

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In the face of dramatic climate change and human pressure acting on remaining forest areas across tropical, temperate and boreal biomes, there has emerged a coordinated effort to identify and protect forests that are currently considered "intact". These forests are hypothesized to be more resilient to future abiotic perturbations than fragmented or degraded forests, and therefore, will provide more reliable carbon storage and/or biodiversity services into an uncertain future. Research in the fields of contemporary and paleoecology can offer valuable insights to enhance our ability to assess resilience of forests and whether these would be comparable across forest biomes. Contemporary ecological monitoring has been able to capture processes acting over the short-to-medium term, while paleoecological methods allow us to derive insights of the long-term processes affecting forest dynamics. Recent efforts to both identify intact forests, based on area definitions, and assess vegetation climate sensitivity globally have relied on satellite imagery analysis for the time period 2000–2013. In this paper, we compare these published datasets and do find that on average intact forests in boreal and tropical biomes are less sensitive to temperature and water availability, respectively; however, the patterns are less clear within biomes (e.g., across continents). By taking a longer perspective, through paleoecology, we present several studies that show a range of forest responses to past climatic and human disturbance, suggesting that short-term trends may not be reliable predictors of long-term resilience. We highlight that few contemporary and paleoecology studies have considered forest area when assessing resilience and those that have did find that smaller forest areas exhibited greater dynamism in species composition, which could be a proxy for declining resilience. Climatic conditions in the Anthropocene will be pushing forest systems across biomes into novel climates very rapidly and with current knowledge it is difficult to predict how forests will react in the immediate term, which is the most relevant timeframe for global efforts to reduce carbon emissions.

Keywords: intact forest landscapes, resilience, tropical forest, boreal forest, paleoecology, climate sensitivity

INTRODUCTION

Intact forests (i.e., that have not experienced large-scale anthropogenic disturbance) have been highlighted as being particularly valuable for conservation due to a number of unique attributes and services, such as climate change mitigation, local to regional weather regulation, invaluable biodiversity habitat, clean water provision, support of dependent indigenous cultures as well as wider benefits for human health (Watson et al., 2018). Further, particularly large, contiguous areas of intact ecosystems are posited to be more resilient to changing climate conditions due to their harboring species with higher functional diversity, and therefore, redundancy. A larger, contiguous area allows for greater species dispersal potential as well as greater genetic diversity within extant species (Thompson et al., 2009; Baho et al., 2017). There is already considerable literature showing the negative effects of even moderate levels of disturbance on forest functioning and biodiversity (Gibson et al., 2011; Barlow et al., 2016; Betts et al., 2017), particularly reduced carbon sequestration and loss of species' habitat due to increases in forest edges (Haddad et al., 2015; Qie et al., 2017). At the same time, the impact of disturbance on forest resilience, particularly over larger time scales such as centuries and millennia, is less clear (see Froyd and Willis, 2008; Cole et al., 2014). For example, are there particular types of disturbance that might make a forest ecosystem more resilient over time and is the impact of early Neolithic cultures relevant for the designation of intact forest areas today (Barlow et al., 2012; Willis et al., 2018)? The overall aim of this paper is to discuss and provide a selection of spatial and temporal metrics to inform efforts to assess forest resilience. In particular, we will discuss these methodologies in the context of the intact forest landscape (IFL) metric (Potapov et al., 2017) to explore: (i) how are intact forests responding to disturbance and climate change, (ii) is it possible to distinguish natural variability of a forest ecosystem from increasing variability due to reduced resilience, (iii) are there common mechanisms underpinning resilience across biomes, and (iv) do larger forest patch areas confer resilience?

With increasing anthropogenic pressure, better understanding the dynamics of intact forests is necessary for human development to remain within planetary boundaries (Steffen et al., 2018). Current efforts to identify forest without evidence of contemporary disturbance and that are sufficiently large to maintain the above listed services have relied on remote sensing methods (Potapov et al., 2017). The IFL metric has identified intact forests across all terrestrial biomes (i.e., tropical, temperate, and boreal ecosystems) using a minimum area definition of 500 km^2 with a minimum width of 10 km and a minimum corridor width of 2 km, which have not shown any sign of human disturbance since 2000 (Potapov et al., 2017). However, these systems have historically experienced very different levels of human disturbance as well as evolved under very different natural disturbance regimes (Thompson et al., 2009). In theory, intactness is considered to be a core aspect of resilience (Parrish et al., 2003), whereby current conditions can be compared to historical baselines to assess the scale of past disturbance or level of "ecological integrity" (see section on "Baselines"). In practice, the assumption that the same area-based definition of intactness would necessarily correlate with resilience across all forests should be examined. Outlining clear baselines for initial anthropogenic disturbance have proved to be challenging (e.g., Nogué et al., 2017). Paleoecological records have already provided evidence of a long presence of human impacts on forest around the world. For example, evidence of agricultural activity has been dated in New Guinea to 7,000 years ago (e.g., Willis and Birks, 2006) and more examples of early anthropogenic impacts have been found in Amazonia (e.g., McMichael et al., 2012), lowland Central Africa (Tovar et al., 2014) and the Canary Islands (de Nascimento et al., 2009). Therefore, the integration of spatial and temporal methodologies is essential to advance our understanding of the resilience of intact forests.

Competing Frameworks for Resilience

Defining forest resilience has its own challenges. First, it is necessary to decide whether resilience is considered to be a return to an equilibrium state (e.g., engineering resilience) or as a dynamic system that maintains certain functions following a disturbance (e.g., ecological resilience) (Holling, 1973). Carpenter et al. (2001) posited the question "resilience of what, to what?" Are intact forest areas largely valued for their carbon storage and sequestration services, which are supported by highly diverse plant and animal communities, or are they primarily more reliable areas of habitat for endangered and rare species, including refugia for poorly dispersed species, that have the added benefit of being a carbon storage facility? The distinction may seem academic, but the metrics for assessing forest resilience in either scenario could be quite different as well as, potentially, policy approaches for achieving each outcome (Newton, 2016). Existing theory to assess resilience suggest a variety of metrics for predicting whether conditions are approaching a tipping point, and by extension, a likely shift in regime. This requires careful consideration of the temporal scale of analysis, which some have argued should be based on the life-cycle of the slowest relevant variable (e.g., at the century-scale for capturing forest dynamics) (Folke, 2006). However, this shift in temporal scale can lead to a mismatch between the extent of our ecological knowledge and current management policies (Willis et al., 2005).

Assuming a stable state theory, Baho et al. (2017) developed a quantitative framework of resilience, consisting of quantifying measures of resistance, persistence, variability, and recovery that can be estimated using ecosystem-level measures of structural and functional attributes following a disturbance. Resistance relates to the amount of change observed in a chosen metric due to a disturbance. Persistence refers to the length of time species co-exist before going extinct. Variability is expected to be low during a state of stability and increasing as a system approaches a tipping point. While recovery relates to the engineering resilience perspective of returning to a known or desired equilibrium state. Conversely, if considering the resilience of a forest as a dynamic adaptive system, it is unlikely it will "recover" to its original state, but could undergo "renewal" or "regeneration" to a new but similarly functioning system (O'Neill, 1998). Evidence for taking a more complex view of ecosystem resilience relates to the likelihood an ecosystem in a specific location could have multiple-stable states, due to climate-lags in species response rates, which can also exhibit hysteresis or path dependence (Blonder et al., 2017). Finally, there is a spatial element to resilience, which relates to how connectivity, gradients, ecological lags, and asymmetries contribute to or feedback on a system's response to a disturbance (Cumming, 2011; Allen et al., 2016).

Spatial and Temporal Metrics for Assessing Resilience

Several studies have attempted to estimate the resilience of remaining forest areas using a wide range of metrics; although, largely reliant on a stability-based understanding of resilience, and to our knowledge, none considering the total size of forest area. For instance, relative variability in a response variable has been used as a proxy for forest resilience, such as variability in latent heat fluxes from eddy covariance measures as a predictor of drought vulnerability (Anderegg et al., 2018), climate sensitivity of vegetation using spectral time series of moderate-resolution satellite imagery (Seddon et al., 2016), or establishing a historical range of variation (HRV) to describe a "basin of attraction" for comparison with contemporary responses to disturbance (Seidl et al., 2016). Through establishing an HRV, Seidl et al. (2016) reinforce the understanding that with climate change the range of variability, disturbance regime and rates of recovery will change, thereby defining resilience as a dynamic property of an ecosystem that is important to quantify for informing forest management. Trends in ecosystem responses have been used to assess whether a system is approaching a threshold, such as comparing regional trends in minimum water-use efficiency (WUE) during dry and wet years (Ponce-Campos et al., 2013) or tree-ring growth and isotope signatures to assess changes in community-level productivity (Sangüesa-Barreda et al., 2015; van der Sleen et al., 2015; Brienen et al., 2016).

Beyond temporal trends, spatial patterns may also be indicative of an approaching shift to an alternative state whereby spatial correlation as well as spatial variability may increase. Although, this has mostly been applied in dry environments (Dakos et al., 2011). Other approaches have focused on functional and structural measures of communities to estimate underlying dynamics, which may consider overall species diversity (Hisano et al., 2018), functional redundancy in species presence and their relative abundance (Baho et al., 2017), functional trait composition of the dominant species in a community (Bartlett et al., 2019), whether combinations of functional traits in species are supported by high phylogenetic diversity (Díaz et al., 2013), or discontinuities in the distribution of measures (e.g., animal body mass) that are expected to relate to overall ecological health and resource availability (Nash et al., 2014; Angeler et al., 2016). There are a limited number of metrics that incorporate both spatial and temporal perspectives, although the climate sensitivity metric developed by Seddon et al. (2016) does produce a globally consistent decadal estimate, they do not consider neighborhood effects or contiguousness of vegetation.

All of the metrics listed above, at best, estimate the probability of an ecosystem shifting to an alternative regime, such as a shift in species composition or in life-forms (e.g., to grassland or savannah). Considering both the temporal and spatial scale over which these kinds of shifts could occur, it becomes invaluable to consider a longer temporal scale that paleoecological data can provide. Paleoecological datasets such as fossil pollen and charcoal coupled with statistical modeling are already producing important insights about how forest ecosystem processes vary in time and if observable variability is predictive of an ecosystem approaching a threshold. For example, previous studies, based on a metanalysis of over 200 pollen-records (covering ∼20,000 years) have estimated the recovery time between periods of forest cover in the tropics to assess regional forest resilience, offering a binary measure of forest or non-forest (Cole et al., 2014). Other paleoecological resilience metrics have entailed innovative analysis of Holocene pollen, charcoal records, functional traits (e.g., bark thickness, plant height), and also diatoms to explore observable forest responses to past biotic and abiotic drivers (e.g., Seddon et al., 2014; Brussel et al., 2018; van der Sande et al., 2019).

Baselines: Providing Trajectories of Intact Forest to Assess Resilience

The approaches listed above allow the range of observed ecosystem responses to be compared to an ecosystem's ecological history. Ecological history is important for determining the degree of change that has occurred from baseline reference conditions (Willis et al., 2005, 2010; Gillson et al., 2011). Moreover, ecological history has been highlighted as crucial to determine the level of intervention required to restore an ecosystem that has been modified by human impacts to a more "naturally functioning state" (Jackson and Hobbs, 2009). Assessing ecological history was undertaken to inform management of island ecosystems, which included consideration of multiple baselines (Nogué et al., 2017). There are also some examples in the policy literature that have highlighted the importance of identifying baselines. For example, the IUCN's "global standard for the identification of Key Biodiversity Areas" have introduced the concept of ecological integrity (criterion c) (IUCN, 2016), which has been defined as "when [an ecosystem's or species'] dominant ecological characteristics (e.g., elements of composition, structure, function, and ecological processes) occur within their natural ranges of variation and can withstand and recover from most perturbations imposed by natural environmental dynamics or human disruptions" (Parrish et al., 2003, p. 852). This definition essentially combines the concepts of intactness and resilience into one. Operationally, the term involves considering both ecological integrity and intactness of the ecological community, which combined refer to the baseline (or historical benchmark) conditions that support intact species assemblages and ecological processes (IUCN, 2016). Baselines therefore, are relevant to identify in intact forest landscapes. Calder and Shuman (2019) introduced an interesting approach to measure resilience by considering the amount and duration of change from a baseline and the potential to measure the rate of recovery. Using paleoecological datasets from Connecticut and

Colorado (USA) the authors suggested that identifying baselines are important to determine recovery, an intrinsic feature of resilience. Trends in recovery rate can also be considered, whereby the ability of a system to recover following disturbances slows before approaching a critical threshold (Veraart et al., 2011). However, the challenge of identifying the accurate baseline applies to nearly any time period (e.g., millennia to decades) and disturbance (e.g., temperature increase, wildfire, and land-use change) (Hansen et al., 2016).

COMPARISON OF STUDIES AND METRICS FOR MEASURING RESILIENCE IN INTACT FORESTS

While it is clear the question of forest resilience is incredibly complex, locally driven, likely path dependent, and therefore, difficult to assess at a global level; there are international policy prerogatives to prioritize forest areas for conservation that can help us achieve meaningful climate mitigation and adaptation. Hence, there is a societal need to understand the conditions required to allow for the unhindered persistence of forests across biomes as we enter an uncertain climate regime, the Anthropocene (Malhi et al., 2014). Early efforts may be overly simplistic, namely identifying arbitrarily-sized patches of forest globally and hypothesizing that their size and contiguousness necessarily confers a level of resilience (Potapov et al., 2017), but it is an interesting assumption to explore. Fragmentation of previously large patches of forest have likely resulted in higher carbon emissions already (Maxwell et al., accepted) and the processes by which they would be further disturbed are likely to make them more prone to further degradation (Putz and Romero, 2014).

To explore the robustness of the IFL assumption that area confers resilience, we assess published global contemporary and local paleoecological studies across forest biomes for evidence. We were interested whether IFL areas exhibited lower contemporary climate sensitivity than non-intact forest and whether this metric varied by biome and continent. Then we illustrate different metrics for understanding resilience from paleoecological studies across these biomes. Although, the studies chosen were not intended to be exhaustive, they are helpful in informing the range of responses intact forest landscapes have exhibited over paleoecological time to disturbance and how they compare to ecological or engineering resilience approaches for understanding resilience today.

Analysis of Contemporary Datasets

The analysis we present is based on a contemporary measure of climate sensitivity developed by Seddon et al. (2016) partitioned into intact and non-intact forest areas using the intact forest landscapes (IFL) dataset generated by Potapov et al. (2017) and forest cover dataset produced by Hansen et al. (2013). The IFL dataset also uses the Hansen et al. (2013) forest cover dataset to identify contiguous forest areas, as previously described. They have produced a series of analyses, estimating IFL coverage and loss between 2000 and 2013 and 2013–2016. We used the analysis by Seddon et al. (2016) to explore whether there is evidence that the area-based metric for IFLs are less sensitive to climate anomalies, and therefore, potentially more resilient than non-IFL forest areas. Although with the caveat that Seddon et al. (2016) are quantifying "sensitivity" and not resilience directly. Their approach uses Moderate Resolution Imaging Spectroradiometer (MODIS) Enhanced Vegetation Index (EVI) time series from 2000 to 2013 (Solano et al., 2010) and various climate variables to asses "variability," under the assumption that greater variability indicates higher sensitivity, potentially lower resilience, and therefore, a higher probability of crossing a threshold to an alternative state. To assess ecosystem sensitivity to short-term climate variability, they developed a new metric, the vegetation sensitivity index (VSI), which compares the relative variance of vegetation productivity (EVI) with three ecologically important MODIS-derived climate variables (air temperature, water availability and cloud-cover) for the months in which EVI and climate are found to be related. They used an autoregressive (AR1) multiple linear regression approach, taking the three climate variables and 1-month lagged vegetation anomalies to identify areas with strong vegetation-climate coupling. Their global VSI is generated from aggregating the EVI sensitivities to each climate variable, weighted by the coefficients from the linear regression modeling. The VSI provides a useful dataset to explore contemporary responses to recent climate anomalies; although, with a monthly canopy response interval, this metric would not be capturing longer term responses. Also, the resolution of the data is 5 km, which would be aggregating the climate response over several landcovers in more fragmented landscapes. While they were assessing the sensitivity of all vegetation, not specifically forest, they found that boreal forest and the wet tropical forests of South America, Southeast Asia and Western Africa were among the most "sensitive." When they parsed the abiotic drivers, tropical forests were more cloud limited and northern latitudes were more temperature sensitive.

For our comparison we focused on the IFL layers for 2000–2013 as that overlapped with the time period of study for Seddon et al. (2016) and non-intact forest pixels for 2013 from Hansen et al. (2013). The details of our analysis are described in **Supplementary Materials**. We found that across the tropical biome, IFL areas were less sensitive to water availability than non-IFL areas. Southeast Asian (SEA) IFLs were more sensitive than non-IFLs for all climate sensitivity variables (**Figure 1**), which according to Potapov et al. (2017) represented 6% of IFL area in 2000 but experienced an almost 15% reduction in IFL area. We also found that this region has considerably less forest area considered intact than non-intact as depicted in the map and histograms in **Figure 1**. South American (SAM) IFLs exhibited lower sensitivity to water availability and African (AFR) IFLs exhibited lower overall climate sensitivity as well as cloud and water sensitivity than non-IFLs (**Figure 1**). When comparing intact forests within biomes across sub-regions, we found that SEA IFLs were significantly more sensitive than both SAM and AFR IFLs for overall climate sensitivity, water and cloud sensitivity (**Figure S1**). SEA and SAM IFLs were similarly sensitive to temperature and both were more sensitive than IFLs in Africa.

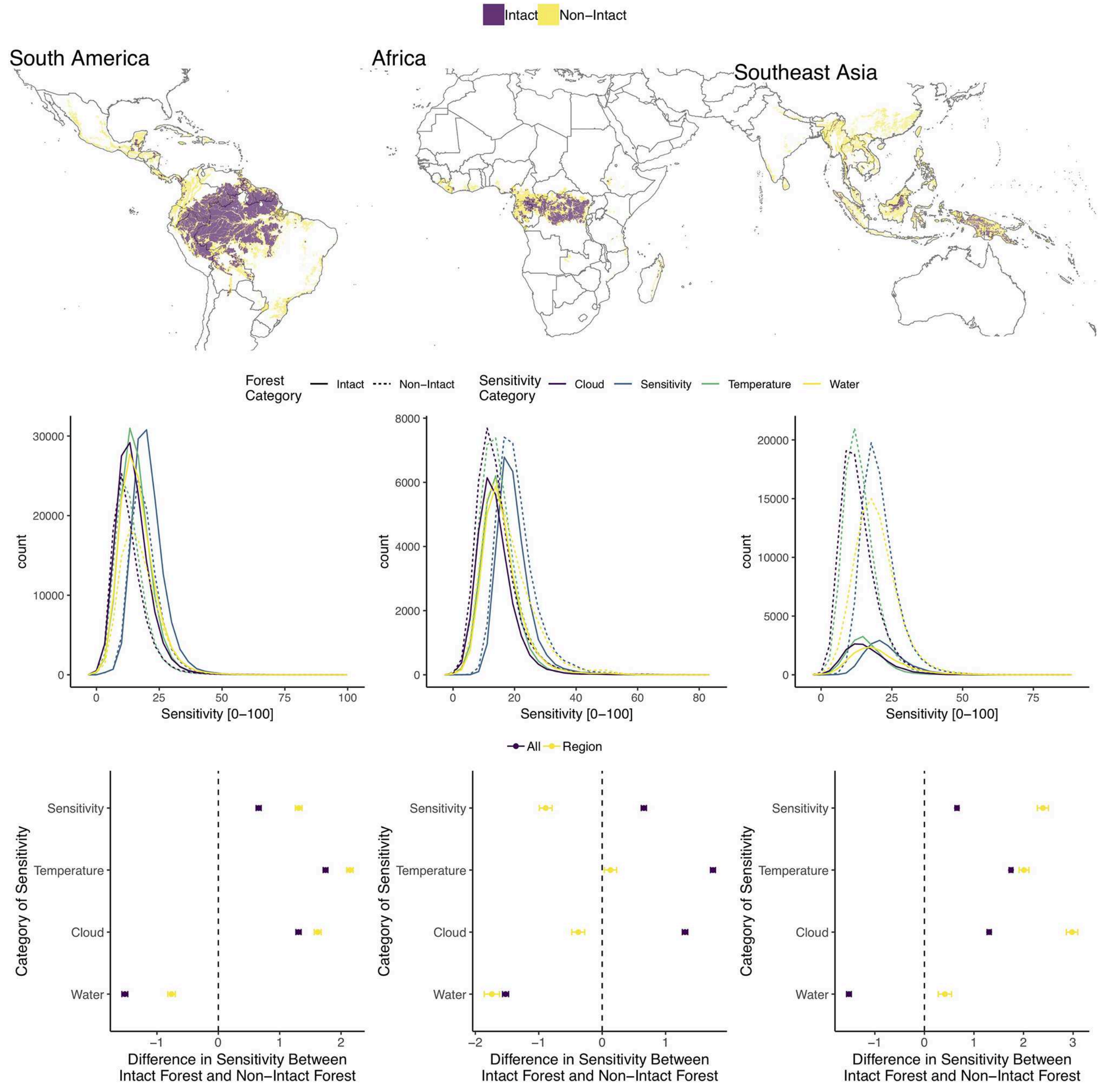

FIGURE 1 | (Top row) Distribution of intact and non-intact pixels for each analyzed continent across the tropics. **(Middle row)** Histograms of four climate sensitivity metrics for intact (solid) and non-intact (dashed) forests for each continent. **(Bottom row)** TukeyHSD values, with confidence intervals, comparing climate sensitivity of intact and non-intact forests for each climate sensitivity metric for all ("All") forest pixels across the tropics and for each continent ("Region"). Negative values indicate intact forest pixels exhibited lower sensitivity for each variable and positive values indicate non-intact forest pixels exhibited lower sensitivity.

Across the boreal biome, IFLs were less sensitive for overall climate and temperature metrics (**Figure 2**). IFLs in Northern European and Asia (NEA) were less sensitive for all climate metrics than non-IFLs, while the opposite was true for North American (NAM) IFLs. However, NAM IFLs were somewhat less sensitive than NEA IFLs for temperature and cloud metrics, while NEA IFLs were less sensitive to temperature (**Figure S1**). Potapov et al. (2017) reported that NAM boreal IFL consisted of 24% of global IFL, suffering a 3.3% loss between 2000 and 2013, while NEA boreal IFLs were only 12% of global IFLs and experienced a loss of 4.4%. When contrasting the area of forest in IFLs and non-IFLs across both continents (**Figure 2**) it is clear that the NEA boreal zone is significantly more fragmented compared to the NAM boreal zone, which exhibits more similar levels of intact

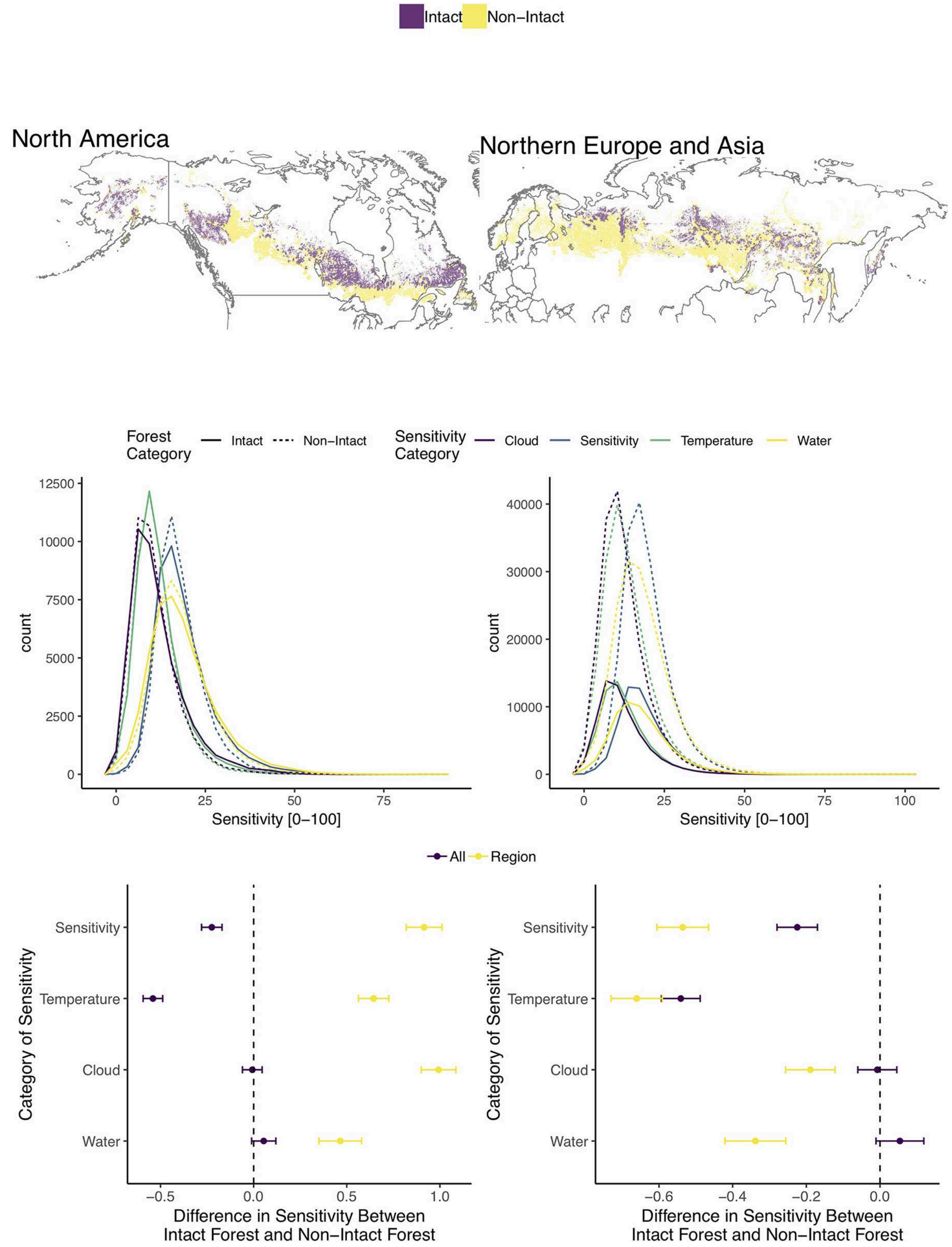

FIGURE 2 | (Top row) Distribution of intact and non-intact pixels for each analyzed continent across the boreal biome. **(Middle row)** Histograms of four climate sensitivity metrics for intact (solid) and non-intact (dashed) forests for each continent. **(Bottom row)** TukeyHSD values, with confidence intervals, comparing climate sensitivity of intact and non-intact forests for each climate sensitivity metric for all ("All") forest pixels across the tropics and for each continent ("Region"). Negative values indicate intact forest pixels exhibited lower sensitivity for each variable and positive values indicate non-intact forest pixels exhibited lower sensitivity.

and non-intact forest area. We performed the same analysis for temperate and southern boreal forests, although across these biomes very small areas of IFL relative to total forest area remain (**Figure S2**). Overall, temperate IFLs were more sensitive than non-IFLs with only NEA IFLs being less sensitive to temperature and Oceania (OCE) IFLs being less sensitive to water (**Figure S2**). Comparisons across biomes are also presented; however the signal was quite complicated.

Identified Paleoecological Studies

Figure 3 presents an overlay of global IFL and non-IFL pixels with the location of several paleoecological studies we discuss as illustrative examples, which are also listed in **Table 1**. These examples were chosen to highlight the complexity and opportunities that paleoecological approaches can provide in terms of measuring resilience in different landscape configurations and forest systems. These studies use a variety of methods: fossil pollen, charcoal, soil erosion and climate proxies, tree rings, and functional traits. The analysis of these long-term datasets involves statistical analysis from population modeling to rates of change. Studies A and G-I, occurred in a currently fragmented agroforestry landscape that revealed the persistence of forest species over the past 6,000 years (Bhagwat et al., 2012; Nogué et al., 2018). Study B implements paleoecological measures of functional traits and how they may be selected for through changes in disturbance (Brussel et al., 2018). Study C combines lake-sediment charcoal record with fire scars on living spruce trees (*Picea*) to assess response of this forest system to increasing human pressure since the gold rush (c. 1902) (Gaglioti et al., 2016). Study D presents a study of *Nothofagus* that revealed a long and stable persistence of this forest system over time (Iglesias et al., 2018). Study E shows a 90,000 year pollen record from an Afromontane site in Cameroon, indicating highly unstable species composition with past climate changes (Lézine et al., 2019). Study F explored the impacts of past human activity on the floristic composition and carbon sequestration of a peatland forest as well as identified "resilience friendly" activities that could effectively conserve and restore this carbon-rich forest system (Hapsari et al., 2018). Finally, study J used population modeling of *Symphonia*, a Madagascan endemic tree, which revealed rapid oscillations in their metric just before a threshold shift in species composition of the community (Virah-Sawmy et al., 2009).

DISCUSSION

How Are Intact Forests Responding Currently?

Increasing concentrations of CO_2 in the atmosphere combined with changes in temperature, are impacting net ecosystem productivity (NEP) and water use efficiency (WUE) of forests, although the direction of the effect varies by biome. For instance, NEP in northern latitudes appear to be increasing with temperature and the tropics are exhibiting greater sensitivity to CO_2 (Fernández-Martínez et al., 2019). There is already contemporary evidence that species composition of forest communities are shifting in response to drying conditions (Fauset et al., 2012) and even with CO_2 fertilization, increases in NEP are in areas that are less water limited (Fernández-Martínez et al., 2019). The carbon sink across the tropical forest biome has been relatively neutral since the 1990s, with sequestration rates roughly equaling emissions from deforestation and degradation (Mitchard, 2018). However, there have been spikes in this signal, where the tropics became a net source of carbon during climate extremes (Liu et al., 2017). Trends in carbon uptake of tropical forests in the Amazon are showing signs of slowing as well as enhanced carbon emissions from slowly decaying necromass, which is modeled to be twice the magnitude of the decline in carbon sequestration (Brienen et al., 2016). In addition, there remains considerable uncertainty around the scale of necromass and its vulnerability to increasing fire incidence (Withey et al., 2018). Trends in carbon uptake can vary within the tropics, whereby forests in Africa are more resource limited and smaller, sub-canopy trees can be responsible for 20% of carbon sequestration even though they may only store 11% of stand biomass (Hubau et al., 2019).

Boreal forests are known to be experiencing warming twice the rate of the global average during the twentieth century (Wolken et al., 2011). However, the impact of temperature increase across its range remains unclear (Frégeau et al., 2015; Girardin et al., 2016). Warming is causing increases in the frequency, size and severity of many natural disturbances, including pest outbreaks that are known boreal forest stressors (Millar and Stephenson, 2015) as well as likely increasing rates of soil respiration (German et al., 2012). Although multi-decadal soil warming experiments suggest that increased respiration of microbes may be short-lived with the dominant impact being enhanced root production (Lim et al., 2019). Increasing temperature has been identified as the most likely factor driving increased mortality across North American forests, which has been outpacing the rate of recruitment over the last few decades (van Mantgem et al., 2009). The hotter, and therefore, drier conditions are believed to be interacting with pathogen and insect incidence to create this "novel forest decline" (Wong and Daniels, 2017). Worryingly, suitable climate zones for the boreal biome have been modeled to be moving to higher latitudes one order of magnitude faster than species are expected to be able to migrate (McKenney et al., 2007).

Unlike tropical or temperate systems, old growth boreal systems are not characterized by tall dense stands in equilibrium. Disturbance is a core aspect of this ecosystem, with fire being the dominant driver followed closely by pest incidence and disease. Fire occurs randomly throughout the landscape independent of stand age resulting in a patchy distribution of forest condition. Therefore, it has been argued that this system would be better understood, and therefore, managed at the landscape-scale, whereby a representative distribution of stand ages are conserved to allow for recovery between disturbance events (Kneeshaw et al., 2018). Evidence seems to be growing that management decisions based on the stand-level could be making boreal regions more susceptible to fire and pest damage regardless of biotic factors (Seidl et al., 2016). Our results suggest IFLs in the boreal biome overall show lower sensitivity to temperature anomalies than non-intact forests,

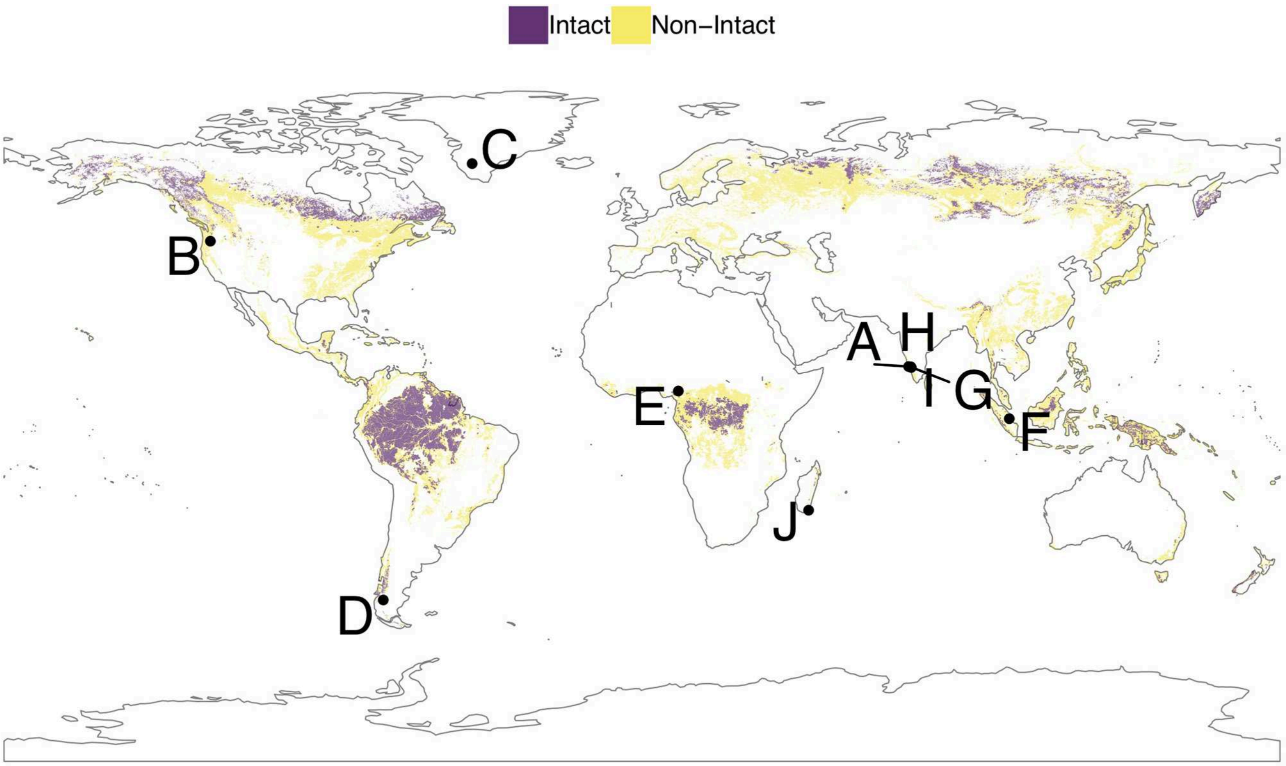

FIGURE 3 | Intact forest landscape (IFL) and non-intact forest pixels with locations of selected paleoecological studies illustrating the range of forest responses to past disturbance. **Table 1** lists the details of each study.

suggesting contiguous forest areas could be more resilient for this biome.

What Does the Paleoecological Record Suggest?

Palaeoecology offers a longer temporal perspective that is important for assessing past forest responses; particularly, being able to assess whether a previous regime shift was driven by a climatological ("extrinsic") or ecological ("intrinsic") event (Williams et al., 2011; Seddon, 2017). Using examples around the world, the aim of this section is to discuss: stability, population, and fragment dynamics as well as forest responses to disturbances.

The paleoecological literature reveals several records that have displayed stability or persistence over time, even with changes in environmental conditions (e.g., Urrego et al., 2013). Therefore, caution needs to be taken when analyzing contemporary changes in variability. Paleoecological methods for detecting stability or variability can rely on the rate of change in a pollen time-series (Iglesias et al., 2018) as well as turnover in pollen composition (e.g., Birks and Birks, 2008). First, in Patagonia, the *Nothofagus* (southern beeches) forest was found to have prevailed relatively unchanged for the past 9,800 years until the twentieth century by calculating the rate of change in pollen records, which was equal to zero (Iglesias et al., 2018) (**Figure 3**, Study D). This stability could be attributed to *Nothofagus*' resistance to environmental change, its ability to rapidly recover or trade-offs in the plasticity within *Nothofagus*' species traits. Stability has also been found in the Afromontane forest in the Eastern Arc Mountains of Tanzania for ∼48,000 years (Finch et al., 2009) as well as in some tepui mountains in Venezuela (Rull, 2005; Nogué et al., 2009). However, we still do not understand the underlying drivers of this dynamic.

In other regions of the world, paleoecological models have found discernible changes in population dynamics that preceded a tipping point. For instance, in Malagasy littoral forest remnants, authors studied the population dynamics of an endemic tree (*Symphonia*) (**Figure 3**, Study J). The results of this case study showed steeper oscillations in the response variance (e.g., species dominance) to a climatic change threshold (Virah-Sawmy et al., 2009), suggesting in this system erratic oscillations provided advance warning of a threshold being reached. At the same time, population models showed that overall, there was coexistence between *Symphonia* and another local species, *Erica*, unless the community was located in a nutrient-rich substrate. In this case, competition seems to have promoted a decline in *Symphonia,* demonstrating that local factors may determine the survival of certain species undergoing abiotic stresses like climate change.

The Western Ghats in India also provides an illustrative example of dynamism in species composition over long-time scales in a fragmented landscape. This region exhibits high levels of forest fragmentation due to heavy pressure to support

TABLE 1 | List of paleoecological studies from intact forests featured in **Figure 1**.

Code	References	Country	Location	Latitude	Longitude	Biome	Forest status	Metric
A	Bhagwat et al., 2012	India	Asia	12.28	75.22	Tropical	Fragmented	Relationship between vegetation cover and drivers of environmental and anthropogenic disturbance. Quantile regressions.
B	Brussel et al., 2018	USA	North America	44.77	−121.78	Boreal	Intact	Time-series of fire-adapted traits Fire frequency.
C	Gaglioti et al., 2016	USA	North America	64.86	−47.93	Boreal	Fragmented	Charcoal analysis preserved in varved lake sediments (annually layered) and fire scars in living trees Local fire return intervals (FRIs) and regional fire activity
D	Iglesias et al., 2018	Chile	South America	−48.20	−73.00	Temperate	Intact	Rate of change
E	Lézine et al., 2019	Cameroon	Africa	5.94	10.24	Tropical	Montane	Pollen % converted to tree or grass dominated biome categories and changing dominance of biomes
F	Hapsari et al., 2018	Indonesia	Asia	−1.24	103.62	Tropical	Peatland	Trends in carbon accumulation rate (CAR) Fire frequency PCA analysis of floristic composition
G	Nogué et al., 2018	India	Asia	12.18	75.82	Tropical	Fragmented	Trajectories of change (generalized mixed models, GAMM)
H	Nogué et al., 2018	India	Asia	12.22	75.79	Tropical	Fragmented	Trajectories of change (GAMM)
I	Nogué et al., 2018	India	Asia	12.05	75.98	Tropical	Fragmented	Trajectories of change (GAMM)
J	Virah-Sawmy et al., 2009	Madagascar	Africa	−24.95	47.00	Tropical	Fragmented	Population modeling

agricultural activities (Giriraj et al., 2010), which is a common reality across tropical forest regions (Karanth and DeFries, 2010). Using paleoecological data obtained from four small forests fragments (∼5 ha) in a coffee (*Coffea arabica*) agroforestry landscape in Karnataka, India, it was possible to reconstruct 7,500 years of vegetation dynamics (**Figure 3**, Studies A and G-I). Taking into account regional climatic changes over this same time period (e.g., monsoon activity) and other environmental variables (e.g., anthropogenic fire, and soil erosion), results suggested that fire was responsible for maintaining low tree cover in the landscape over the past 3,500 years. In addition, it appeared that retaining tree cover in this fragmented landscape, was key to maintaining its ecological resilience to subsequent environmental and anthropogenic disturbance (Bhagwat et al., 2012). In addition, by investigating the dynamics of vegetation (tropical forest, cultivated, grasses, and herbaceous taxa) and environmental variables (biomass burning, canopy closure, and habitat specialist trees) over the past 900 years across four of the Western Ghats' fragments, it was found that agricultural activity had not precipitated a collapse of the Western Ghats forests, but instead had enhanced the dynamism of vegetation within and between forest patches. Furthermore, these results are also relevant for conservation as it suggests that small and informally protected-forest patches (e.g., sacred groves) in human-dominated agricultural landscape might sustain high quality tropical forests, temporally and spatially (Bhagwat et al., 2014; Nogué et al., 2018). Although, this heightened dynamism could indicate lower resilience of these fragments to novel climatic conditions.

Finding general patterns and responses to disturbances (e.g., temperature increase and fire) for the boreal forest in the paleoecological record proved to be challenging. Most of the studies are focused on long-term shifts, and the fire regime data are spatially limited and generally of low resolution. Therefore, we discuss major regional temperature-related changes together with local fire responses. First, paleoecological studies of forest responses to the increase of temperature across the Pleistocene-Holocene boundary (Levesque et al., 1997; Hou et al., 2007) suggest different patterns across the boreal biome worldwide (Shuman et al., 2002a,b; Wolken et al., 2011). For example, in Alaska, spruce (*Picea*) forests have been dominant since the early Holocene; however, during the deglacial period into the early Holocene the woody vegetation was deciduous (e.g., *Betula*, *Salix*, and *Populus*). Second, in addition to changing temperatures, wildfire frequency also seems to control the long-term dynamics of species composition in boreal forests (Carcaillet et al., 2010). However, there is good evidence that in Alaska, climate change drove species composition which in turn drove changes in the fire regime (e.g., Lynch et al., 2002; Higuera et al., 2009). When looking at specific case studies this complexity arises further. Brussel et al. (2018) (**Figure 3**, Study B) found that fire frequency may have driven selection pressure for fire-adapted traits. This finding is consistent with ^{14}C dated and botanically identified charcoal (Frégeau et al., 2015) together with sedimentary sequences (Carcaillet et al., 2010) showing the maintenance of both fire-prone and less fire-prone tree species over time. At a very local scale, Gaglioti et al. (2016) (**Figure 3**, Study C) found that even with a 4-fold increase in regional burning following the arrival of gold miners near to Fairbanks, Alaska, the permafrost and watershed of Ace Lake stayed mainly intact. However, these authors worry that the legacy of this heightened fire activity may make this region more susceptible to megafires in the future as temperatures continue to increase. The dynamics described above may suggest the ability of the boreal biome to maintain its structure and function following fire-related disturbances, which could be interpreted as an overall resilience to changes in fire regimes (Carcaillet et al., 2010; Frégeau et al., 2015). However, Johnstone and Chapin (2006) showed that too many fires might also push the composition from evergreen to deciduous forest in the Yukon region.

Can We Distinguish Natural Variability From Variability Approaching a Tipping Point?

If we consider an engineering approach to resilience, how can we discern the natural variability of a dynamic ecosystem from increasing variability due to its approaching a threshold? The danger of using an equilibrium/stable state model of resilience for a complex adaptive system, like a forest ecosystem, is that management to maintain stability may have the effect of reducing resilience through dampening its natural variability (Holling and Meffe, 1996). Also, without considering a comparable baseline of responses to past disturbance, it is very difficult to establish whether contemporarily observed variation is predicting the approach of a system threshold. Being able to combine the temporal-scale of paleoecological studies with short-term and more spatially explicit contemporary ecological studies, is difficult. For one, from the paleoecological record, it is still challenging to analyse species interactions or how vegetation dynamics may have varied spatially in a study landscape. Therefore, being able to differentiate whether more biodiverse vegetation is necessarily more sensitive to recent climate changes (e.g., Willis et al., 2018), or if that “sensitivity” is actually a function of vegetation dynamics within the normal historical range of those ecosystems, remains a challenge.

Southeast Asia is home to more than half of tropical peatland area and 77% of tropical peat volume, storing 68.5 Gt of carbon (Page et al., 2011). Deforestation since 1990 on Southeast Asian peatlands has been dramatic, with only 28% of original peat swamp forest cover remaining (Miettinen et al., 2012). Deforested peatland areas have also been more prone to fire incidence, worsening carbon emissions as well as lower carbon accumulation rates (CAR), which might suggest a shift in regime. A paleoecological study by Hapsari et al. (2018) (**Figure 3**, Study F) were able to discern a reduction in floristic composition and CAR with human activities during the Malayu Empire 1,200 years ago in Central Sumatra (Indonesia); however, with reduced pressure due to population migration they saw a rapid recovery of both measures within 60–170 years of abandonment. From their findings, they were able to suggest appropriate methods for sustainable use of peatswamp forests as well as appropriate species for reforestation. Unfortunately, CAR across tropical peatlands are expected to slow with increasing temperatures and to become a net source by the end of the century (Gallego-Sala et al., 2018). It is unclear the extent to which restoring peatswamp forest would have a dampening effect on those predictions; however, as evidenced by Hapsari et al. (2018) these systems can recover, and therefore, returning them to a more “intact” state would be advisable.

Proposed Mechanisms for Resilience

There are known and hypothesized physiological limits to abiotic drivers across forest species, such as temperature and water availability. However, photosynthesis appears to be more impacted by drought than by temperature (Cusack et al., 2016). Some groups suggest that there are intrinsic system-level sensitivities to water availability across biomes (Ponce-Campos et al., 2013) with the majority of trees exhibiting relatively narrow hydraulic safety margins (Choat et al., 2012). This would indicate low adaptive capacity to rapid changes in temperature and rainfall regimes, resulting in higher mortality rates for trees more at risk of embolism (Trugman et al., 2018). Predictions for the tropics are that species dominance will shift to those with drought tolerant traits, with concomitant loss of evergreen species, particularly in sites exhibiting increasing drought duration (Aguirre-Gutiérrez et al., 2019; Bartlett et al., 2019). This transition is likely to entail large-scale die-off of the tallest trees in old-growth forest, resulting in a pulse in global carbon emissions (McDowell and Allen, 2015). For instance, heightened mortality has been observed for the largest trees or those with the lowest wood density (Phillips et al., 2010), a dynamic that has been echoed in experimental conditions replicating long-term droughts via through-fall exclusion (TFE) (da Costa et al., 2010). However, in *Nothofagus* dominated forest in Patagonia, it was the trees exhibiting the most variable growth patterns, not the largest or oldest, that were more likely to die (Suarez et al., 2004). Studies in Latin America have found the smallest and youngest trees exhibiting greater mortality, with concomitant impacts on community composition (Enquist and Enquist, 2011). In addition, a pan-tropical, tree-level study by Johnson et al. (2018) found that climatic conditions, such as mean annual temperature (MAT) and cumulative water deficits (CWD), were better predictors of mortality across size classes, suggesting that size alone was not a reliable predictor.

The primary underlying mechanisms inducing tree mortality seems to be a combination of hydraulic failure and availability of non-structural carbohydrates (NSCs) (Adams et al., 2017; McDowell et al., 2018). How these dynamics manifest at the community-level via competitive or facilitative plant-plant interactions will also determine the resilience of a forest ecosystem to changing climate (Ploughe et al., 2019). For instance, in the Canadian boreal region, Luo and Chen (2015) identified a significant increase in tree mortality over their three decade study and found the dominant drivers appeared to be due to resource competition between individual trees and stand age. Allen et al. (2015) review how tree mortality might be impacted by climate change and identify several worrying drought trends, namely: droughts will be hotter, they will occur everywhere, mortality can be faster with hotter droughts, deaths can outpace growth creating novel forest systems and vapor pressure deficit increases non-linearly with temperature. Worryingly, it is emerging that the compound effects of extreme vapor pressure deficit (VPD) and low soil moisture are occurring with increasing frequency due to reinforcing feedback mechanisms (Zhou et al., 2019).

Another commonality across biomes would be a relationship between forest resilience and biodiversity. Seminal work in grasslands has shown the importance of diverse systems for being able to maximize niche differentiation, thereby enhancing productivity and stability (Tilman et al., 2014). However, this assumes biodiversity measures relate to functional diversity (Cadotte et al., 2011). This recognition has led to the advancement of trait-based diversity assessments, which focus on the functional attributes of individuals based on their morphological, physiological and phenological attributes, how those contribute to performance traits like productivity and their ability to persist in a community through environmental filters (Violle et al., 2007). This has been simulated for the Amazon using a range of plant functional traits, which found with greater biodiversity biomass recovery could be up to 95% of pre-shock levels, granted only after several centuries (Sakschewski et al., 2016). Díaz et al. (2013) proposed a framework assessing specific effect functions (SEF) and specific response functions (SRF), where the former relates to the outcome of a species' functional traits on an ecosystem and the latter relates to the ability of a species to maintain its functions while undergoing environmental change. They add a community-level risk assessment for an ecosystem service by considering the phylogenetic diversity of the SEF, which if high would suggest redundancy of the functional response to environmental change. Much of these assessments are based on community weighted means for each species, and therefore, rely on their relative abundance to relate to a community-level resilience. However with current understanding, it is difficult to predict how important rare species may be for an ecosystem's resilience, as sometimes these species can have a unique combination of functional traits that may disproportionately impact a systems' adaptive capacity during a time of disturbance (Mouillot et al., 2013). Nevertheless, studies have found that forest systems dominated by a small number of species can be more vulnerable to rapid climate changes (Fensham et al., 2015).

Climate change impacts on biodiversity are predicted to be significant, and particularly if species are not able to thermally adapt to new conditions, their loss could be greater than losses due to drought or deforestation (Feeley et al., 2012). CO_2 fertilization seems to be beneficial for fast-growing, light-demanding pioneer species (Cusack et al., 2016), which as highlighted above may be more vulnerable to hydraulic failure during drought conditions. One method for assessing the impact of climate change on community-level biodiversity is the community temperature index (CTI), whereby species relative abundance and their known thermal optima are combined to produce an average temperature preference for the community (Stuart-Smith et al., 2015; Gaüzère et al., 2018). With repeat measures in the same site, it can be possible to assess whether more thermophilic species are migrating into a community, suggesting one mode of adaptation to climate change. This dynamic has been found along an Andean transect since 1990, whereby plot-level CTI have been increasing with species migration up-slope. However, these species movements have been halted at the barrier between ecotones (e.g., montane forest to cloud forest) (Fadrique et al., 2018), suggesting physically-imposed limits to species migration. The 90,000 year pollen record from the Afro-montane forest of Cameroon (**Figure 3**, Study E) showed a highly variable upper limit to the forest zone with a relatively stable lower forest zone (Lézine et al., 2019), also indicating long-term, complex constraints on species dispersal. This dynamic contrasts starkly with the stability the Afromontane forests in Tanzania exhibited over a 48,000-years record (Finch et al., 2009) and further complicates the question of how spatially constrained "natural variability" or a "baseline" for current forest dynamics can be compared.

Do Larger Forest Patch Areas Confer Resilience?

By combining paleoecological and contemporary perspectives, can we answer the question of whether size of forest is positively correlated with resilience? We do know that tropical forests across the world are threatened by fragmentation (e.g., the conversion of large areas of forest into smaller patches) as a result of rapid land use conversion from forest to agriculture (Curtis et al., 2018; Taubert et al., 2018), with extreme predictions resulting in severe fragmentation of half the Amazon Basin (Gomes et al., 2019). We also know that the process of fragmentation has been associated with large-scale biodiversity loss (Laurance et al., 2011; Haddad et al., 2015) and reduction of carbon sequestration (Qie et al., 2017), due to edge effects and habitat loss. However, the debate as to whether several smaller forest fragments vs. the equivalent forest area in one contiguous patch, keeping total habitat area constant, have significantly different biodiversity outcomes is ongoing (Fletcher et al., 2018; Fahrig, 2019). It is not clear the extent to which this can be said of carbon sequestration rates or forest resilience more generally, whereby following habitat fragmentation, vegetation dynamics of intact forests' systems are altered. For example, fragments might display an increase in the frequency and/or amplitude of population, community, and landscape dynamics initially, and then gradually stabilize and approximate the pre-fragmentation conditions (Laurance et al., 2002, 2011). Conversely, fragments may not gradually stabilize toward the pre-fragmentation conditions, and potentially, undergo a regime shift. Unfortunately, more evidence is needed before relying on an area-based definition for predicting the resilience of forest fragments.

Studies from the tropics suggest that forest patches experience exceptionally large variability in vegetation dynamics especially when disturbances associated with shifting cultivation are frequent; yet these records are restricted to relatively short temporal scales (<50 years). In a >30 year project in Amazonian forest fragments, Laurance et al. (2011) found that different fragmented landscapes can diverge to a surprising degree in species composition and dynamics. Understanding how and why the dynamics of fragmented landscapes are altered will improve our ability to predict and manage the consequences of intact forest landscape fragmentation. Our comparison of IFL areas and climate sensitivity suggest that larger contiguous forest patches in the tropics are exhibiting lower sensitivity to water availability, and therefore, may be more resilient in their response to CO_2 fertilization. This would be consistent with canopy drought responses, measured as anomalies in EVI, which found shorter recovery times in dense forests compared to secondary and degraded forests over the Amazon for a similar time period to our analysis (Anderson et al., 2018). Additionally, our results identified IFLs in Africa as being less sensitive than both South American and Southeast Asian tropical forest. This seems to be corroborated by analysis of canopy responses to drought over West and Central Africa, using QuickSCAT canopy backscatter data, which found significantly shorter recovery times for the continent compared to similar climate shocks in South America. The authors attributed this observed resilience to the protracted drying trend West and Central Africa has been undergoing since the 1970s (Asefi-Najafabady and Saatchi, 2013).

In boreal systems, the dynamic between fragmentation, fire and timber harvesting are complex and it is difficult to discern whether there are discernible changes with climate change. In principle, due to the boreal region's adaptation to disturbance it is considered to be less impacted by fragmentation (Harper et al., 2015). A 30-years Landsat based analysis of the Canadian boreal region showed lower rates of fragmentation and higher rates of recovery in forests being actively harvested than unmanaged areas driven by fire. However, the authors posit this could relate to harvesting occurring in more productive and less fragmented forests, while more fragmented forest areas could be more susceptible to fire (Hermosilla et al., 2019). Lehsten et al. (2016) focused specifically on the boreal shield and boreal plains to compare fire dynamics within managed and unmanaged systems in a similar ecotone. They found that managed forest areas, particularly fire suppression activity, not only did not reduce the number of large fires but decreased the natural phenomenon of fuel fragmentation, increasing the probability of more severe fires. Finally, fragmentation in the boreal region can also be driven by climate change itself, whereby climate suitability of species may shift so dramatically over the next several decades that populations of vegetation, birds, and mammals could be physically bifurcated at the continental-scale (Murray et al., 2017) or sporadic thawing of permafrost may shift currently forested areas to treeless wetlands (Carpino et al., 2018).

CONCLUSIONS

This paper was intended to summarize the range of observable responses of intact forest to environmental change and a selection of contemporary and paleoecological metrics used to assess forest resilience to these changes (see **Figure 4**). Primarily, resilience metrics seem to fall into three main categories, namely

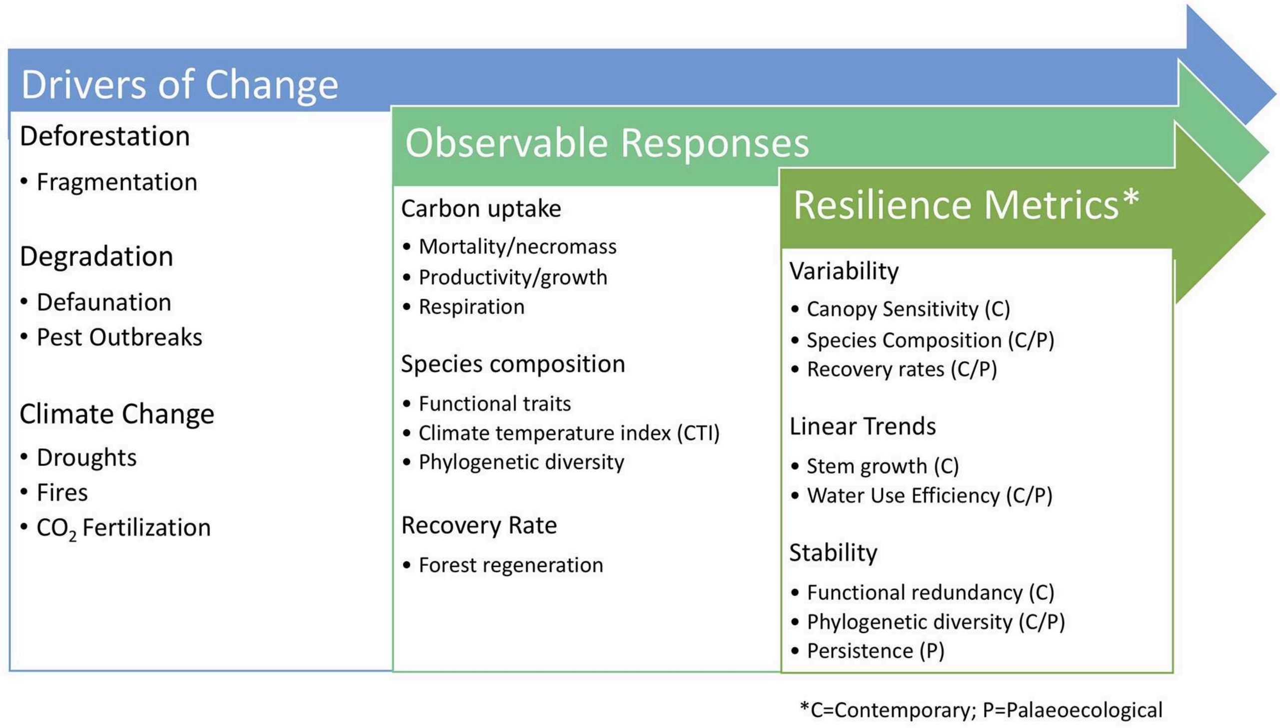

FIGURE 4 | Summary figure of key drivers of change to forests, observable responses, and the existing contemporary and paleoecological metrics to assess the resilience of forest ecosystems to these drivers of change.

measures of variability, linear trends, and stability of observable forest response such as carbon uptake, species composition, and recovery rate. In general, these metrics do not describe the underlying driver that may be reducing the overall resilience of a forest system, which are included in **Figure 4** and have been reviewed at length by Malhi et al. (2014). However, they are, or should be, intended to assess the ability of a forest ecosystem to respond to climate changes, and therefore, will be an aggregated measure at the community level. The analysis we performed and presented was comparing the variability in canopy response to climate anomalies for large, contiguous intact forest areas with non-intact forests across and within biomes. We do not assert that the dataset produced by Seddon et al. (2016) necessarily captures the underlying mechanism that may be causing an increase in discernible vegetation sensitivity to climate anomalies, as there may be "intrinsic" ecosystem dynamics contributing to climate responses of vegetation that are not currently captured by coarse-resolution imagery (e.g., degradation or low adaptive capacity).

By comparing canopy responses within biomes rather than between them, our results suggest that intact forest areas exhibit lower sensitivity to climate drivers that a biome is known to be susceptible to, namely temperature in the boreal region and water availability in the tropics. However, this pattern varied across continents within the same biome. For instance, African forests in the tropics seem to exhibit the lowest canopy sensitivity to climate anomalies and are known to have experienced significant climate variability, which has perhaps selected for more drought resilient traits. If we take exposure to past climate variability as a predictor of future vulnerability, the tropical forests of Southeast Asia, which are dominated by tall trees that have experienced little seasonality historically and which our analysis shows to be exhibiting the highest sensitivity to climate anomalies, would be particularly important for understanding the mechanisms of forest resilience.

Even by combining contemporary and paleoecological perspectives, it remains up for debate how forest resilience will manifest under rapidly accelerating climate change and whether insights can be generalized for biomes or regions. Theory as well as evidence from the literature reveals that resilience is an emergent property of a complex system. Individual tree responses to disturbance are influenced by life histories and functional attributes, and therefore, the ecosystem-level response will, to some extent, be path dependent. At the century to millennium-scale, paleoecology tells us that many intact forests have persisted and been able to adapt to new environmental conditions, which may entail shifts in species, or vegetation structure. However, it is over the short term that many in the forest research community are looking to ensure resilience of forest systems, and particularly, maintain forests as reliable storage of carbon and habitat for threatened biodiversity. A precautionary approach over this time frame, might be to prioritize conservation of large forest areas as they have a higher probability of supporting greater biodiversity and generally have lower opportunity costs to protect. However, with the benefit of hindsight through long-term studies, we can see that past disturbance does enhance aspects of resilience (e.g., recovery rate) and even forest in fragmented landscapes can persist for millennia. With the scale and rapidity of precipitation and temperature changes expected, the immediate future of carbon storage and sequestration services of forest is hard to predict. However, the greater uncertainty seems to be the degree to which the global community is able to dramatically reduce carbon emissions, and by extension, at what concentration of CO_2 the atmosphere will eventually stabilize. Ensuring carbon storage in forests cannot be achieved without dramatic reductions in fossil fuel emissions.

AUTHOR CONTRIBUTIONS

Idea for review developed and analysis performed by AM. AM and SN contributed equally to writing and editing the manuscript.

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SUPPLEMENTARY MATERIAL

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Conserving the Last Great Forests: A Meta-Analysis Review of the Drivers of Intact Forest Loss and the Strategies and Policies to Save Them

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The conservation of Earth's remaining intact forests (IFs) is a global priority, but improved understanding of the causes and solutions to IF loss is urgently needed to improve conservation efforts. This meta-analysis examines 207 case studies of IF loss occurring since 1970 to synthesize the drivers of IF loss and the proposed case-specific interventions. The goal of this study is to build a portfolio of conservation best practices for retaining IFs. The most frequently reported direct drivers of IF loss were logging, agriculture, ranching, and infrastructure expansion. Mining and fire were also prominent threats to IFs in selected areas. Indirect drivers of IF loss varied between continents, with high demographic pressures driving forest loss in Latin America, Asia, and Africa, contrasting with North America and Europe-Russia. Indirect economic and socio-political drivers were most frequently reported at the national scale for all continents studied, indicating a central role for national institutions in IF loss and conservation. Decisive socio-political factors underlying IF loss worldwide include political failures, institutional failures, and pro-development policies. A wide range of interventions were recommended in the case studies to conserve IFs. The proposed actions were most frequently within the forest, finance, and education and science sectors, and also emphasized inter-sectoral activities. Based on the results of this study, three core approaches to IF conservation that can be combined at the landscape scale are identified: protected areas, payments for ecosystem services, and agricultural reforms. Related enabling conditions include cooperative landscape management, effective enforcement, and political advocacy. The success of IF conservation efforts ultimately depends on sustained political support and the prioritization of high-value forest landscapes. Such efforts should mitigate socio-economic pressures through policy mixes that are cross-sectoral and place-based. Key policy priorities for IF conservation include addressing the systemic failures of public institutions, increasing political support for IF conservation, and countering harmful development activities.

Keywords: intact forest, forest conservation, deforestation, drivers, policy, strategy, meta-analysis

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INTRODUCTION

Intact forests (IFs) are a global conservation priority because they provide ecosystem services and vital resources and cultural benefits to local and global societies, especially forest-dependent indigenous people (Finer et al., 2008; Olivero et al., 2016). The loss of these relatively undisturbed native forests has both local and global consequences because human and natural ecosystems are dependent upon stable global carbon and hydrologic cycles and the ability of IFs to mitigate climate change impacts (Seymour and Busch, 2016; Watson et al., 2018). Documenting the loss of IFs has been a long-term priority in biodiversity conservation because the core habitats for many threatened forest-dependent species worldwide are found in IFs (Gibson et al., 2011; Betts et al., 2017; Donald et al., 2019). The threats to and losses of relatively undisturbed native forest ecosystems continue to be reported and recent estimates suggest that only ∼25% of global forests are classified as intact (11 million km^2) (Heino et al., 2015). Between 2000 and 2012, ∼324,000 km^2 of IF was lost, which is equal to a land area 1.3 times the size of the United Kingdom (Heino et al., 2015). Scientists and policy-makers have worked for decades to understand the causes of forest loss and to develop effective interventions (e.g., World Resources Institute, 1997; Lambin et al., 2003; Nepstad, 2005; Kissinger et al., 2012). While past efforts have helped to reduce deforestation in some areas (Nepstad et al., 2014; Thaler et al., 2019) and have improved the science of forest conservation (Puri et al., 2016; Min-Venditti et al., 2017), more effective approaches are needed to address the continued and widespread loss of IFs. Current research priorities include improved understanding of the causes of IF loss (Heino et al., 2015) and the development of more evidence to inform the design of place-based forest conservation efforts (Puri et al., 2016; Min-Venditti et al., 2017).

Underlying our need to better understand the drivers of IF loss is the reality that conservation interventions must be matched to the multi-scale drivers threatening IFs. Developing this knowledge can be difficult because the drivers of forest loss vary regionally and temporally due to variations in socio-economic conditions, land-use dynamics, population density, forest condition, and local biophysical conditions, among other factors (Lambin et al., 2003; Geist et al., 2006). This variation implies that efforts to conserve IFs must be place-based and informed by direct deforestation drivers, which operate locally (e.g., logging and mining), and indirect drivers, which are often external to the local area and outside the control of local land-users (e.g., market prices and technology; Geist et al., 2006). A diversity of scholars with different academic backgrounds have studied the direct and indirect drivers of forest change at several scales—global, regional, and local (e.g., Geist et al., 2006; Soares-Filho et al., 2006; Kissinger et al., 2012; DeFries et al., 2013). The existence of various disciplinary frameworks to understand the drivers of forest change suggests that IF conservation efforts be based on an interdisciplinary, and therefore holistic, approach to forming knowledge of the drivers of IF loss.

Designing effective IF conservation interventions must account not only for the location-specific drivers of forest change, but also overcome a lack of evidence regarding the efficacy of conservation policies and programs. In general, the field of evidence-based policy and program design for biodiversity conservation remains immature (Miteva et al., 2012; Baylis et al., 2016). Various forest conservation policies have been rigorously evaluated in recent decades, but even the most well-studied interventions suffer from a limited study of intervention outcomes and are not geographically representative (Puri et al., 2016). Limited evaluation data for past conservation efforts is problematic because the impacts of interventions, including unintended tradeoffs (Ferraro and Pattanayak, 2006; Puri et al., 2016) such as increased inequality or leakage (Hirsch et al., 2011), cannot be predicted accurately. Insufficient evaluation data may also hinder projections of conservation interventions because policy impacts can vary by efficacy, efficiency, equity, legitimacy, and partisan appeal (Salamon and Lund, 1989). Given the paucity of rigorous evaluations of forest conservation interventions and the multitude of potential outcomes, expanding the evidence used to inform IF conservation efforts and developing best practices for IF conservation efforts is an urgent scientific challenge.

In addition to insufficient knowledge about the impacts and trade-offs of IF conservation efforts, another key challenge is implementation. Even if a set of well-informed policies is designed to counter the drivers of forest loss, weak governance, institutional failure, and corruption may inhibit implementation and negate desired effects (Geist and Lambin, 2002; Laurance, 2004; Kissinger et al., 2012). The importance of institutional and political failure in policy implementation is rooted in the tradition of command-and-control governance widely used to regulate land-use (Lambin et al., 2014). Implementing conservation policies and enforcing compliance often requires adequate governance capacity and monitoring capabilities, which is problematic in most tropical forest countries (Kissinger et al., 2012; DeFries et al., 2013). Likewise, political support is necessary to enforce IF conservation laws and to develop new legislation, but political will may be lacking due to corruption (Ascher, 1999; Laurance, 2004) and the primacy of economic development (Geist et al., 2006; Nepstad et al., 2014). Policies that conserve IF may also create economic trade-offs that can be difficult to overcome in the face of powerful political actors and market forces (Wunder and Verbist, 2003). Thus, developing effective approaches to conserve IFs that identify and mitigate governance and institutional deficiencies and overcome existing economic and political trade-offs is a research priority.

To inform the aforementioned gaps in knowledge and the design of IF conservation efforts, this study examined the following questions: (1) what are the drivers of IF loss with respect to the case study literature?; (2) what IF conservation policies and activities are recommended in the case study literature?; and (3) can the synthesis of the case study's reported deforestation drivers and conservation recommendations inform the design of IF conservation policies and strategies?

MATERIALS AND METHODS

Meta-analyses of case studies are widely used to provide systematic knowledge of scientific topics (Khan et al., 2001), including case-based analyses of the drivers of tropical deforestation (e.g., Geist and Lambin, 2002; Rudel, 2007). Like all research methods, the case-oriented meta-analysis approach has strengths and limitations (Rudel, 2008). An important strength of the approach is the method's ability to identify broad patterns that explain the causes of land-cover change and inform policy development (Rudel, 2008; Magliocca et al., 2015). Drawing inferences from unique case studies can also present methodological challenges, including potential issues with inter-coder variability in the analysis of case studies (Rudel, 2005) and potential bias if cases are mostly focused on popular issues or regions of interest (Rudel, 2008). The following case-oriented meta-analysis sought to avoid potential biases by collecting a global sample of case studies of IF loss, extracting relevant data from each case study using two independent reviewers, and analyzing the case studies at continental and global levels. Continents studied were North America, Latin America, Europe-Russia, Asia, and Africa. Only two cases were identified related to IF loss in Australia-Pacific, so this area was excluded from the continental analyses. To reduce inter-coder variability and ensure that each reviewer utilized a similar approach to extracting information from a case, the reviewers were trained by the lead author using sample case studies. Reviewers then evaluated each assigned case independently before comparing and synthesizing their results with the reviewer who analyzed the same case. The data extracted from the cases was categorized and assessed using existing conceptual frameworks (**Table 1**).

The final dataset included 207 case studies from 193 publications documenting the drivers of IF loss at the local, regional, or national scale. Cases were identified and screened using the PRISMA-P meta-analysis protocol (Shamseer et al., 2015) (see **Appendix 1** for complete PRISMA search results). All cases included were peer-reviewed research articles, dissertations or master's theses, or related institutional publications. Cases were obtained using keyword searches in Google Scholar and the Web of Science database from the first 30 pages, showing 10 results per page. The following search terms were used: agricultural frontier, forest frontier, and deforestation frontier, as well as keyword searches constructed using the following methodology: "forest" + *climate* or *condition* keyword + *change* keyword. *Climate* keywords included dry, rainforest, tropical, subtropical, boreal, and temperate. *Condition* keywords included old-growth, intact, and primary. *Change* keywords included deforestation, conversion, and loss. For example, search strings included "dry forest deforestation" and "tropical forest loss." To be included, each case study had to describe IF loss at the local, regional, or national scale, occur partly or entirely after 1970, and contain information on the drivers of IF loss.

Based on the keyword searches and after screening the titles for relevance to the study, a total of 1,113 case studies were identified and a total of 483 duplicate studies were removed. The abstracts of the remaining 630 cases were then screened and 441 were excluded, leaving 189 cases (see **Appendix 1** for reasons for exclusion). An additional 41 records were obtained from reference lists and Google Scholar alerts, resulting in 230 records for full-text screening. After full-text screening 37 records were excluded, which resulted in a database of 193 records for study. Cases were organized and analyzed in Excel. The following data was extracted from each case study by each reviewer: direct and indirect drivers of change, institutional failures, political

TABLE 1 | The drivers of IF loss and the proposed conservation interventions extracted from the case studies.

Variable extracted	Variable definition	Variable structure
Direct drivers	Drivers locally responsible for forest conversion or degradation	(1) agricultural expansion; (2) infrastructure development; (3) wood extraction; (4) natural disturbances (e.g., fire, pests, drought); (5) mining and hydrocarbon extraction; and (6) ranching
Indirect drivers	Drivers that enable or encourage conditions that lead to forest conversion or degradation.	(1) demographic; (2) economic; (3) sociopolitical; (4) cultural and religious; and (5) scientific and technological. Drivers were recorded by spatial scale of local, national, and international
Institutional failures	Failures in public institutions that lead to forest loss or degradation	(1) weak or inadequate law enforcement; (2) poorly designed policies; (3) insufficient capacity; (4) failures in tenure regime; (5) poor planning; (6) poor coordination or collaboration; and (7) institutional corruption
Political failures	Failures by political actors that lead to forest conversion or degradation	(1) absent policies or insufficient political will; (2) political corruption; (3) failed policy effort; (4) unclear or ambiguous policies; (5) political instability or uncertainty; (6) insufficient or weak policies; and (7) insufficient funding
Pro-development policies	Forest development, natural resource extraction, or immigration policies implemented by political leaders or policy-makers	(1) encourage resource extraction; (2) encourage agriculture/pasture expansion; (3) encourage migration/colonization projects; (4) subsidies or tax incentives to deforest; (5) encourage/support infrastructure development; and (6) promotion of general economic growth.
Forest conservation interventions	Policy recommendations of case study authors to conserve forests	(1) sectoral policies; (2) inter-sectoral policies; and (3) unique policies and strategies

The direct drivers of IF loss were extracted using a modified version of the framework of Geist and Lambin (2002) and indirect drivers were identified using the framework developed by Nelson et al. (2006). The institutional and political failure typologies were produced based on results of the case studies and the political science concepts of policy failure, government failure, and institutional failure (Acheson, 2006; Howlett and Ramesh, 2014; Press, 2015).

failures, pro-development policies, and proposed conservation policies or activities. The data extracted by each reviewer was then refined based on discussions between the paired case study reviewers. Bias was present in the form of the unequal global distribution of case studies. To control for this bias, extracted data was quantitatively analyzed and synthesized as a percent of the case studies at the global and continental scales. For a detailed description of each variable extracted see **Table 1**.

RESULTS

Case Studies of IF Loss Reviewed

The review of 193 publications produced 207 case studies of IF loss that formed the database used in this study. Data was collated across all major forest types, five continents, and 49 countries (**Appendices 2**, **3**). The most common reported forest type was tropical-subtropical wet forests (63% of cases), followed by tropical-subtropical dry forests (20%), temperate forests (8%), and boreal forests (8%). The case studies were mostly focused on Latin America (57%), followed by Asia (22%), Africa (10%), Europe-Russia (6%), and North America (5%). Eighty-nine percent of the cases were from developing countries and the remaining 11% were from developed countries.

Global and Continental Direct Drivers

By order of frequency reported, the global direct drivers (i.e., proximate causes) of IF loss were agriculture, logging, and ranching (**Appendix 4**). However, logging was most frequently reported as the greatest contributor to IF loss in all continents studied with the exception of Latin America. In Asia, logging was followed by agriculture and infrastructure development, with ranching infrequently reported. In North America and Europe-Russia, logging was followed by natural factors (i.e., fire), with many of the fires reported caused directly or indirectly by humans. In Latin America, the most frequently reported direct driver of IF loss was agriculture followed by ranching and infrastructure development. Infrastructure development was reported to play a role in ≥50% of each of the continental analyses and mining and oil/gas drilling was reported in 19–31% of cases by continent. A continental analysis of the co-occurrence of agriculture and logging as driving IF loss found that 50% of the Europe-Russian cases and 40% of the North American cases reported logging as the primary reason for IF loss without identifying agriculture as a driver. In contrast, logging without agriculture was reported in only 13% of the cases from Africa and Asia and 4% of the cases from Latin America. Agricultural crops commonly reported to replace IFs at the continental level were soy in Latin America, palm oil and rubber in Asia, and corn in Africa.

Global and Continental Indirect Drivers

The indirect drivers (i.e., underlying causes) of IF loss reported in the cases reviewed varied widely by continent and driver type (**Appendix 5**). Socio-political and economic indirect drivers were most commonly reported at the national scale for all continents at 55 and 63% of all cases, respectively. National and international economic drivers of IF loss were higher in Latin America, Asia, and North America compared to Europe-Russia and Africa. Notable economic factors identified across the cases included increasing commodity and land prices, poverty, and economic recession. National demographic factors were most commonly reported as IF loss factors in Africa (63% of cases), Latin America (48%), and Asia (36%). A continental analysis of the association between demographic factors and IF change identified four IF loss-demographic scenarios: high internal population growth, general internal migration, internal immigration caused by instability, and immigration from abroad. In Latin America, Asia, and Africa, the demographic factors of importance were internal population growth (34, 29, and 31% of cases, respectively), internal migration (39, 22, and 50% of cases, respectively), and migration due to internal instability (5, 2, and 19%, respectively). In Latin America and Asia, immigration was often associated with government-sponsored immigration projects and spontaneous colonist expansion due to poverty, whereas in Africa, immigration was associated with poverty and refugee movements caused by war and political unrest. With a few exceptions, cultural and religious drivers and scientific and technological drivers were reported in ≤10% of the continental case studies. Examples of cultural drivers reported included the transition from traditional hunting and gathering practices to subsistence agriculture and changes in traditional land-use practices. Examples of scientific and technological drivers reported included advances in seed varieties, improved irrigation technologies, and increased mechanization of logging operations and wood processing.

Pro-development Policies and Political and Institutional Failures

A global and continental analysis of "pro-development" policies leading to IF loss found that 49% of all cases reported one or more pro-development policy, and the number of policies reported varied widely by continent. Pro-development policies were more commonly reported as driving IF loss in North America (50% of cases), Latin America (47%), and Asia (44%) compared to Europe-Russia (30%) and Africa (19%). In Latin America, the most frequent pro-development policies were associated with agriculture and pasture expansion, colonization schemes, and promotion of resource extraction (e.g., gold mining and logging). In Asia, the most common pro-development policies were agriculture expansion, promotion of resource extraction (i.e., logging), and infrastructure development. In North America, the pro-development policies most often reported were the promotion of resource extraction (i.e., logging) and agriculture expansion.

A common socio-political factor leading to IF loss is political failure (59% of all cases studied) due to the absence of political will or policies to conserve IFs (30% of all cases) (**Table 2**). Absence of political will or policies was most frequently reported on all continents except Asia, where political corruption and failed policy efforts were more frequently reported. In Africa, a multitude of factors drive political failure contributing to IF loss, including political corruption, lack of policies or political will, political instability, and insufficient or weak policies.

TABLE 2 | The table below shows the reported political failures at the global and regional scales leading to IF loss.

Political failures	Global cases	Latin America	Asia	Africa	Europe—Russia	North America
% of cases with political failures	59	55	67	69	40	70
Absent policies or political will	30	30	18	44	30	50
Political corruption	10	6	20	19	0	0
Failed policy effort	11	11	20	0	0	0
Political instability or uncertainty	10	9	4	38	10	0
Insufficient or weak policies	8	4	7	25	10	30
Lack of funding	5	5	0	13	10	0

Results shown as a percentage of the total case studies reporting a political failure.

TABLE 3 | The table below shows the reported institutional failures at the global and regional scales leading to IF loss.

Institutional failures	Global cases	Latin America	Asia	Africa	Europe—Russia	North America
% of cases with institutional failures	57	55	69	69	30	30
Inadequate law enforcement	26	25	36	31	10	0
Poorly designed policies/planning	5	4	9	13	10	10
Insufficient institutional capacity	12	13	11	6	10	0
Issues with land tenure	9	11	9	6	0	0
Poor resource/development planning	10	11	11	13	10	20
Inadequate collaboration/coordination	1	1	2	0	0	10
Institutional corruption	2	2	4	0	0	0

Results shown as a percentage of the total case studies reporting an institutional failure.

In North America, 80% of the cases reviewed reported the absence of political will or a lack of policies and insufficient or weak policies to conserve IFs. Another common indirect socio-political factor leading to IF loss is institutional failure, with 57% of all cases reporting a related institutional failure (**Table 3**). Globally, the most commonly reported institutional failure was inadequate law enforcement (26% of cases), followed by insufficient institutional capacity (12%), and poor resource/development planning (10%). Similarly, inadequate law enforcement was most frequently reported in Latin America, Asia, and Africa, followed by insufficient institutional capacity, and poor resource/development planning. Institutional failures were reported less frequently in Europe-Russia and North America.

Recommended Policies and Strategies for IF Conservation

In the 207 case studies, a total of 456 interventions were recommended to address forest loss. Each intervention was classified and organized by its respective governance sector (**Appendix 6**). The most frequently recommended sectoral intervention was forest-conservation (53% of all recommendations), followed by inter-sectoral actions (13%), efforts within the finance sector (8%), and public education and science (8%). A sample of the policies and activities proposed within each sector is shown in **Appendix 6**. Interventions were assessed by how frequently they were recommended to address indirect or direct drivers of IF loss. The most frequently recommended interventions were forest governance (20% of cases), forest management activities (15%), protected areas (10%), collaboration and landscape governance (7%), and law enforcement and monitoring (7%). The least recommended interventions were sustainable land-use planning (2%), political advocacy and lobbying (<1%) and addressing corruption (<1%) (**Appendix 6**).

DISCUSSION

The basic assumption of this research is that the long-term conservation of IFs depends on the integration of scientific knowledge and conservation efforts. Results from this meta-analysis show that the drivers of IF loss vary at the continental level, which adds further support to existing evidence that place-based conservation strategies are needed. As shown by this study, a wide variety of forest conservation policies are available. However, further research is needed to inform the design of IF conservation interventions for specific locations and to develop a portfolio of best practices. Improved understanding of the causes of IF loss and an overview of best practices for IF conservation is the focus of the following sections.

Understanding and Linking the Drivers of IF Loss to Conservation Efforts

The meta-analysis results presented provide an overview of the case study literature describing the global and continental drivers of IF loss and their recommended conservation interventions. While the drivers of tropical forest loss are well understood (Geist and Lambin, 2002; Rudel, 2005; Kissinger et al., 2012), knowledge gaps remain with respect to the causes of IF loss (Heino et al., 2015). Echoing previous research on the causes of deforestation (Geist and Lambin, 2002; Kissinger et al., 2012), this study finds that IF loss is often directly due to a combination of factors, including agriculture, logging, infrastructure expansion, and ranching. Agriculture was the most frequently reported direct driver of IF loss at the global level, but logging was the most frequently reported continental direct driver, occurring in >85% of the case studies not in Latin America. This finding aligns with research conducted by Potapov et al. (2017), who used remote sensing to show that IF loss 2000–2013 was most frequently due to logging. Logging, agriculture, and ranching co-occurred with high frequency on most continents, but in North American and

European-Russian forests, logging was reported as a direct driver on its own at a higher frequency than Latin America, Asia, and Africa. This finding highlights how the boreal and temperate forests of North America and Europe-Russia are particularly threatened by the logging industry (Hansen et al., 2013; Potapov et al., 2017). Another key continental difference was the high frequency of ranching in Latin America but relatively low frequency in Asia. Also, while agriculture is a frequent driver on all five continents, the most commonly reported crops replacing IFs on three continents were distinct. The individual case studies also demonstrate that direct drivers often vary at regional and local levels. For example, at the local level, Scullion et al. (2014) found that the direct drivers of forest loss in Madre de Dios, Peru varied by land-use designations. At the regional level, Caldas et al. (2015) found that cattle ranching was the largest driver of change in the Paraguayan Chaco, which contrasts with other dry forest case studies in Latin America where conversion due to soya expansion was dominant (Pacheco, 2006; Volante et al., 2016). Common to all continents was the ubiquity of infrastructure development resulting in IF loss. A number of cases also reported mining and oil and gas extraction as drivers, but at lower frequencies. Overall, the direct drivers of IF loss vary widely at the continental level and often at regional and local levels as well. The broad geographic diversity of deforestation threats and the ubiquity of IF loss worldwide (**Appendices 2**, **3**) indicate that IF conservation efforts should focus on high-value regions. The strategy of regional prioritization of IF conservation efforts is reinforced by the finding that many "IF landscapes" (Potapov et al., 2008) lack the full complement of their native fauna (Plumptre et al., 2019). In other words, fully intact forests are increasingly rare and should be targeted for conservation efforts based on priority IF landscapes.

The indirect causes of IF loss also vary widely at the continental level. The three most frequently reported indirect drivers of IF loss were factors related to demographics, economics, and socio-politics. These factors can be summarized as increasing human demand for natural resources and the global trade in commodities, which drive local-to-global teleconnections (Carrasco et al., 2017) and endanger not only IFs but also wildlife (International Union for the Conservation of Nature, 2009; Estrada et al., 2019). In agreement with trends of global population growth and immigration (United Nations, 2019), clear differences were found between reported demographic pressures across continents, including higher frequencies of population growth and internal migration affecting IFs in developing countries. The causes of migration affecting IFs within developing countries were also variable, with colonization projects, poverty, and population growth being most reported in Latin America and Asia, and population growth, poverty, and refugee movements being most reported in Africa. These findings are insightful because they draw attention to the important and diverse role of human migration in IF change, which can include reductions or increases in forest cover depending on the circumstances (Radel et al., 2019). Economic factors were the most frequently reported indirect driver worldwide and most commonly reported on the same three continents with high levels of pro-development policies: Latin America, Asia, and North America. The economic drivers reported were often linked to economic growth, but economic contraction and poverty also led to IF loss. These findings demonstrate that an important factor driving the continued loss of IFs, which are often geographically remote (Potapov et al., 2008), is their continued integration into global commodity supply chains. Since this integration threatens IFs, this study therefore suggests that conservation efforts should target the leading industries and pro-development policies on each continent. For example, in Latin America, the most frequently reported pro-development policies are the promotion of agriculture, pastures, and logging. Thus, primary targets in Latin America include the beef and soya industries and companies engaged in tropical forest logging. Similarly, priority conservation targets in Asia should include palm oil and logging companies, and in North America, logging companies. Interestingly, the least reported indirect drivers of IF loss, scientific and technological factors and cultural and religious practices, are likely relevant in far more cases than reported due to the central role of culture in influencing human behavior (Brislin, 1993; Schultz, 2011) and the importance of science and technology in driving economic expansion and environmental degradation (Millennium Ecosystem Assessment, 2005). Taken together, this study finds that meta-analysis studies of cases describing IF loss can inform the design and targeting of conservation interventions and confirms that the meta-analysis approach is limited by the biases and reporting of case study authors (Rudel, 2008).

The need to simultaneously target both market forces and national development policies and institutions to conserve IF is evident in this study by the high frequency of reported political and institutional failures driving IF loss. More than half of the case studies reviewed reported one or more political failure. Lack of political will or absent policies were especially problematic and pronounced in North America and Africa. Many studies have identified the role of political failures, including failed policy efforts, political corruption, political instability, and insufficient or weak policies as major threats to forests in the tropics (e.g., Ascher, 1999; Geist and Lambin, 2002; Kissinger et al., 2012). This study confirms these findings and shows that such drivers are worldwide threats to IFs. Similarly, echoing previous findings on the important role of institutional failure in forest loss (e.g., Dourojeanni, 1999; Kissinger et al., 2012; Rodrigues-Filho et al., 2015), this research found that institutional failures leading to IF loss occur worldwide and were reported in more than half of the cases studied. Overall, institutional failures were more frequently reported in developing countries than in developed countries. Across all continents, except for North America, inadequate law enforcement was the most frequently reported institutional failure, which aligns with other research showing that weak law enforcement is a persistent problem facing forests in developing countries (Kissinger et al., 2012). The relatively high frequency of failures related to law enforcement worldwide demonstrates that preventing IF loss is often not about writing new laws, but enforcing existing laws and regulations. Likewise, the frequency at which the lack of political will is cited indicates the importance of political advocacy to change the domestic politics that surround IFs. However, increased political advocacy on behalf of IFs was rarely mentioned as a recommended conservation intervention. In many cases, the political reforms required to address issues of weak law enforcement and insufficient political will need to address the social inequities that often lead to IF loss (Dourojeanni, 1999) and the strengthening of political constituencies in favor of IF conservation and government accountability (Nepstad, 2005).

A key finding of this study is the relatively high frequency of indirect drivers of IF loss at the national level, including demographic, economic, and socio-political factors. The importance of these national-level factors in IF loss, particularly decisions made by national governments and corporations, is supported by others who have noted the key role of national-scale institutions in driving tropical deforestation (Wells et al., 2015; Nolte et al., 2017) and maintaining protected area effectiveness (Brandon, 1998; Bradshaw et al., 2015). Related evidence showing the importance of national-scale institutions in forest conservation outcomes includes the recent success of national initiatives to conserve large areas of forests in China, Vietnam, and Brazil (Liu et al., 2008; Meyfroidt and Lambin, 2009; Nepstad et al., 2014). Opportunities exist for international actors to catalyze domestic reforms through multilateral agreements that provide economic assistance or increased market access in return for reform. One example is the US-Peru trade agreement that required forest governance reforms in Peru for greater market access to the United States (Del Gatto et al., 2009). Similarly, international actors can incentivize nation-states to strengthen government institutions that manage IFs through international aid, such as the recent investments of Norway in Liberia, Indonesia, and Brazil (Rainforest Foundation Norway, 2018). While prioritizing conservation efforts at the national scale makes intuitive sense given the hierarchical structure of modern nation-states and the importance of national-level drivers of IF loss, this research also shows that important indirect drivers of IF loss are nested at local and international scales. In summary, future IF conservation efforts should design policies that target deforestation drivers at specific geographic scales and emphasize the targeting of national-level political systems, economic systems, and public institutions whose mission and activities influence IFs.

Core IF Conservation Interventions

Individual conservation policies and activities can be understood as "tools in the toolbox" of potential forest conservation interventions because policy instruments are viewed as substitutable (Landry and Varone, 2005). That is, as shown in this study, a wide range of policies and strategies exist to conserve IFs and many of these approaches are useful under a range of circumstances. However, some policy instruments, such as payments for ecosystem services, are more specialized and only effective under certain conditions (Scullion et al., 2011; Wunder, 2013). Given the variation of policy impacts in different contexts and the lack of "policy panaceas" to resolve the overuse of natural resources (Ostrom, 2007), intelligent combinations of policy instruments, known as "policy mixes" (Howlett, 2004), are needed to conserve IFs. The strength of policy mixes is that they are designed to create positive synergies between individual policies and contextual conditions (Howlett, 2004). The wide variety of policies identified in the case studies shows that numerous IF conservation policies are available. While there are many options available, we identified a set of conservation interventions that when implemented together at the landscape scale are likely to lead to long-term IF conservation: protected areas, payments for ecosystem services, and agricultural reforms. These policies were chosen because of their ability to target key drivers of IF loss identified in this study: land conversion for agriculture, logging, and ranching as well as market prices and politics favoring converted forests over IFs. The trade-offs of these core interventions and their related enabling conditions are discussed below.

Protected Areas

Protected areas (PAs) form the foundation of global biodiversity and forest protection and are designed to prevent land-use change (United Nations Environmental Program, 2016). The effectiveness of PAs in conserving forests has been studied extensively with most studies finding that PAs slow or stop deforestation compared to unprotected lands (Joppa and Pfaff, 2011; Geldmann et al., 2013). The success of PAs depends on internal and external conditions, such as adjacency and intensity of nearby development and the density of park guards (Bruner et al., 2001; Joppa and Pfaff, 2011). Not all PAs are effective as many fail to maintain their biodiversity (Laurance et al., 2012) or are degazetted due to political pressure (Mascia and Pailler, 2011; Kroner et al., 2019). Establishing PAs on expanding forest frontiers may be helpful in the short-term, but without other supporting initiatives, such as regional land-use planning and law enforcement, their long-term maintenance may be too costly economically and politically. The main reasons for this being that PAs can result in the displacement of other land-uses (Dewi et al., 2013) and create political opposition (Mascia and Pailler, 2011). PA success is especially challenged in developing countries where institutions and political support for conservation are weaker (Ascher, 1999). Similar options but with fewer restrictions, such as indigenous reserves and multiple-use community forestry systems, have also been shown to be effective in maintaining forest cover (Nepstad et al., 2006; Blackman et al., 2017). Based on the aforementioned, we hypothesize that government-led PAs are more likely to effectively conserve IFs in North America and Europe-Russia and community-based systems more effective in Latin America, Asia, and Africa.

Payments for Ecosystem Services (PES)

PES programs are an increasingly popular forest conservation strategy that can be used to conserve IFs in lieu of or in addition to PAs. PES programs come in a variety of forms, including carbon payments (e.g., REDD+) and payments for hydrological services (Porras et al., 2008; Angelsen and Rudel, 2013). The strength of the PES approach is that under the right conditions they create a market price for the services of intact ecosystems that can compete with market prices for ecosystem conversion (Wunder, 2005). PES programs may also be advantageous because they can provide an equitable way to offset opportunity costs borne by land-users whose land-use is reduced by conservation efforts (Grieg-Gran et al., 2005). Major drawbacks to PES programs are that the payments are often marginal to the income of land-users and they may not compete with high returns from agriculture (Fisher et al., 2011; Scullion et al., 2014). PES interventions also require existing tenure regimes and effective law enforcement (Wunder, 2005), which are often lacking in remote or frontier regions. PES policies may also increase economic resources in poor regions and ultimately increase deforestation (Assunção et al., 2013). Nonetheless, as evidenced by the rush of national governments seeking to receive REDD+ funds, PES programs can provide a strong incentive to conserve forests (Kissinger et al., 2012). The REDD+ program and other multilateral funding programs that exchange cash for commitments to conserve forests offer promising ways to conserve IFs, but program criteria need to be adjusted to explicitly include IFs (Watson et al., 2018). In summary, given low payment prices, PES programs will work best to conserve IFs when land-use alternatives have low economic value. Also, effective law enforcement and stable public institutions are needed, which frequently excludes IF landscapes in developing countries.

Agricultural Reforms

Because PAs are insufficient to conserve all species and landscapes (Soares-Filho et al., 2006) and because agricultural expansion is a leading cause of IF loss and forest loss worldwide (Kissinger et al., 2012), reforming the agricultural sector and including private lands in landscape-level conservation strategies is a key priority. Agricultural policies and programs designed to reduce deforestation include approaches known as "supply chain interventions" (Lambin et al., 2018), which aim to create market incentives to conserve forests and disincentives for deforestation. Transformation of the agricultural sector to conserve forests has increased rapidly in recent years due to consumer demand and the limited effect of public policies in slowing deforestation (Nepstad et al., 2013). Key efforts underway to transform agricultural supply chains include commodity roundtables, crop certification schemes, and corporate procurement policies, such as "no-deforestation" pledges (Nepstad et al., 2013; Rainforest Foundation Norway, 2018). A major downside to supply chain interventions is that they require other supporting policies because they are vulnerable to leakage and spillover effects (Schielein and Börner, 2018). Also, for local producers, crop certification schemes often have low returns because of high certification costs and low-price premiums (Nepstad et al., 2013). In areas of the landscape where PAs and PES payments are less effective due to weak governance or existing private land, agricultural reforms may be useful in all regions of the world studied. Also, while deforestation caused by smallholder shifting cultivation appears to be decreasing in relative terms compared to industrial agriculture (Austin et al., 2017), in Africa, Asia, and Latin America this form of farming remains a threat to IFs (Geist and Lambin, 2002; Potapov et al., 2017). Thus, efforts to reduce the impacts of smallholder agriculture are also needed. Overall, the major related policy challenge is how to pair agricultural reforms with other multi-sectoral efforts that together ensure IF conservation, food security, and local income generation.

Enabling Conditions for IF Conservation

Enabling conditions are necessary for the efficacy of the core IF conservation interventions described above and include cooperative landscape management, enforcement, and political advocacy. These three conditions were selected based on the high frequency of interventions recommended related to law enforcement and multi-sectoral actions, as well as their ability to increase political will for IF conservation.

Cooperative Landscape Management

The diversity of cross-sectoral deforestation drivers and proposed inter-sectoral conservation interventions reported in this study highlight the necessity of cooperative landscape management. Cooperative landscape management involves collaborative management of mixed-use landscapes by land-users and institutions with management authority at the landscape-scale (Jacobson and Robertson, 2012), including combinations of PAs, working forests, and agricultural landscapes. The strength of this approach is that landscape-level collaborative efforts can break down sectoral silos, increase co-learning, and create shared responsibility to solve natural resource issues (Jacobson and Robertson, 2012; Kissinger et al., 2012). Various IF conservation interventions can be applied through cooperative landscape management, or "territorial approaches" (Nepstad et al., 2014), including strategic road planning (Laurance et al., 2014), deforestation bans and moratoriums (Fagan et al., 2013), forest zoning (Potapov et al., 2008), and land tenure reforms (Busch and Ferretti-Gallon, 2017).

Enforcement

This study found that weak or absent law enforcement was the most frequently reported institutional failure in Latin America, Africa, and Asia. This situation is problematic because enforcement of the rules and laws underlying natural resource management is a prerequisite for conservation success (Ostrom, 1990). In general, effective law enforcement is associated with positive forest conservation outcomes (Agrawal et al., 2014). However, law enforcement can be economically costly and may present opportunity costs to land-users (Börner et al., 2014). Effective law enforcement also has the potential to exacerbate rural poverty and can raise questions about social justice and the legitimacy of force (Brechin et al., 2002). If used inhumanely or without policies to offset its opportunity costs to land-users, law enforcement will be politically unpopular and increasingly difficult to maintain (Brechin et al., 2002). These challenges may be overcome through community-based conservation efforts where local communities make and enforce their own rules (Ostrom, 1990; Cox et al., 2010). Relatedly, corruption threatens IFs worldwide and related law enforcement efforts are essential.

Political Advocacy

Absent policies or political will was the most frequently documented political failure on all continents besides Asia. Political advocacy is necessary to conserve IFs in a democratic society to generate political will, challenge powerful actors, win political debates, and ensure government transparency. An engaged citizenry is also needed to conserve IFs because the ultimate cause of most conservation challenges is human behavior (Schultz, 2011), which manifests through politically negotiated outcomes and government institutions (Dietz et al., 2003; Fischer et al., 2012). Social movements and grassroots advocacy whose agendas are to influence environmental politics have long been instrumental in the legal protection of IFs, including wilderness protection in the United States (Turner, 2012) and the recent soy moratorium in the Brazilian Amazon (Rainforest Foundation Norway, 2018). Maintaining and expanding the protection of IFs will thus require increasingly effective political advocacy. Such advocacy should emphasize persuasive storytelling and building influential and diverse political constituencies, including corporations, politicians, young people, and forest-dependent communities.

CONCLUSION

This study demonstrates that the synthesis of case studies of IF loss worldwide can be used to identify distinct continental patterns of indirect and direct drivers. This knowledge can be used to inform the design of place-based conservation interventions. A key finding from this study is the diversity of reported drivers of IF loss external to the forest-conservation sector. This reality implies that many of the most effective policy interventions will be extra-sectoral (Wunder, 2004). Critical non-forest sectors identified in this research include infrastructure, finance, and education and science. Ultimately, the inter-sectoral nature of IF loss implies the need to shift from a linear conservation dominated approach to a holistic multi-sectoral approach. Similarly, gaps in the recommended conservation interventions in the case studies include a lack of recommendations to address corruption, insufficient political will, and institutional weakness. Whether this issue is restricted to the case study literature or is a broader problem facing IF conservation efforts requires further analysis, but additional efforts are surely needed to increase political support, eliminate subsidies and tax incentives, and address corruption.

This meta-analysis shows that IFs face a variety of direct and indirect threats around the world. Successful IF conservation efforts require holistic, place-based, and multi-scale approaches focused on priority IF landscapes. Conservation efforts at the landscape-scale cross jurisdictional borders which creates challenges and opportunities for public-private partnerships (Scarlett and McKinney, 2016). Ultimately, the current paradigm of economic development must shift to make IF conservation the preferred policy option and not a trade-off that must be made. This approach requires the concerted efforts of scientists, policymakers, corporations, NGOs, and engaged citizens operating in governance regimes that link actors and institutions across global-to-local scales. To conserve IFs locally and globally thus requires many different actors to work together and for governance regimes to account for the telecoupled nature of resource flows and collective decision-making (Munroe et al., 2019). The structure for such collaborations is multi-scale governance whereby global and domestic institutions provide guidance, coordination, and monitoring and local and regional institutions ensure policies are fit to local conditions and include local stakeholders. Developing these polycentric governance systems (Nagendra and Ostrom, 2012) focused on landscape-level IF conservation will take generations, but the effort is surely worthwhile.

AUTHOR CONTRIBUTIONS

JS devised and directed the project. JS, BD, SW-S, and ML extracted the data and conducted the analysis of the results. JS and KV wrote the article. All authors discussed the results and commented on the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2019.00062/full#supplementary-material

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The Dilemma of Maintaining Intact Forest Through Certification

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Intact forests are natural and often extensive forests free from apparent anthropogenic degradation. Intact forests have important intrinsic and societal values, making their protection a high conservation priority. They are, however, vulnerable to being lost and degraded due to high opportunity costs and a lack of positive incentives to their preservation. Market-based mechanisms, such as voluntary certification, might provide a means to conserve intact forests while maintaining income through sustainable forest uses. Yet possibilities to ensure strict protection of large areas of intact forests through certification remain limited as long as premiums from certification are bound to the units of forest products that are sold. We explore challenges for incorporating intact forests into certification processes, and of maintaining intact forests within forest management units. To circumvent these challenges, it might be necessary to create a form of compensation payment scheme to overcome the foregone costs of intact forest preservation. Alternatively, certification systems might need to consider permitting some degree of regulated extraction in exchange for recognition and implementation of stringent forest preservation. This will require a re-evaluation of the way intactness is treated within current certification standards and the requirements for forestry within intact forests. Eventually, intact forest conservation and socially and economically viable forest management can only be reconciled on the landscape scale.

Keywords: land sharing land sparing, protected areas, REDD+, forest management, FSC, sustainable intensification, boreal forest, tropical forest

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INTRODUCTION

Global efforts for biodiversity conservation are not sufficient to be distributed equally around the world. In order to target those areas with the highest conservation value, two contrasting concepts have emerged, both prioritizing landscapes that are biodiverse, but one focussing more on hotspots the other more on coldspots of human activities. Hotspots are global centers of biological diversity and endemism that are threatened by human activity, especially from habitat loss (Brooks et al., 2002). Coldspots are extensive and largely intact and undisturbed natural regions where the threat of loss is less immediate, but where the problem of degradation is increasingly important. The maintained integrity of coldspots is important for their large carbon stores and the extensive habitats of many disturbance-sensitive species (Watson et al., 2018). According to recent research, areas that have been identified as global hotspots currently contain an average of only 15% of their natural, intact vegetation (Sloan et al., 2014). Coldspots, in contrast, include the last large intact forests that remain free of human activities. Intact forests tend to be remote from populated areas and urban centers, and often occupy mostly inaccessible and agriculturally marginal regions in both tropical and boreal regions. One commonly used definition defines intact forest landscapes (IFL) as areas of at least 500 km^2 that do not show any sign of remotely detectable human activity or habitat fragmentation (Potapov et al., 2008). Intactness is in itself a valued aspect of conservation quite apart from the biodiversity that such IFL might contain, and therefore preserving intactness is an additional and complementary component of conservation. The expansion of exploitative activities even into some of the most remote corners of the globe is stimulating efforts to maintain these extensive areas of permanent forest cover, especially in countries where pressure to harvest timber or convert forest to agricultural uses is high.

THE ECONOMIC IMPERATIVES OF USING AND NOT USING INTACT FORESTS

Just as avoided deforestation is a cost-effective way for climate mitigation (Griscom et al., 2017), conserving intact forests has been described as a cost-effective way of delivering conservation benefits (Potapov et al., 2008). The underlying assumption is that maintaining an intact forest by avoiding human interventions of any kind has lower direct costs than maintaining, managing, or restoring smaller forested areas located in populated biodiversity hotspots. Large countries, such as Canada and Russia in boreal regions, or Brazil and the Democratic Republic of Congo in the tropics, could potentially maximize conservation outcomes for lower cost by preserving existing intact forests.

Yet, while on global scale the protection of intact forests can be a win to society, locally some people lose their assets. Many intact forests overlap with commercial logging interests (e.g., Courbin et al., 2014; Gaveau et al., 2014; Kleinschroth et al., 2017) and have been or will be exploited for timber under a business as usual scenario. The opportunity costs for avoided exploitation of resources within intact forests can be very high (Nasi et al., 2012). Areas of intact forests often have high commercial value for wood production, due to the age of forest stands, and the prevalence of large old trees. Forest companies have a strong financial interest to access the "primary forest premium," and governments are attracted to the tax revenues generated from commercial logging. If governments do protect intact forest areas to the exclusion of extractive industries, some form of compensation payments (e.g., for ecosystem services) might be demanded by concession holders. Both REDD+ and mitigations for environmental impacts elsewhere could, theoretically, fund this. Yet, such compensation schemes are only viable if the funds are competitive with the expected extractive revenues (Butler et al., 2009). Additionally, in countries with limited statehood, characterized by weak institutional capacity in the periphery, the commitment to preserve forests might weaken over time, or might never materialize, as happened to Ngoyla-Mintom forest, one of the last intact forests outside national parks in Cameroon (Ongolo, 2015).

The long-term preservation of intact forests is also threatened by national development agendas. Nations typically seek to improve transport and power infrastructures in order to aid the extraction of natural and mineral resources, and reduce post-harvest losses in the food sector by increasing accessibility to rural lands. Logging is often a first step in this process, as it generates revenue and requires investment in initial infrastructure upon which subsequent development can be based.

FSC AS AN AGENT TO IMPLEMENT INTACT FOREST CONSERVATION

Forest certification is a voluntary, market-based incentive mechanism to validate sustainable forest management for wood production in addition to legal compliance as a form of non-state governance. As such, it relies for its effectiveness on the marketing of forest products from responsibly managed forests. There is a need for market rewards to compensate owners for the cost of certification. The process of forest management certification implicitly follows a "land sharing" approach, based on the assumption that improved management across the whole management unit delivers overall benefit on social, environment and economic grounds.

FSC certification rules require a minimum of 10% of the management unit area to be set aside for conservation purposes (FSC Policy Standards Unit, 2010). In practice, this is complemented by areas designated as High Conservation Value (HCV) and un-operable areas, meaning that the percentage of protected forest within the management unit may be much higher. In 2014, FSC set itself the target to include IFL as an HCV criterion (FSC Policy Standards Unit, 2017), with far-reaching consequences for the implementation of certification in boreal and tropical forests (Kleinschroth et al., 2019). The opportunity costs introduced by the mandatory protection of IFL as part of certification depends on the individual location of a forest management concession and on the economic value of the IFL. The larger the overlap between concession and valuable IFL, the higher the opportunity costs (Karsenty and Ferron, 2017). Intactness, as defined in the IFL concept, can only be maintained through strict protection. Yet, the price premium from certification is bound to the units of wood sold, not to the area protected (**Figure 1**). A company with concessions that include large overlaps with IFL areas will therefore be disadvantaged, unless it is compensated for the opportunity costs in a different way.

The influence of FSC over global IFL is small. In Russia, 1.6% of the 225 Mio ha of IFL area fell into certified concessions (Ptichnikov et al., 2017) and in the Congo Basin 1.2% of the 84 Mio ha of IFL are found within certified concessions of Republic of Congo, Gabon, and Cameroon (based on own calculations for 2016). Other major overlaps between IFL and FSC certified areas occur in Canada and Brazil, where we were unable to find complete spatial data of certified areas. Total certified area in the six main IFL countries has stagnated since 2014 (**Figure 2**). In Africa, for example, the area of FSC certified forest has declined by 9% (from 7,421,322 to 6,784,372 ha) from February

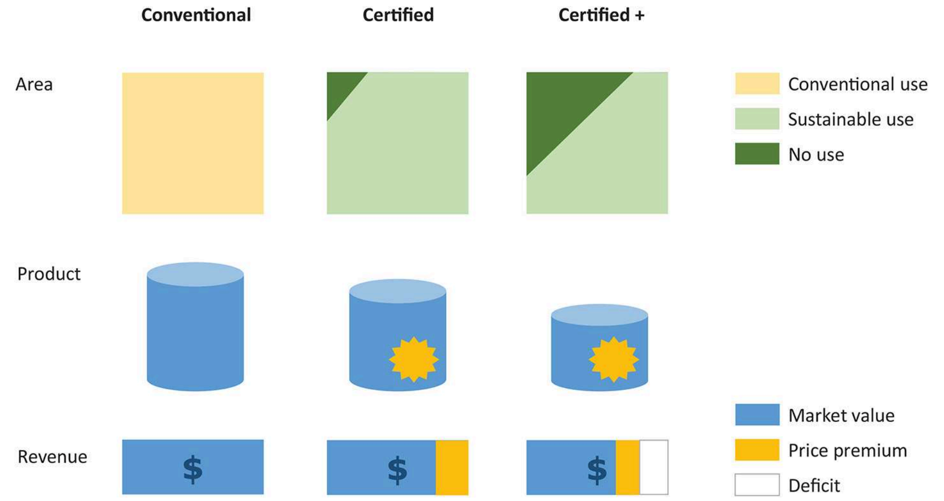

FIGURE 1 | Conceptual comparison between produced yields and income for the same area of forest under conventional and certified management. "Certified +" stands for certification that includes protection of IFL.

2016 to 2019 (https://fsc.org/en/page/facts-figures). This reflects, at least in part, the current atmosphere of uncertainty in the forestry sector regarding FSC certification to which the new IFL policy is contributing (Rotherham, 2016). Obtaining forest certification is a long process, and considerations as to whether to maintain a certificate might last longer than a few years, and such considerations might therefore not yet be reflected in currently reported certified areas. More remarkable is the strong increase of the area under double certification by FSC and the competing scheme Programme for the Endorsement of Forest Certification (PEFC). Data published jointly by FSC and PEFC shows a strong increase of the area under double certification in the three main IFL-countries Brazil, Canada, and Russia, as well as in all other countries from 2017 to 2018 (**Figure 3**). Around 43% of all FSC certified forest in Canada is now also certified by PEFC, with equivalent values being 27% for Russia and 51% for Brazil. This can be interpreted as a signal that the industry is seeking a backstop solution through an alternative certification scheme in the event that FSC is no longer tenable for them.

INCORPORATING IFL WITHIN THE FSC VOLUNTARY FRAMEWORK

The voluntary nature of certification means that the standards can only be as demanding as the marginal value of the certified label to the certified company. If standards become too demanding, certification will be a net cost, rather than a benefit to timber companies, resulting in "flight" from FSC. In order to prevent this, and to remain a viable influence in the timber trade, FSC could take either an "Exclusion Strategy," abrogating responsibility by excluding intact forests from certified areas, or a "Reduced-impact Strategy," allowing timber production in intact forests while attempting to reduce the impact of this activity with additional requirements. For other strategies to become viable, certification would need to move further to a landscape scale, as we propose in the last section of this article.

The Exclusion Strategy excludes forest concessions that overlap with intact forests from certification, by not allowing any new certificates in IFL areas or by revoking existing certificates from IFL areas. The FSC has been criticized for certifying logging inside intact forests (Greenpeace, 2017). Removing IFLs from the certified area protects the reputation of the FSC brand at a superficial level, but fails to address the drivers of intact forest degradation. From a conservation perspective, the Exclusion Strategy is only useful if areas excluded from FSC certified forestry operations are also excluded from any other uses and become protected by governments. Yet, protected areas around the world experience strong human pressures (Jones et al., 2018; Schulze et al., 2018) and the effectiveness of strict protected area management is limited (Oldekop et al., 2016). Furthermore, while the wider implementation of REDD+ payments remains deadlocked (see e.g., Nantongo and Vatn, 2019), governments have few if any sources of compensation for the creation of additional protected areas. The likely outcome is that many IFLs would be exploited by companies using conventional (non-certified) harvesting methods, or companies using other certificates that lack IFL considerations (Karsenty and Ferron, 2017).

Alternatively, FSC could follow the Reduced-Impact Strategy, in the expectation that impacts on intact forests would be much less under light and highly regulated extractive management than alternative exploitation scenarios. This approach would allow timber extraction from an agreed portion of IFL areas within certified concessions, on the basis of tighter requirements on timber harvesting practice, post logging controls and increased permanent conservation set asides in critically important areas. This would allow FSC to govern actions

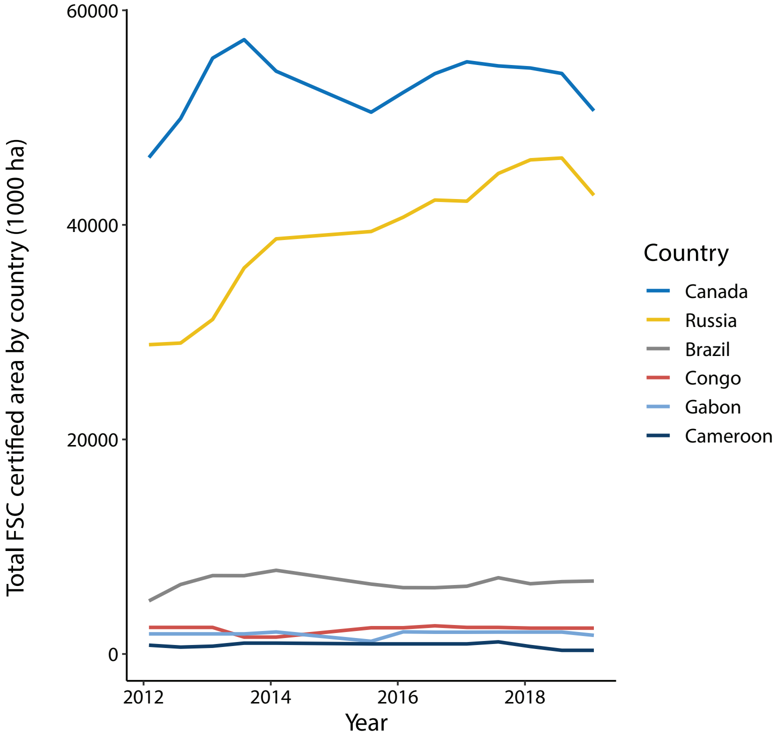

FIGURE 2 | Total FSC certified area between 2012 and 2019 in six countries with large IFL (source: https://fsc.org/en/page/facts-figures).

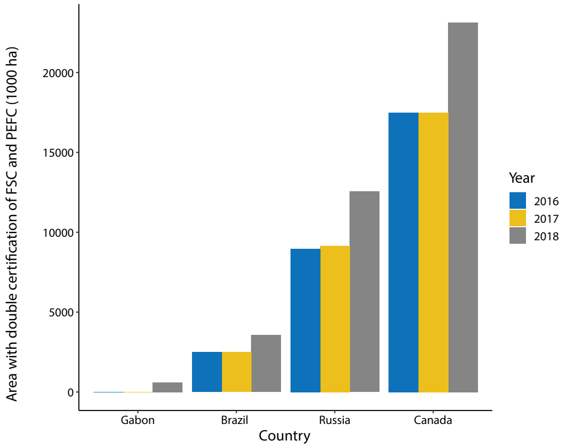

FIGURE 3 | Area (ha) with double certification by FSC and PEFC for countries with large IFL (sources: https://fsc.org/en/page/facts-figures, https://www.atibt.org/en/press-release-of-our-partner-pafc-gabon-the-forest-certification-pacf-gabon-continues-its-development-and-commitment-to-the-gabonese-forests-by-rose-ondo-president-of-pafc-gabon/).

in IFL portions of certified concessions, but will require a reinterpretation of FSC policy toward IFL and the practices allowed within them.

From an ecological point of view, there are two main arguments against logging in intact forests: modification of the forest stand due to tree harvesting (Martin et al., 2015), and provision of access to other land uses due to road building (Kleinschroth and Healey, 2017). Both processes can have severe impacts on plant and animal communities. Forest recovery strategies should, therefore, be an integral part of any forest management considerations. Forest recovery strongly depends on logging intensity (Kleinschroth et al., 2013). Common logging cycles of 30 years are considered too short to sustain yields of commercial species (Karsenty and Gourlet-Fleury, 2006), resulting in the strong contrast in standing value between intact and logged forests. At the same time carbon stocks in managed Amazonian forests have been shown to recover within <21 years at logging intensities below 30 m^3 ha^{-1} (Rutishauser et al., 2015). For disturbance sensitive animal species such as the woodland caribou (*Rangifer tarandus caribou*) in Canada, habitat recovery after clearcutting forestry operations takes at least 50 years (Environment Canada, 2012). In contrast, populations of chimpanzees (*Pan troglodytes troglodytes*) and gorillas (*Gorilla gorilla gorilla*) in tropical managed forests returned to baseline within <10 years after logging (Morgan et al., 2017). Especially in Central Africa, well-managed forests make an important contribution to species conservation (Clark et al., 2009; Stokes et al., 2010; Poulsen et al., 2011; Maisels et al., 2013). Forest and species recovery after logging are highly variable depending on geographical contexts. This highlights the importance of regional assessments of forest intactness to be used in forest management standards implemented on the ground.

The current identification of IFL is based on remote sensing and the most visible traces of industrial logging are the roads that are constructed for access. Definitions of intactness that could work within the FSC system could take into account ecological values on finer scales, and differentiate for the actual impact of different types of disturbance depending on the duration of time they occur, and on how quickly and effectively habitats can be restored afterwards. In such a case, the intact forest is maintained as an extensive forest unit that has not lost the main functions, carbon storage and the provision of habitat to disturbance sensitive species. The only forestry activities allowed would be constrained and regulated by strict adherence to FSC guidelines. Criteria for the definition of intact forests could include the extensiveness (e.g., more than 500 km^2) of continuous cover forest with viable populations of monitored umbrella species such as the above mentioned woodland caribou in boreal regions and primates in the tropics. Further management would need to incorporate ecosystem service outcomes that are accommodated within a carefully managed and certified concession. Human activities would be limited to those permitted by the certifications standards, and any interventions (e.g., logging areas and roads) should no longer be discernible through remote sensing within 5 years of their implementation (Kleinschroth et al., 2015). The Reduced-impact Strategy presupposes that effective monitoring and verification of the efficacy of certification guidelines in maintaining biodiversity and ecosystem services and functions across intact forest areas.

THE CONSEQUENCES FOR FOREST MANAGEMENT IN NON-INTACT AREAS

If FSC requires companies to retain the oversight and management of IFLs, it is likely that timber production from these areas will have to be reduced in line with more stringent operational requirements, even to zero under current IFL standards. This may drive the intensification of timber extraction outside IFL areas to maintain current levels of timber output with implications for the implementation of certification standards and the marketing of certified wood. The potential for companies to do this while remaining within the standards expected of FSC certification remains uncertain, and will no doubt vary on a case by case basis, but the more general point is that we might expect pressure to increase on non-IFL forests within concession areas. Sustainable intensification is an approach to minimize the environmental footprint of productive systems by increasing outputs per area for multiple purposes (Rockström et al., 2017), but the extent to which this can be achieved in natural (i.e., not plantation) tropical or boreal forests has yet to be assessed in detail.

In clearcutting regimes of boreal forests, sustainable intensification would mean higher investments in silvicultural interventions before and after harvesting, requiring investment from forestry companies in technology, recruitment and training of skilled employees (Naumov et al., 2016). For tropical forests with selective logging regimes, intensification could be achieved through higher extraction regimes in previously disturbed forest to increase light availability for faster regeneration of light-demanding timber species (Fredericksen and Putz, 2003). Other improvements include more careful mapping and planning processes, and using remote sensing and precision forestry before any operations take place. Increased efficiency in timber processing and transformation to reduce waste, and the marketing of a broader range of species, offer additional options for sustainable intensification (Karsenty et al., 2008; Horne, 2013). Current forestry regimes in remote regions with low tenure security may not, however, favor intensification on account of the costs relative to the returns when compared to conventional logging systems (Mathey et al., 2008).

URGENT NEED FOR LANDSCAPE SCALE SOLUTIONS

Land use changes in increasingly remote regions push back the forest frontier through degradation and forest clearance, and increased vulnerability to fire and illegal encroachment (Ahrends et al., 2010). To preserve intact forests, expansion into the forest frontier needs to halt. Buffers of managed natural forests might have an important function in maintaining a stable frontier between intact forests and agricultural land (Gaveau et al., 2013), provided that these activities are genuinely sustainable, and managed in a way that does not facilitate "hidden" encroachment as has been observed in agroforests that expand into natural forests legally or otherwise.

Care should be taken to ensure that "Exclusion Strategies" do not lead to displacement of unsustainable forest uses to other areas or countries with weaker law enforcement (Lambin and Meyfroidt, 2011). Such leakage has been observed in the context of REDD+, where deforestation was avoided where it was been paid for, but this led to forest losses elsewhere (Fisher et al., 2011). FSC provides some leverage to protect more intact forest areas, while ensuring financial benefits flow to forests country governments. Yet, any effort of FSC to protect intact forests will be spatially limited to those areas where certified concessions overlap with intact forests. Intact forests are generally larger than certified forest areas, meaning that measures to afford permanent protection to intact forests still depend on the creation, financing and management of protected areas. If certified forest management is to play a major on-the-ground role in intact forest protection, forest management certification of intact areas should be spatially aligned with protected areas.

Moving certification from the concession to the landscape scale, allows thinking beyond the land sharing—land sparing paradigm. Land use allocations in forested landscapes that strike a balance between productivity and conservation have been proposed. In a case study in Borneo, setting aside two-thirds of the land as protected areas could potentially be compensated by the incomes from certified selective logging and wood fiber plantations on the remaining third of the land (Runting et al., 2019).

Yet the landscape approach demands a coordination process that operates above the concession scale. Coordinated planning that encompass a range of degraded, productive and intact forests in order to direct optimal spatial configurations of forest uses and restoration is not currently possible through management unit based voluntary certification. Moreover, supply chains emanating from regions such as the Congo Basin are structured around specific timber commodities, and a business plan built around plantations, even if only a small proportion of the land, is not necessarily viable. The proposed differential land allocation solution requires action from a range of stakeholders, including governments, and new paradigms for land use planning and conservation finance.

The protection of intact forests is gaining momentum and support from society, but existing certified companies view the IFL issue as a challenge to their continued viability in important timber producing regions (Rotherham, 2016; Karsenty and Ferron, 2017). To protect more intact forest, we need to explore ways of overcoming the concerns of certified companies that are often the most progressive actors in IFL frontier areas. Since these companies agreed to be certified, we can assume that they have some degree of willingness to respect and enforce ecological considerations in response to the demands of their target markets. To bridge this challenge, we might need to compromise on the strict non-intervention IFL approach, while still retaining the core elements of its agenda, including the preservation of extensive forest areas, the biodiversity they contain, and the services they provide. Alternatively, incentives could be provided in the form of compensation payments for non-exploitation, and these can be within the context of landscape-level payments for ecosystem services (Ghazoul et al., 2009). In other words, certification that includes the protection of IFL areas could make a company potentially eligible for REDD+ payments. Making a stronger link between the ecological necessities of intact forest protection and the economic possibilities of certification can eventually strengthen both, for the benefit of livelihoods in production and conservation forests.

DATA AVAILABILITY STATEMENT

Publicly available datasets were analyzed in this study. This data can be found here: https://fsc.org/en/page/facts-figures.

AUTHOR CONTRIBUTIONS

FK conceived of the paper, wrote the first draft, and coordinated the writing. TR provided important input to content and structure of the text. JG led the research and finalized the writing of the paper.

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Measuring Forest Biodiversity Status and Changes Globally

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The world's forests are crucially important for both biodiversity conservation and climate mitigation. New forest status and forest change spatial layers using remotely sensed data have revolutionised forest monitoring globally, and provide fine-scale deforestation alerts that can be actioned in near-real time. However, existing products are restricted to representing tree cover and do not reflect the considerable spatial variation in the biological importance of forests. Here we link modelled biodiversity values to remotely sensed data on tree cover to develop global maps of forest biodiversity significance (based on the rarity-weighted richness of forest mammal, bird, amphibian and conifer species) and forest biodiversity intactness (based on the modelled relationship between anthropogenic pressures and community intactness). The strengths and weaknesses of these products for policy and local decision-making are reviewed and we map out future improvements and developments that are needed to enhance their usefulness.

Keywords: forest cover, remote sensing, biodiversity, Biodiversity Intactness Index (BII), IUCN Red List

INTRODUCTION

The world's forested biomes are crucially important for terrestrial biodiversity but humanity's growing demands for resources have led to the removal of natural forest for agriculture and the degradation of forest landscapes through hunting and timber removal, fragmentation, pollution, and other human impacts (Foley et al., 2005; Song et al., 2018). Such pressures are impacting forest biodiversity (Newbold et al., 2013, 2016; Phillips et al., 2017), as many sensitive species are reliant upon intact forest landscapes and "primary" forests (Gibson et al., 2011; Betts et al., 2017).

Remote sensing has been established for over 40 years as a vital tool for understanding how land cover and land use are changing over time. As satellite technology and analytical methodologies have improved, computing power has increased and data have become increasingly freely accessible, the available products have increased greatly in sophistication and spatial and temporal resolution. For forest biomes, these developments have resulted in the creation of the world's first global 30-m resolution tree-cover status and change product (Hansen et al., 2013), which in turn facilitated the development of a suite of academic papers and freely available products within the "Global Forest Watch" partnership, covering forest status and trends (Hansen et al., 2013), forest carbon (Tyukavina et al., 2015), and forest tree height (Hansen et al., 2016).

However, measurements of tree presence and absence alone are a poor surrogate for biodiversity value and biodiversity loss (Tropek et al., 2014). Biodiversity, including measures such as species diversity, species endemism, or genetic diversity, is unequally distributed, with major biological differences among and within the forested ecoregions of the world (Olson et al., 2001; Dinerstein et al., 2017). This variation means that equally sized areas of tree cover, mapped through remote sensing, often differ dramatically in biological value (however this may be defined) among different continents, and at different locations, latitudes, and elevations. While these patterns have been explored for particular taxa by linking species distribution data to global tree cover loss data (e.g., Buchanan et al., 2011), until now there has been no global analysis of biological values of forests (covering a broad suite of taxa) linked to the newly available tree-cover data enabled by Hansen et al. (2013).

In this paper we present approaches that estimate how forest cover change affect two aspects of biodiversity value, through a combination of modelled biodiversity data that are spatially linked to remotely sensed data. The first approach uses data from the IUCN Red List (www.iucnredlist.org), a widely used dataset relating to species' risk of extinction, including spatial distribution maps for each species. We use these maps to estimate and map biodiversity significance, based on rarity-weighted richness (through aggregate scores of range-size rarity), for all forest-dependent mammals, birds, amphibians and conifers across the forested regions of the world, highlighting locations that make a disproportionate total contribution to the global distributions of these species (Williams et al., 1996).

The second approach uses data from the PREDICTS database, a large taxonomically and geographically representative global database of the impact of anthropogenic pressures on local biodiversity (Hudson et al., 2017). This database is analysed statistically to estimate and map biodiversity intactness, following the framework outlined by Newbold et al. (2016) and Purvis et al. (2018), reflecting the proportion and abundance of a location's original forest community that remain.

These two layers are both informative about how different facets of forest biodiversity are distributed; considering them together provides added information, such as highlighting areas that are potentially suitable for restoration or conservation.

MATERIALS AND METHODS

Tree Cover Change

Gridded tree cover, tree-cover loss and tree-cover gain data as described by Hansen et al. (2013) were accessed in December 2017 from the Google Earth Engine (Gorelick et al., 2017) data repository. However, tree cover for 2010 was accessed from the USGS Land Cover Institute (2017). Thresholds of minimum crown cover/closure (MCC), from here on referred to as tree cover, for delimiting forested land vary greatly within scientific literature (Lund, 2002, 2015; Magdon and Kleinn, 2013; Magdon et al., 2014). The US National Vegetation Classification System defines forests as areas with a 60% tree cover (Grossman et al., 1998), UNEP (2001) use a threshold of 40% tree cover to distinguish closed forests, Kohl and Päivinen (1996) use a threshold of 20% tree cover for distinguishing European forests and the Vegetation Resources Inventory (for Canadian forests) defines a treed area as having 10% tree cover (Sandvoss et al., 2005). The FAO uses a threshold of 10% MCC to determine whether an area has been deforested (FAO, 2000) in contrast to Hansen et al., 2010 who suggest that a value <25% MCC can be used for measuring global deforestation across all biomes, due to its ability to "identify tall woody vegetation unambiguously in multispectral imagery." Tropical and more forested countries typically use higher tree cover in their national assessments relative to countries primarily outside of forest biomes, for example, Zimbabwe defines forest using a tree cover of 80% (Magugu and Chitiga, 2002) whereas Australia uses a tree cover of 20–50% (ABARES, 2018). The scale of the reference area is important, with forest area positively correlated to reference area size (Magdon and Kleinn, 2013). For this study we selected the more conservative value of 60% tree cover to indicate the presence of forest; however, for comparison, we also calculated biodiversity intactness and biodiversity significance maps using a forest definition of 25% tree cover and have included the results within the Supplementary Material (**SM Figures 1–3**).

Tree cover data may not distinguish between natural forests and forests that have been planted for human uses, yet the biodiversity value of such plantation forests is typically considerably lower (e.g., Gibson et al., 2011; Newbold et al., 2015; Phillips et al., 2017). If the rotation length of plantations is greater than the time span of the tree-cover data, and other criteria such as height and density of trees are met, then treating plantation forests as though they are natural would lead us to overestimate their biodiversity value. To distinguish between natural forests and plantation forests we used the Spatial database of Planted Trees (SDPT; Harris et al., 2019), a compilation of mapped and modelled plantation data from multiple countries, that focuses on including intensively managed plantations and excludes semi-natural forests with intensive natural regeneration. Plantations in China and Papua New Guinea in the SDPT could not be included due to data restrictions. Further details of spatial datasets used in this study can be found in **SM Table 2**.

Biodiversity Significance

Tree cover data for 2018 and annual tree-cover loss data between 2000 and 2018 were used in this analysis.

Using the IUCN Red List dataset (www.iucnredlist.org), we extracted spatial data on distributional boundaries and tabular data on habitat preferences and elevation limits for birds, mammals, and amphibians (provided by IUCN in October 2017) and conifers (in November 2017). Following Tracewski et al. (2016), we defined forest-dependent species as those birds coded by BirdLife International as having high or medium forest dependency (Buchanan et al., 2008; Bird et al., 2012), and those mammals and amphibians coded by Rondinini et al. (2011) and Ficetola et al. (2015), respectively, as having high forest dependency. Differences in forest-dependency selection criteria (i.e., high, medium etc.) between birds and other taxa reflect variation in how dependency is defined. We defined forest-dependent conifers as those coded for forest habitats only (IUCN, 2017). This produced a list of forest-dependent mammals ($n = 1,463$), amphibians ($n = 3,563$), birds ($n = 6,841$), and conifers ($n = 393$), totalling 12,260 species for further analysis. These taxonomic classes are the only ones in which all or nearly all terrestrial species have been assessed for the IUCN Red List and for which spatial distribution maps are available (BirdLife International Handbook of the Birds of the World, 2016; IUCN, 2017).

Biodiversity Significance of Remaining Forest in 2018

To calculate the significance of remaining forest habitat for each forest-dependent species, we produced an "Extent of Suitable Habitat" (ESH) map [now known as Area of Habitat: (Brooks et al., 2019) through exclusion of areas within the species' distribution with (1) <30% tree cover in 2000, or (2) any tree cover loss between 2000 and 2018, and/or (3) altitude outside the species' elevational limits as defined by IUCN (2017). Spatially explicit elevation data was obtained from the GMTED2010 dataset (Danielson and Gesch, 2011). We also removed areas of plantations based on the SDPT dataset (Harris et al., 2019), except for ∼20% of species that were listed with affiliations coded as "Suitable" for either Plantations or Subtropical/Tropical Heavily Degraded Former Forest habitats (IUCN, 2017). For such species, composed primarily of birds, including plantation areas in the ESH calculations represents their ability to utilise both habitats. Where these are present within the species' range this will then lead to lower significance scores in natural forest areas, reflecting their lower dependence on natural forest habitat.

The range-size rarity for each species within a grid cell was calculated as the contribution of each ∼30 m cell toward the global extent of suitable habitat for the species (i.e., the inverse of the ESH within each species' distribution). For those species coded with having different seasonal distributions, we calculated range-size rarity scores for each of these distributions separately. Range-size rarity scores were summed across all species present within a grid cell to give an overall rarity-weighted richness score, or the "biodiversity significance" of the cell. Cells with high values for biodiversity significance typically contain more species for which the cell comprises a larger proportion of their global distribution. Loss of forest in such cells is therefore of disproportionate significance in terms of loss of biodiversity (at least for the taxonomic groups considered). We note that there are many alternative ways of estimating biodiversity importance, but we use the term "biodiversity significance" for this metric as "rarity-weighted richness," "range rarity," and related terms are not widely understood by non-specialists.

We converted species' distribution polygons to raster format at ∼1 km resolution. This resolution is more relevant to the accuracy of the species distribution data than the high resolution (∼30 m) forest data. However, to calculate the area of forest habitat (ESH) per species, and for creating final outputs, we used the forest data at ∼30 m resolution. Therefore, the coarser resolution of the underlying species data remains in the final outputs, i.e., biodiversity significance values for forest pixels do not vary within ∼1 km cells. All analyses were completed in Google Earth Engine (Gorelick et al., 2017).

Significance of Forest Loss 2000–2018

To calculate the significance of loss, we followed a similar approach, but instead calculated range-size rarity values based on ESH using forest cover from 2000. This shows how significant a pixel of forest was for a species in 2000. We then summed this value across all species per cell to calculate the biodiversity significance of forest cells lost during 2000–2018.

Biodiversity Intactness

To model biodiversity intactness, we analysed the PREDICTS database which comprises well over 3 million rows of geographically and taxonomically representative data of land-use impacts to local terrestrial biodiversity derived from the primary literature and other databases (Hudson et al., 2017). As our intention was to explore the impacts of forest change, the database was first subset to sites within forested biomes (Olson et al., 2001) yielding a dataset from over 550 studies encompassing over 19,700 sites, 2.3 million observations and ∼25,000 taxa. A generalised linear mixed-effects model framework was used to assess how community abundance was impacted by land use and human population density (extracted from HYDE 3.1: Klein Goldewijk et al., 2011) within forest biomes, following the methods outlined in Newbold et al. (2016). Briefly, the random-effects structure included a study-level random effect to account for the innate variability between samples collected using different methodology and focused upon varying taxa, and a biome-level random effect with human population density as a random slope to account for differences in the influence of human population density among biomes. A random slope of land use within study accounted for the study-level variation in the influence of land use on community abundance. The fixed-effects structure was selected using backwards stepwise selection using likelihood ratio tests to select the most appropriate model. The model of compositional similarity followed the methodology of De Palma et al. (2018) (see also Newbold et al., 2019, Nature Ecology and Evolution). In brief, a matrix of paired site-level comparisons was first prepared where all sites within a study were compared to all minimally-used primary vegetation sites within that same study. The asymmetric Jaccard Index was employed to calculate abundance-based compositional similarity for each paired comparison, and a mixed-effects model was fitted to predict the influence of land use, the environmental distance between sites and the geographic distance between sites, on logit-transformed compositional similarity. The community abundance and compositional similarity model coefficients were multiplied to produce the abundance-based Biodiversity Intactness Index (BII), our biodiversity intactness metric.

To estimate how the spatial patterns of forest change have affected biodiversity intactness, we used the layers of tree cover, loss, and gain during 2000–2014 (Hansen et al., 2013 updated) to produce a map of land-cover change. The downscaled land-use map produced by Hoskins et al. (2016) provides data on anthropogenic land uses (such as cropland, pasture and urban) at a spatial grain of ∼1 km^2; we used this map to infer the land use after deforestation. Each deforested pixel was allocated the proportions of the anthropogenic land-use categories within the corresponding grid cell of the downscaled land-use map.

We defined 12 Boolean conditions describing important boundaries within the input data layers (**SM Table 1**). Mutually exclusive expressions were then built to describe each of the land covers as a function of the Boolean variables (Equations 1–7). It was important to include a distinction between tropical and temperate areas due to the input data informing the model coefficients. The PREDICTS database, which populates and informs the models for BII, uses different classification schemas for tropical and temperate environments: specifically, tropical secondary forest characterised as "young" cannot be older than 10 years, whilst in temperate biomes "young" secondary forests can be up to 30 years old. This reflects the speed with which succession takes places in temperate vs. tropical areas, and especially how intactness can recover faster in the tropics. The expressions below reflect this by introducing variable I (**SM Table 1**), which differentiates tropical and temperate biomes.

$$A_{\text{Primary, Mature Secondary}} = P' \cdot T \cdot L' \cdot G' \cdot V' \tag{1}$$

$$\begin{aligned} A_{\text{Intermediate Secondary}} = {} & P' \cdot (T \cdot L' \cdot (G + V)) \\ & + ((T' + L) \cdot D' \cdot R' \cdot I) \end{aligned} \tag{2}$$

$$A_{\text{Young Secondary}} = P' \cdot (T' + L) \cdot D' \cdot ((R \cdot I) + I') \tag{3}$$

$$A_{\text{Cropland}} = P' \cdot (T' + L) \cdot D \cdot C \tag{4}$$

$$A_{\text{Pasture}} = P' \cdot (T' + L) \cdot D \cdot B \tag{5}$$

$$A_{\text{Urban}} = P' \cdot (T' + L) \cdot D \cdot U \tag{6}$$

$$A_{\text{Plantation}} = P \tag{7}$$

A primary or mature secondary forest is defined as an area which is not a plantation, meets the forest cover in 2010 criteria, and which has not experienced forest loss (Equation 1). It must also not have recorded growth, and tree cover must have been stable (±20%) between 2000 and 2012 (Equation 1). An intermediate secondary forest is defined as an area which is not a plantation and which is either: an area which experienced loss or does not meet 2010 cover criteria, but which is not disturbed and is both tropical and over 10 years old; or which meets cover criteria and has not experienced loss but is either still growing or unstable in its cover between 2000 and 2012 (Equation 2). A young secondary forest is defined as an area which is not a plantation and has experienced loss or does not meet 2010 cover criteria, but which is not disturbed, and is either tropical and under 10 years old, or temperate (Equation 3). Cropland is defined as an area which is not a plantation and does not meet 2010 cover criteria or has experienced loss, which is also sufficiently disturbed, was not disturbed by natural fires, and is dominated by cropland (Equation 4). Pasture is defined as an area which is not a plantation and does not meet 2010 cover criteria or has experienced loss, which is also sufficiently disturbed, was not disturbed by natural fires, and is dominated by pasture (Equation 5). Urban land is defined as an area which is not a plantation and does not meet 2010 cover criteria or has experienced loss, which is also sufficiently disturbed, was not disturbed by natural fires, and is dominated by urban areas (Equation 6). Finally, plantations are defined as areas which are covered by the plantations layer, independent of all other variables (Equation 7). A description of the Boolean conditions used to define land use can be found in **SM Table 1**.

This resulted in a map within forested biomes with the following land use classes: Primary/mature secondary forest, Intermediate secondary forest, Young secondary forest, Cropland, Pasture, and Urban. The statistical models were crossed with global maps of biomes, land use, and human population density to make global spatial projections of both abundance and compositional similarity, which were then multiplied together to provide a map of modelled biodiversity intactness.

RESULTS

Forest Biodiversity Significance

Our forest biodiversity significance layer shows that the relative importance of forest locations—in terms of their contribution to the distributions of mammal, bird, amphibians and conifer species occurring in them—varies around the world (**Figure 1**). The areas with low values across most of the temperate region tend to support fewer species and these tend to have larger geographical distributions. While lowland tropical forests in the Amazon and Congo basins are species-rich, these species also tend to have large distributions, so the contribution of any individual location to the overall distributions of these species tends to be low. Conversely, montane forests in South America, Africa and SE Asia all contain many species with small geographical distributions, as do the lowland forests of insular SE Asia, coastal Brazil, Australia, Central American, and Caribbean islands. These regions all show high values for biodiversity significance on our map; as well as being species-rich these individual locations make a greater contribution to the overall distributions of the species occurring within them.

The forest biodiversity significance of tree-cover lost from 2000 to 2018 gives an indication of the impacts of removal of forested habitat (with the caveat that some forest loss may be from natural causes, such as hurricane damage). Our results (**Figure 2**) highlight those regions where tree cover loss (change from above 60% tree cover to 0% tree cover within a 1 km^2 pixel) has resulted in disproportionate loss of the distributions of the world's forest-dependent species (in the taxonomic groups considered): Madagascar, parts of eastern Brazil, central America, SE Asia, West Africa, Australia, and northern New Zealand. Intermediate levels of loss are seen across large regions of the forests of continental and insular SE Asia. Although areas of particularly significant forest biodiversity loss occurred in the tropics during this period (a reflection of the higher species richness as well as the density of endemic species within the tropics), it should be noted that the map also highlights the biodiversity significance of the substantial extent of deforestation that has occurred over the last 18 years within temperate areas. Scandinavia, Russia, Canada and the USA have all undergone considerable losses in forest cover, mainly due to large-scale logging and fires (Curtis et al., 2018). Although these areas support relatively fewer species and these species tend to have larger global distributions, the aggregate biodiversity impacts may be substantial. The layer does not distinguish between forest

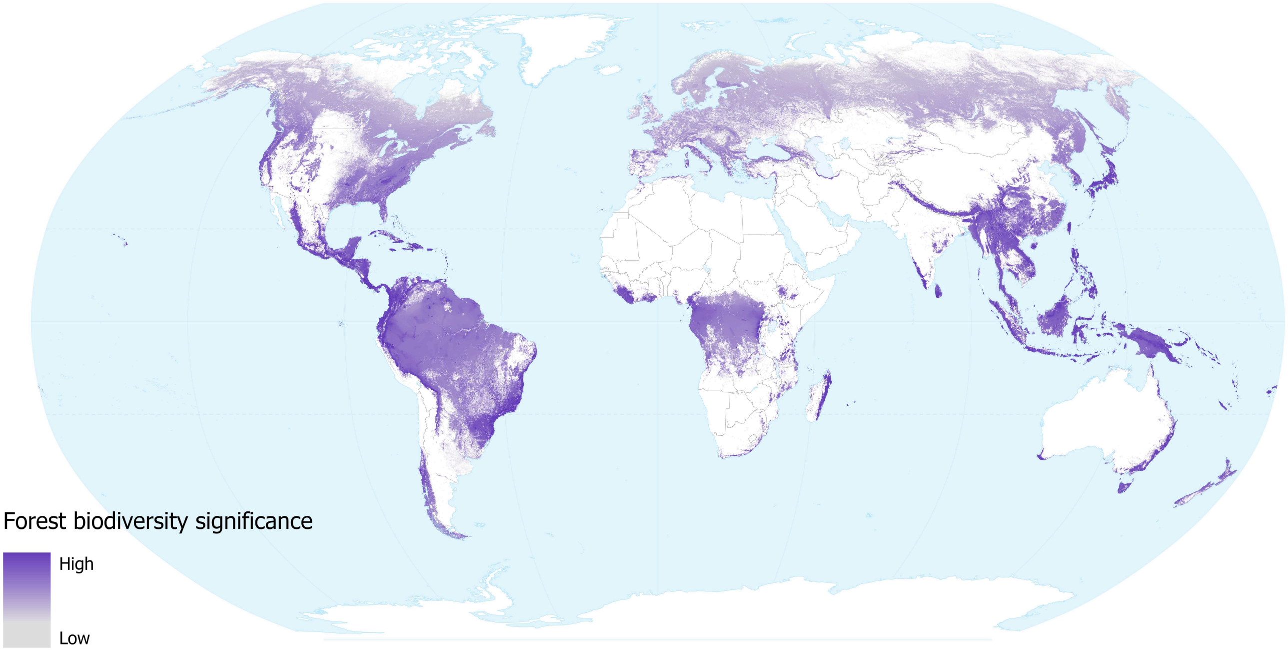

FIGURE 1 | Forest biodiversity significance in 2018, in terms of the contribution of each location to the distributions of forest mammal, bird, amphibian, and conifer species occurring in them. Grey shows low and dark purple shows high significance values. White shows areas not classified as forest (i.e., tree cover values were <60% in 2000, lost between 2000 and 2018, or mapped as plantations).

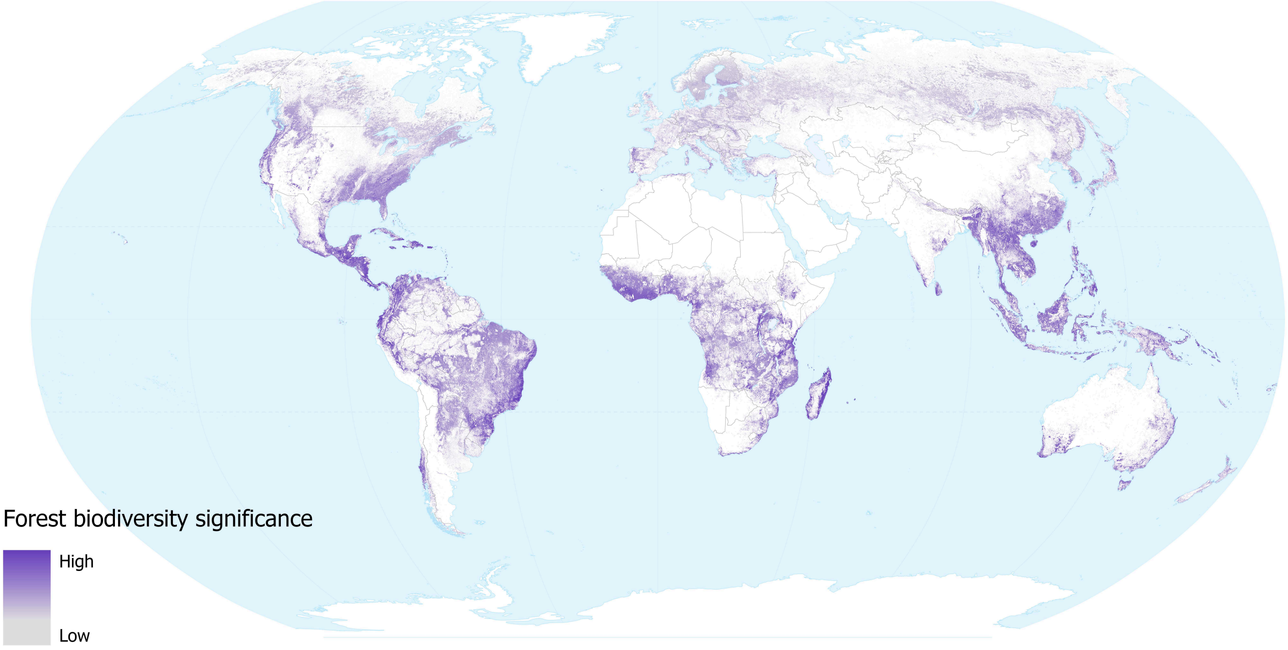

FIGURE 2 | Forest biodiversity significance for areas of forest loss during 2000–2018, in terms of the contribution of each location to the distributions of forest mammal, bird, amphibian, and conifer species occurring in them. Values are for the year 2000 in areas where forest was subsequently lost. Grey shows low and purple shows high significance. White areas are not classified as forest in 2000 (i.e., tree cover was <25% in 2000, or area was mapped as plantation), or where forest remains in 2018 (i.e., no loss during 2000–2018).

loss that is likely to be permanent in the foreseeable future (e.g., conversion to agriculture) and forest loss that may only be temporary (e.g., resulting from fires or sustainable forestry practices in parts of Canada and Scandinavia). We did not consider forest gain in our assessment, but this is unlikely to overestimate biodiversity loss substantially during the period, as most forest-dependent species do not recolonise young regrowth.

Forest Biodiversity Intactness

The forest biodiversity intactness layer reveals the impact that forest change and human population density has had on species assemblages.

Our models revealed that land use and human population density are significant predictors of community abundance ($\chi^2 = 38.04$, $df = 7$, $p < 0.001$ and $\chi^2 = 7.99$, $df = 1$, $p = 0.005$, respectively). Heavily utilised areas of the world are unsurprisingly less intact (**Figure 3**), for instance, much of Europe and the more densely populated areas of India, North America, Bangladesh, and China. In these areas, the impact of dense human populations together with the urban and agricultural land use required to support them has led to severe losses of biodiversity intactness. Madagascar, coastal Brazil, South Africa, southern Australia, and northern Africa, are also identified as areas with striking losses in biodiversity intactness. These regions have undergone intense removal of natural forest, but retain more of their native biodiversity due to lower levels of urbanisation.

Comparison of Biodiversity Significance and Intactness

Overlaying biodiversity intactness and significance provides insight into areas with high values for both, and areas that score highly for one but not the other. Regions with high values for both metrics include the Northern Andes and Central America, south-eastern Brazil, the western, and eastern parts of the Congo basin, southern Japan, the Himalayas, and various parts of Southeast Asia and New Guinea (**Figures 4**, **5**). By contrast, Europe (**Figure 5D**) is dominated by large areas of biodiversity intactness in the north-east and areas of high biodiversity significance in the south, but lacks large areas where both are high.

DISCUSSION

We present two new biodiversity layers for the world's forests, derived from existing data but in novel ways that aim to add contextual meaning to forest data for use in conservation decision-making.

The layers describe two different dimensions of biodiversity and so are not expected to show the same geographic patterns. Biodiversity significance combines spatial variation in both species richness and levels of endemism, and hence shows the relative contribution of any location to the persistence of forest species. However, the degree to which the values in any particular location are driven by one of these characteristics or the other cannot be determined without further analysis. Furthermore, high endemism may result from either natural endemism, human-induced geographic restriction, or a combination. By contrast with biodiversity significance, biodiversity intactness is highest where ecological assemblages remain intact, irrespective of natural macroecological variations in species diversity or endemism; intermediate values can reflect a range of combinations of reduced overall abundance and reduced compositional similarity to an intact assemblage. In general, biodiversity significance is higher within the tropics (especially in topographically heterogeneous regions) and lower in northern, boreal regions, whereas biodiversity intactness is generally low across most of Europe, India and eastern Asia and high within wilderness areas in northern European and North American forests, as well as within tropical forest cores across Central America, South America, Africa, and Asia.

Safeguarding areas of high significance is important as their loss results in a disproportionate loss of species' distributions, especially narrow-range endemics, elevating species' risk of extinction. High intactness is important to safeguard in order to (a) maintain ecosystem functioning; (b) retain community resilience against pressures such as climate change; and, in the case of forest ecosystems, (c) help mitigate climate change through greenhouse gas regulation (Steffen et al., 2015). Biodiversity intactness is also relevant to efforts to define wilderness regions, intact forest landscapes, or areas that have been described as the "last of the wild" (Potapov et al., 2008; Watson et al., 2016, 2018).

At a more local scale, comparison of the layers may provide information relevant for conservation. For example, landscapes of high significance but low intactness may be appropriate targets for restoration efforts. Landscapes that contain both high intactness and high significance reveal locations with relatively high density of geographically restricted native species. Such areas may therefore be important to safeguard through broad-scale policy responses or site-scale conservation measures such as designation of protected areas. However, biodiversity has multiple dimensions and here we have chosen to focus on just two. When considering prioritisation of areas for conservation management other aspects of biodiversity may also be relevant such as phylogenetic diversity or the presence of charismatic species.

The biodiversity significance layer shows similar patterns to those revealed by the distribution of endemic bird areas and biodiversity hotspots that were identified in the 1990s (Myers, 1990; Mittermeier et al., 1998, 2004; Stattersfield et al., 1998). The advantage of our approach is that it is based on many more species than used in these earlier analyses, and the distribution of each species considered is spatially explicit, allowing much finer resolution maps. Furthermore, the analytical approach is repeatable and allows the layer to be updated as more species and taxonomic groups are added.

The biodiversity intactness later broadly accords with Newbold et al.'s (2016) map, with areas of greatest loss in densely populated and heavily converted regions such as most of western Europe, northern China, and the southern coast of South Africa. However, our estimates for plantation-rich parts of Southeast Asia are notably lower than those of Newbold et al. (2016), which

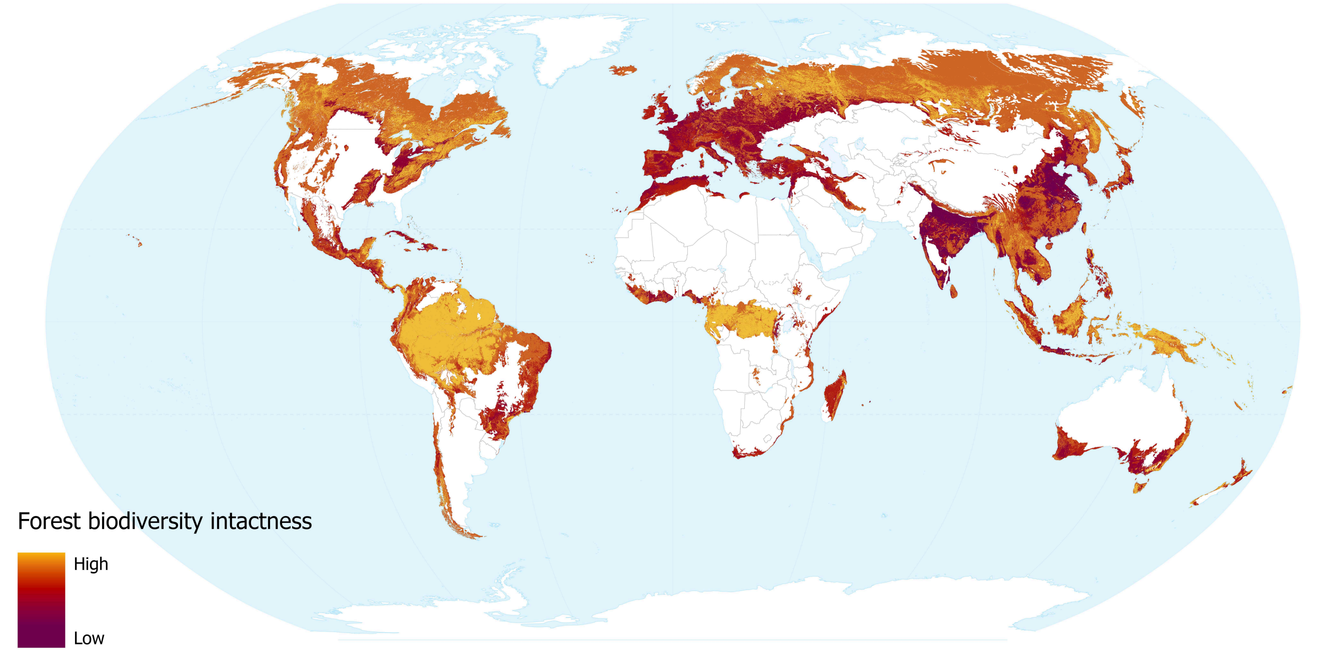

FIGURE 3 | Forest biodiversity intactness, showing the impacts of forest change and human population density. Yellow shows more intact areas and dark red shows more degraded areas.

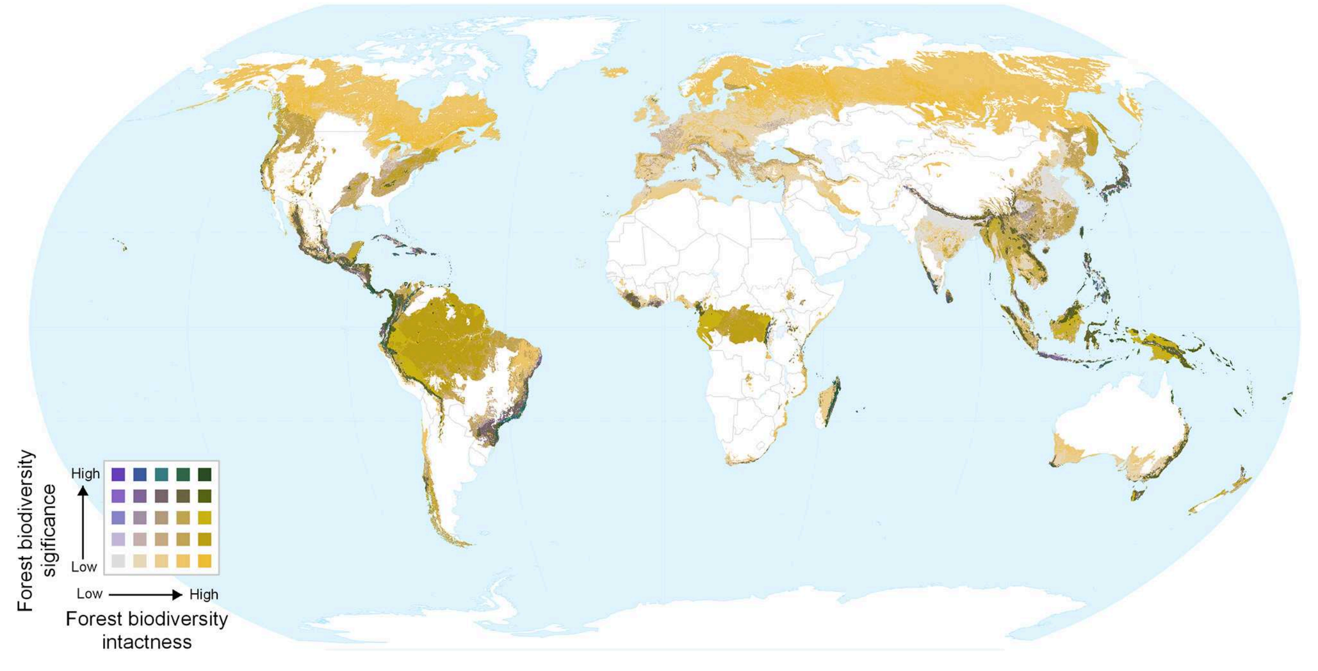

FIGURE 4 | Bivariate map of forest biodiversity significance and intactness. Dark green areas show both high intactness and high significance.

were criticized by Martin et al. (2019) as being too high. Our forest biodiversity intactness map is also able to distinguish areas of recent (post-2005) forest change, such as lowland Mexico and regions in Southeast Asia.

The outputs we highlight here are relevant to international and national policy including the Convention on Biological Diversity (CBD) (Parties' National Biodiversity Strategies and Action Plans, and National Reports), the Paris Agreement of

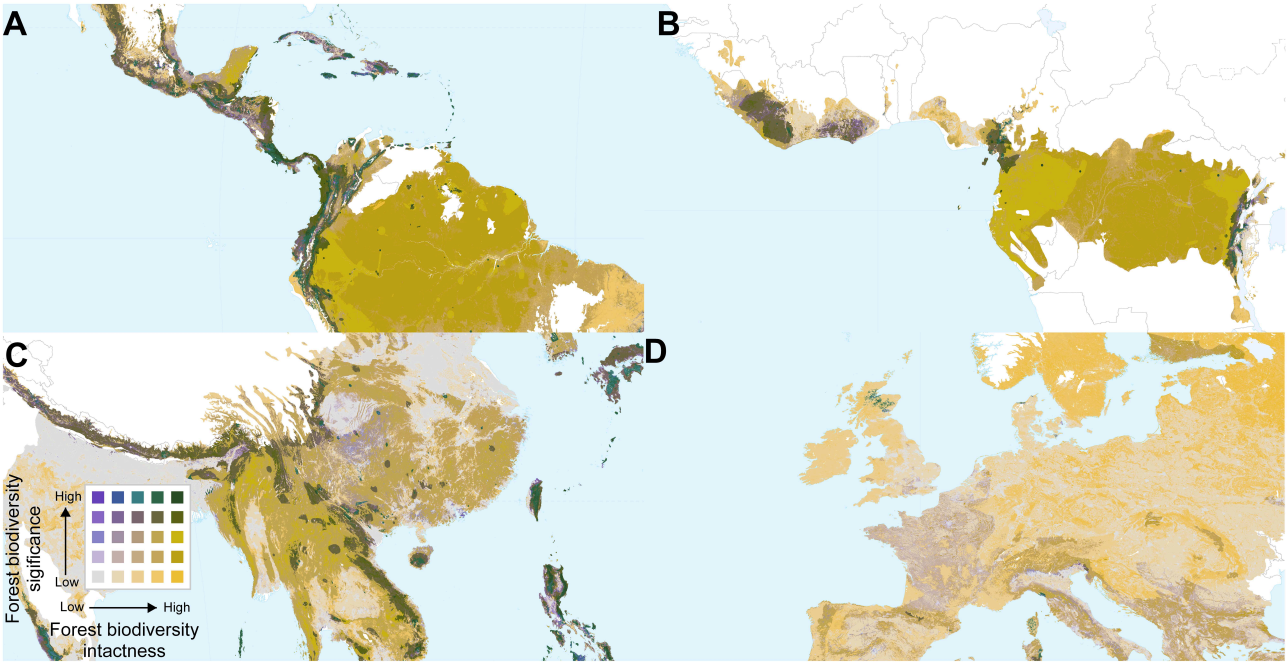

FIGURE 5 | Bivariate maps of forest biodiversity significance and intactness within forest biomes, focused on parts of **(A)** Central and South America, **(B)** Central and West Africa, **(C)** China and South East Asia, and **(D)** Western Europe. Spatial scales differ among the panels.

the UN Framework Convention on Climate Change, Bonn Challenge, and global environmental assessment processes such as the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services and the Global Biodiversity Outlook. The layers are potentially useful both for targeting policy responses and on-ground interventions, and for tracking progress towards goals and targets. For example, global, regional and national maps and indicators of the proportion of areas of high forest biodiversity significance or intactness lost over time are relevant to Aichi Target 5 in terms of measures of loss and degradation of habitats, Aichi Target 11 in terms of areas of biodiversity significance, and Aichi Target 12 in terms of preventing extinctions and declines of threatened species. Data on tree-cover loss linked to biodiversity can also be used for national REDD+ planning and monitoring other commitments to international, regional and nation agreements, policies, and laws. The layers are also relevant to the safeguard policies of investors, financial institutions, and companies.

The data that we have brought together here are the best available, but have a number of limitations. For instance, the Hansen et al. (2013) dataset does not allow for regional calibration, yet the height and density of natural tree cover will vary depending upon local variations in environmental conditions (Tropek et al., 2014). We were not able to account for the variation of natural tree cover on a local scale and, as no standard definition of the tree cover associated with natural forests exists at larger scales, our conservative literature-based choice of a 60% tree cover threshold is unlikely to optimally delimit natural forest across the entire area of our analysis. A comparison of the biodiversity significance and intactness maps derived using a 25% tree cover threshold to indicate forest presence (**SM Figures 1–3**) illustrates this issue. For instance, when considering the biodiversity significance layer, landscapes with high endemicity and a naturally low forest cover are highlighted in the layer at this lower threshold, including the Okavango Delta in Botswana, the South African coast, and the western coast of Madagascar (**SM Figure 1**). Likewise, the biodiversity intactness layer produced using the 25% threshold reveals intactness with northern boreal forests and dry forests in Zambia, which have a naturally sparse tree cover, that are not highlighted in the 60% threshold layer. However, the 25% threshold intactness layer does not show degraded areas within West Africa, including south-east Ghana, which would naturally be covered with dense tree cover (**SM Figure 3**). The Hansen et al. (2013) dataset does not provide gain data across all years of our analysis, which meant that it could not be used within the biodiversity significance layer. However, this is unlikely to bias our results substantially given that forests often take considerable time before becoming suitable for forest-specialist species (Newbold et al., 2014).

When producing the biodiversity significance layer, the forest species' distribution maps were clipped by forest cover and suitable elevations to create maps of the Extent of Suitable Habitat (sensu Beresford et al., 2011), which are finer resolution representations of distribution. However, they do not map occupancy *per se*, and contain commission errors (e.g., owing to extirpation caused by over-exploitation, invasive alien species etc.), although this is not likely to bias the broad patterns across >12,000 species that are shown in the resulting layer. The layer does not take account of variation in abundance within species' distributions, spatial data for which are not available for the large set of species considered. The data used are not currently taxonomically representative—for instance, no invertebrates are included—and clades may have systematically different degrees of spatial resolution in their distributions resulting in the species with the most resolved maps obtaining higher values. The coding of forest dependence in the IUCN Red List does not capture finer-scale variation. In the coming years, the layer will be updated to incorporate data on the distributions of all forest reptiles and a number of forest plant groups (e.g., trees, gingers, rattans) and invertebrate taxa (e.g., dragonfly, monarch and swallowtail butterflies) as these are assessed and mapped for the IUCN Red List.

Likewise, the biodiversity intactness layer has caveats (though our analysis overcomes many of the issues raised by Martin et al., 2019; see also Newbold et al., 2019). For instance, the layer is based upon data extracted from the (Hansen et al., 2013) (updated) tree cover change dataset which only dates back to 2000. Therefore, we are not able to distinguish between forest that had recovered by 2000 and pristine forest. The biodiversity intactness layer reflects how species communities are impacted by land use change and human population density. However, we know that other anthropogenic pressures—such as climate change, hunting and exploitation—are also important, but will only be accommodated in our analysis to the extent that land use or human population density serve as proxies. Although climate change has a significant impact on biodiversity, it is not possible to disaggregate the impacts of a changing climate from the impacts of land use change and human populations over the short time period on which our analysis focuses. Roads open forest areas and affect biodiversity through harvesting (Sodhi et al., 2004), the introduction of alien species (Hulme, 2009), alterations in the microclimate and creating light gaps (Laurance et al., 2009) but these subtle changes were not captured in our analysis.

We have used the plantation data for countries where such data is available in the SDPT, but it is not possible to distinguish all plantation forests from natural forests, notably for countries not represented in the SDPT dataset. Furthermore, it should be noted that China and Papua New Guinea are present in the SDPT dataset but we were not able to obtain permission for their data to be included in this analysis. This deficiency impacts both approaches. In the forest biodiversity significance layer, plantations may wrongly appear as highly significant if the forest they replaced had high values (but not so otherwise). In the intactness layer, plantations that contained mature trees in 2000 are indistinguishable from primary or mature secondary forests, but those plantations composed of primarily non-native species or high intensity, monoculture plantations will have markedly lower intactness than indicated.

Technological revolutions over the last few years, including in our ability to obtain and process satellite-derived data with freely available supercomputer power, are opening up new areas of opportunity for conservation science. We are moving closer to near-real-time habitat and biodiversity-change products that can ingest remotely sensed data and run algorithms to show both areas of forest loss and the consequences for multiple facets of biodiversity, within time periods that can lead to rapid responses and interventions on the ground. Our work represents a further contribution to this aim.

The layers described here have been integrated into the Global Forest Watch platform (www.globalforestwatch.org), which aims to provide the data necessary to document and conserve forests worldwide. It provides information relevant to monitoring fires, documenting illegal activities, screening estates for deforestation and analysing trends in forest change.

Humanity has long relied upon forests, and the varied and complex species assemblages they encompass and support, but in recent times human impacts have become unsustainable, creating areas depauperate in biodiversity. The layers presented here help to evaluate and map how we have impacted forest biodiversity and can inform what measures can be taken at a local scale to conserve and restore forests.

DATA AVAILABILITY STATEMENT

The datasets analyzed for this study can be found in the NHM data portal (data.nhm.ac.uk), and through request at www.iucnredlist.org/resources/spatial-data-download, and www.datazone.birdlife.org/species/requestdis, and the resulting layers can be visualized on the Global Forest Watch portal (data.globalforestwatch.org).

AUTHOR CONTRIBUTIONS

SH and AA led all analyses. CM carried out analyses. SH, AA, CM, SB, CH-T, CC, CD, AP, and NB devised the methodology. All co-authors assisted in the production of the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2019.00070/full#supplementary-material

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Hunting and Forest Modification Have Distinct Defaunation Impacts on Tropical Mammals and Birds

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The mammalian and avian assemblages of intact tropical forests are among the most diverse vertebrate communities on Earth and influence the structure, composition, and functioning of these forests in myriad ways. Over recent centuries, however, increasing human domination of the tropics has led to widespread defaunation, or the decline, local-, or global extinction of tropical animal species. Defaunation is one of the defining features of the Anthropocene and is best documented for vertebrate species, especially mammals and birds. Defaunation is driven by several direct (e.g., hunting) and indirect (e.g., habitat alteration) anthropogenic threats, but how these threats differ in the nature and magnitude of their impacts on tropical mammal and bird species remains unclear. Using a meta-analysis of 82 studies on 254 mammal and 1,640 bird species from across the tropics, we assess the effects of three major regional-scale drivers of tropical defaunation, namely hunting, forest degradation and forest conversion, on measures of abundance for tropical mammal and bird species belonging to different dietary guilds and IUCN conservation status groups. Mammal species across dietary guilds either declined or did not change, on average, in response to the three drivers, with hunting having the most consistent negative impacts on abundances of carnivores, frugivores, herbivores/granivores, large-bodied species, and species of high conservation importance. By contrast, bird species declined most strongly in response to forest conversion, with responses varying widely across different dietary and conservation importance groups, and not consistently related to body size. Our results reveal that hunting, forest degradation and conversion are associated with distinct types of defaunation of mammal and bird species, and are therefore likely to have distinct implications for animal-mediated interactions and processes, ecosystem functions, and conservation of tropical forests. Addressing major gaps in our empirical understanding of defaunation effects—e.g., hunting impacts on smaller-bodied mammals and birds, and responses of species in southeast Asian forests—is key to better understanding, predicting, and mitigating the impacts of this pervasive global threat.

Keywords: anthropocene, avifauna, habitat change, hunting, mammal, meta-analysis, species traits, tropical forest

INTRODUCTION

Tropical forests are among the most biodiverse global biomes and harbor c. 50–70% of all terrestrial vertebrate diversity (Whitmore, 1990; Pimm and Raven, 2000). The rapidly expanding footprint of anthropogenic disturbance is a leading driver of species population declines, resulting in widespread losses of tropical biodiversity (Gibson et al., 2011; Lewis et al., 2015; Watson et al., 2018). Such anthropogenic biodiversity loss, termed *defaunation* when focusing on animal species, is pervasive among all biomes, terrestrial, freshwater, or marine, and is one of the defining features of this epoch, commonly referred to as the Anthropocene (Dirzo et al., 2014; Young et al., 2016).

There are numerous drivers of Anthropocene defaunation, operating across a variety of scales, ranging from global (e.g., climate change, environmental pollution) to local or regional (e.g., direct harvest) scales (Young et al., 2016). Major regional-scale defaunation drivers include direct (e.g., hunting), and indirect (e.g., habitat degradation), threats (Young et al., 2016). Direct harvest for commercial and subsistence hunting is prevalent in most tropical forest regions (Fa et al., 2002; Peres and Palacios, 2007), including within protected reserves (Harrison, 2011; Laurance et al., 2012). In some regions such as Southeast Asia, hunting is considered the predominant threat to vertebrates including birds and mammals (Harrison et al., 2016). Indirect drivers of faunal change in tropical forests include forest degradation (e.g., fragmentation and unsustainable logging) (Potapov et al., 2008; Malhi et al., 2014), and conversion of forests to plantations, cropland and pastures (Gibson et al., 2011; Young et al., 2016), which affect virtually all tropical landscapes.

Because hunting, forest degradation, and forest conversion are very different types of disturbances, the nature and magnitude of their impacts on different mammal and bird species would be expected to vary. For example, species' responses to hunting depend strongly on the traits preferred by hunters, such as large body size, or herbivorous diet (Fa et al., 2002; Fa and Brown, 2009; Benítez-López et al., 2017). By contrast, forest degradation and conversion drive changes in animal communities by altering resource availability for different dietary guilds (Gray et al., 2007), or by constraining dispersal across degraded or modified landscapes (Şekercioğlu et al., 2002). Understanding variation in the nature of trait-mediated animal community change is useful not only for assessing conservation threats posed by different defaunation drivers, but can also improve our ability to predict knock-on impacts on forest vegetation dynamics and ecosystem functions such as carbon sequestration (Osuri et al., 2016; Berzaghi et al., 2018). However, even as previous studies have examined faunal responses to individual drivers such as hunting (Benítez-López et al., 2017) or selective logging (Burivalova et al., 2014), or responses of particular species groups such as frugivores to multiple drivers (McConkey et al., 2012), variation in the responses of tropical forest faunal communities to different defaunation drivers has not been systematically assessed.

In this paper, we present a pan-tropical meta-analysis of mammal and bird species responses to three major regional-scale drivers of tropical defaunation, namely hunting, forest degradation and forest conversion (Young et al., 2016). We ask how abundance or relative abundance metrics of different dietary guilds (e.g., carnivores, frugivores) of mammal and bird species vary in response to these drivers, and whether the strength of these responses are influenced by body size.

MATERIALS AND METHODS

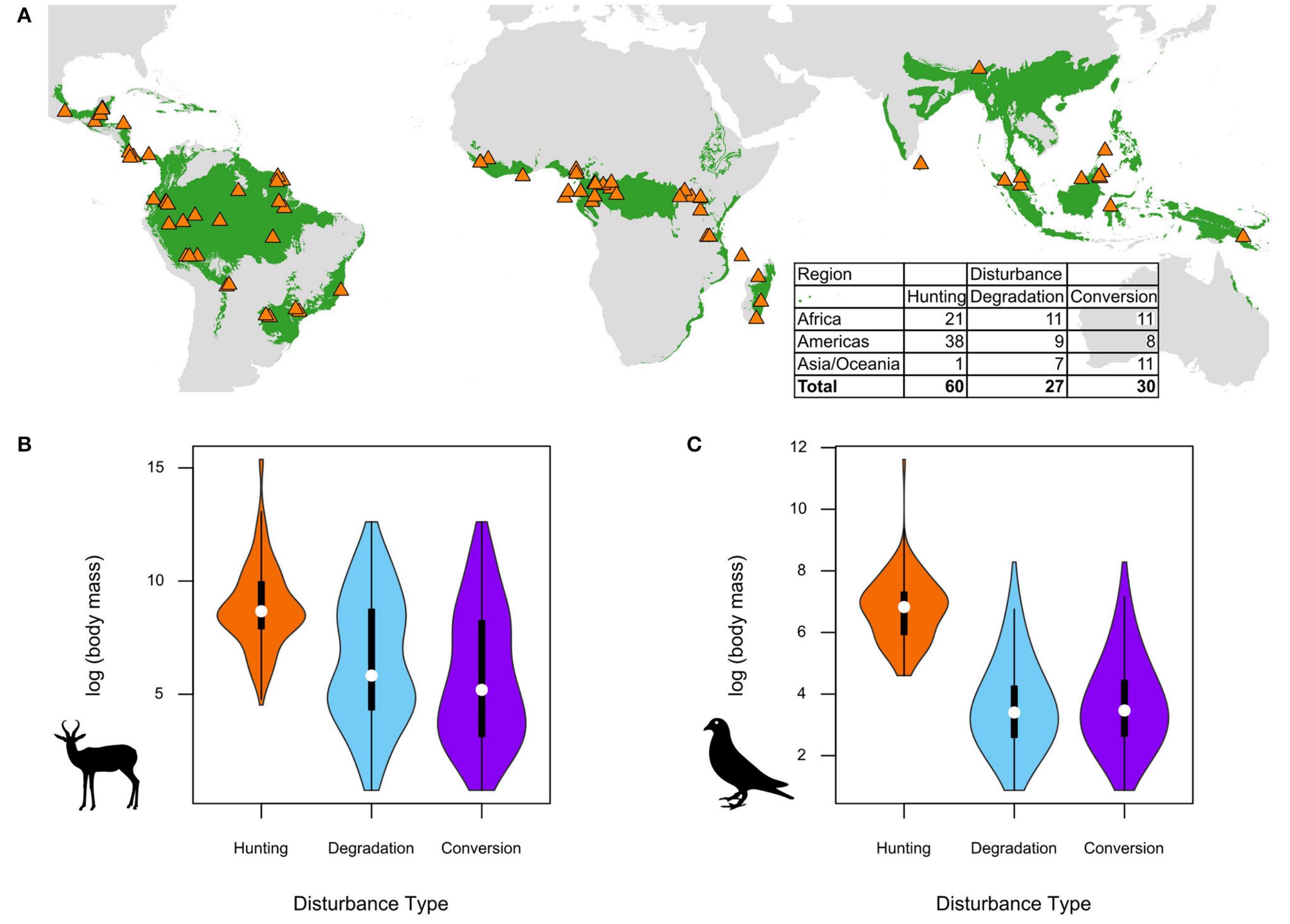
Datasets

Data on the responses of bird and non-volant mammal species to hunting, forest degradation and forest conversion were extracted from published literature and databases. For hunting, a list of potential data sources was derived from a recent pan-tropical meta-analysis of the effects of hunting and distance from human settlements on abundances of mammal and bird species (Benítez-López et al., 2017). We examined all the publications included in the above meta-analysis and retained those studies that were in English, available online, and which explicitly compared and reported metrics of abundance or relative abundance for at least one mammal or bird species from hunted forests and forests experiencing little to no hunting.

For forest degradation and conversion, we extracted data from the PREDICTS database (2016 release) of species responses to anthropogenic habitat disturbance (Hudson et al., 2017). Studies from tropical forests reporting metrics of abundance or relative abundance for at least one bird or mammal species from relatively undisturbed habitats (Predominant_land_use = "Primary vegetation") and at least one disturbed (Predominant_land_use = "Secondary vegetation") or converted (Predominant_land_use = "Plantation forest" OR "Pasture" OR "Cropland") habitat were retained for analysis. The "Secondary vegetation" class included selectively logged forests, forest fragments, and secondary forests growing on shifting or abandoned agriculture.

We extracted the geographic coordinates of each study site and retained only those studies situated within the tropical forest biome as defined by Olson et al. (2001). Next, we reviewed study area and design descriptions of each study to characterize sole or primary disturbances as one of hunting, forest degradation or forest conversion. Studies assessing single disturbance types [e.g., undisturbed vs. hunted forests—Endo et al. (2010)], and studies assessing multiple disturbances separately [undisturbed vs. degraded vs. converted forest—Barlow et al. (2007)], were retained, whereas studies looking at combined impacts of multiple disturbances [e.g., undisturbed vs. hunted + logged forest—Marshall et al. (2006)] were excluded from subsequent analyses.

Our final dataset comprised 117 comparisons (e.g., species abundances in hunted vs. non-hunted forests) in total (from 82 publications), including 60 comparisons based on hunting, 27 on forest degradation, and 30 based on forest conversion, with 37% of the publications reporting more than one type of comparison (**Figure 1**; **Table S1**). The dataset spanned 254 mammal and 1,640 bird species belonging to 17 and 28 taxonomic orders, respectively (**Table 1**). We detected a bias among studies on hunting, which mostly reported responses of species targeted by hunters (e.g., Lwanga, 2006), while responses of non-target species were less frequently reported (e.g., Carrillo et al., 2000), resulting in a skew toward larger-bodied species in hunting



Region	Disturbance		
	Hunting	Degradation	Conversion
Africa	21	11	11
Americas	38	9	8
Asia/Oceania	1	7	11
Total	**60**	**27**	**30**

FIGURE 1 | (A) Locations of 82 studies from different parts of the tropical forest biome (green) included in the meta-analysis. The distribution of body sizes of **(B)** mammal and **(C)** bird species included in the meta-analysis across different defaunation drivers.

studies relative to studies on forest degradation and conversion in our dataset (**Figures 1B,C**). We explore the implications of this bias in our Discussion.

The above dataset was transformed into a species response table that comprised, for every species in each comparison, information on disturbance type, average abundance or relative abundance in undisturbed (control) and disturbed (treatment) habitats. Average body mass (g) and broad dietary guilds of the species were extracted from the EltonTraits 1.0 database (Wilman et al., 2014). For dietary guild, species were assigned one of the following diet classes based on which of those classes represented 40% or more of their known dietary affinity—Carnivore, Frugivore, Herbivore (including Granivore), Insectivore, Nectarivore, and Generalist (including Omnivore). The aggregation and handling of species with ≥40% affinity to more than one class is described in **Table S2**, and body size characteristics of species in different diet classes are described in **Table S3**. Information on species' conservation threat status were obtained from the International Union for Conservation of Nature's (IUCN) Red List of Threatened Species (https://www.iucnredlist.org/).

Analyses

The log response ratio (LRR) between observed abundances, densities, relative abundances or encounter rates of species in disturbed and undisturbed treatments was used as a response variable [LRR = ln(disturbed/undisturbed)]. The processing of data to avoid artifacts in the LRR due to log transformation of zeroes is described in the Supplementary Methods section of the **Supplementary Material**. Analyses were run separately for non-volant mammals and birds using linear mixed-effects models (lme4 package: Bates et al., 2014) in the R statistical and programming environment (version 3.4.4) (R Core Team, 2017). The three-way interaction between disturbance type (hunting, degradation, and conversion), feeding guild (carnivore, frugivore, herbivore, insectivore, generalist, and nectarivore), and species body mass (log transformed) was used as the independent predictor. A unique identifier for study was used as a random factor. Pseudo-replication due to multiple occurrences of the same species across studies was accounted for by including species identity as a second random term.

Phylogenetic similarity between species could be a source of bias when responses of multiple species are aggregated at different treatment levels. This bias stems from the possibility of closely related species, which have similar evolutionary histories, responding in a more consistent manner than those that are more distantly related. To check if phylogenetic similarity influences parameter estimates and differences detected in our analyses, we compared results from the mixed model described above with a separate model, where the species random term was nested within order. Models with and without the nested species-order random term were compared using model BICs and the amount of variation attributed to the random term (following Benítez-López et al., 2017). The premise of this comparison is that if phylogenetic similarity is an important determinant of observed differences in the response variable, it would be reflected in relatively lower BICs (i.e., better model fit) of the model with the nested species-order random term, as well as greater variance associated with the random term. Our analyses showed that the nested random term model did not account for more variation and was a poorer fit to the data relative to the non-nested model (based on model BICs) for both mammals and birds. Hence, we concluded that phylogenetic similarity did not influence the analyses, and we report and interpret results from mixed models with the non-nested random term structure (i.e., where random terms were study identifier and species identity).

A linear mixed-effects model was also used to assess the consistency of effects across species when grouped by IUCN threat status. To ensure adequate sample sizes (numbers of species) in each IUCN threat category, we reclassified threat status into three levels—Critically endangered and Endangered (CR-EN), Vulnerable and Near Threatened (VU-NT), and Least Concern (LC). Log response ratios were modeled as a function of the two-way interaction between disturbance type and our reclassified IUCN threat category. Again, study identity and species identity were used as separate random factors.

We interpreted our results based on modeled effect sizes, their associated 95% confidence intervals (CIs) and biological relevance, rather than relying on *p*-values. Our inferences were categorized into three classes—(1) where modeled effects were large and CIs do not span zero (directional and consistent effects); (2) where effects were $\geq$10% change, but CIs span zero (directional, but inconsistent effects); and (3) where effects were $<$10% change with CIs spanning zero (no effects). The basis for the second interpretation class is that for effects having 95% CIs that span zero, there is as much support for twice the estimated effect (counternull) as there is for no effect (Rosenthal and Rubin, 1994; Stephens et al., 2007), which can be biologically meaningful when average effect sizes are large (e.g., $\geq$10% in our definition).

RESULTS

Mammal and bird species' abundances varied in response to hunting, forest degradation, and conversion. Mammal species abundances were consistently lower (-49%; LRR mean $= -0.67$; LRR 95% CI $= -0.97$ to -0.38) in hunted forests than in forests with little to no hunting (**Figure 2A**). Forest degradation and conversion also reduced mammal species' abundances by 16% and 27%, respectively, on average, but with 95% CIs

TABLE 1 | The representation of different mammal and bird orders across different disturbance types included in the meta-analysis.

Order	Hunting	Degradation	Conversion
Mammals			
Afrosoricida	0 (0)	3 (3)	6 (3)
Artiodactyla	100 (21)	12 (7)	8 (6)
Carnivora	65 (29)	17 (15)	13 (12)
Cingulata	16 (4)	2 (2)	7 (4)
Didelphimorphia	13 (11)	1 (1)	9 (5)
Erinaceomorpha	0 (0)	1 (1)	1 (1)
Hyracoidea	3 (2)	0 (0)	0 (0)
Lagomorpha	3 (1)	0 (0)	0 (0)
Macroscelidea	3 (3)	0 (0)	0 (0)
Perissodactyla	12 (2)	1 (1)	1 (1)
Pholidota	1 (1)	0 (0)	0 (0)
Pilosa	14 (5)	1 (1)	1 (1)
Primates	165 (69)	10 (9)	0 (0)
Proboscidea	7 (2)	0 (0)	0 (0)
Rodentia	60 (29)	36 (25)	36 (24)
Scandentia	0 (0)	12 (8)	7 (7)
Soricomorpha	0 (0)	13 (13)	13 (12)
Birds			
Accipitriformes	14 (14)	27 (21)	73 (46)
Anseriformes	0 (0)	1 (1)	6 (4)
Apodiformes	0 (0)	59 (55)	80 (65)
Bucerotiformes	15 (9)	15 (10)	25 (16)
Caprimulgiformes	0 (0)	2 (2)	9 (7)
Charadriiformes	0 (0)	1 (1)	5 (2)
Ciconiiformes	0 (0)	1 (1)	1 (1)
Coliiformes	0 (0)	0 (0)	1 (1)
Columbiformes	3 (3)	70 (51)	128 (69)
Coraciiformes	0 (0)	34 (26)	60 (34)
Cuculiformes	0 (0)	44 (28)	95 (47)
Eurypygiformes	0 (0)	1 (1)	1 (1)
Falconiformes	4 (4)	8 (7)	13 (10)
Galliformes	37 (21)	27 (21)	32 (27)
Gruiformes	6 (3)	6 (4)	12 (8)
Leptosomiformes	0 (0)	2 (1)	1 (1)
Mesitornithiformes	0 (0)	1 (1)	0 (0)
Musophagiformes	3 (3)	6 (3)	7 (4)
Passeriformes	0 (0)	865 (639)	1433 (883)
Pelecaniformes	0 (0)	2 (2)	20 (10)
Phaethontiformes	0 (0)	0 (0)	1 (1)
Piciformes	4 (3)	91 (66)	177 (103)
Psittaciformes	3 (3)	40 (37)	53 (47)
Pteroclidiformes	0 (0)	1 (1)	0 (0)
Strigiformes	0 (0)	10 (10)	31 (22)
Struthioniformes	1 (1)	0 (0)	0 (0)
Tinamiformes	11 (4)	12 (10)	11 (10)
Trogoniformes	0 (0)	19 (13)	27 (15)

The number of comparisons (number of species in parentheses) of every order-disturbance combination are reported.

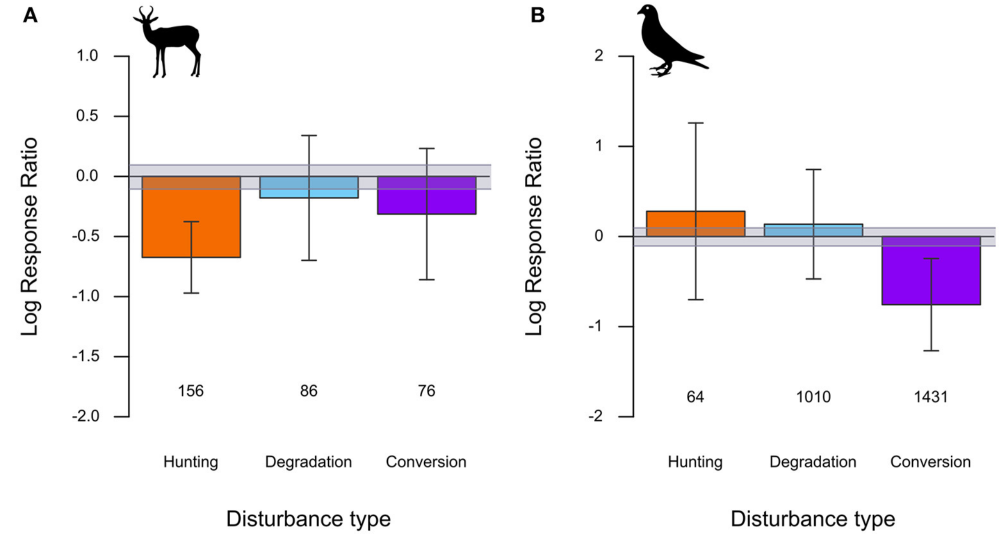


FIGURE 2 | Estimated average effect sizes and 95% CIs from linear mixed-effects models of **(A)** mammal and **(B)** bird species Log Response Ratios (LRRs) in comparisons of hunted, degraded, and converted forests to relatively undisturbed forests. Numbers below each bar represent the number of species of that particular category included in the analysis. The gray band depicts a $\leq$10% difference in species' abundance between disturbed and undisturbed habitats.

overlapping zero, their overall effects on mammals were less consistent, relative to hunting (**Figure 2A**). For birds, by contrast, hunting and forest degradation were associated with increasing but highly variable overall species' abundance responses of 32% and 16%, respectively, while bird species declined consistently by over 53% in response to forest conversion (LRR mean = −0.76; LRR 95% CI = −1.27 to −0.25; **Figure 2B**). The full set of model estimated parameters and 95% CIs is provided in **Table S4**.

Mammal species responses to hunting were negative on average across all major dietary groups, with declines being relatively more consistent among carnivores, frugivores, and herbivores than insectivore and diet-generalist species (**Figure 3A**). The responses of different mammalian diet groups to forest degradation and conversion were more variable, ranging from negative but inconsistent responses of carnivores and frugivores to positive but inconsistent responses of insectivores (**Figure 3A**). Among birds, forest conversion was associated with consistent declines of frugivores and insectivores and increases of herbivores/granivores and nectarivores, and inconsistent declines of insectivores, while guild-wise responses to hunting and forest degradation were weaker and more variable (**Figure 3B**). The full set of model estimated parameters and 95% CIs is provided in **Table S4**.

The effect of hunting on mammals was consistently more negative for larger-bodied than smaller-bodied species (LRR vs. Log body mass slope = −0.34; Slope 95% CI = −0.46 to −0.21), particularly among carnivores (Slope = −0.4; Slope 95% CI = −0.81 to 0) and frugivores, (Slope = −0.64; Slope 95% CI = −1.29 to 0.01) and less consistently for herbivores, insectivores, and generalists/omnivores (**Figure 4A**). By contrast, mammal species' responses to forest degradation and conversion were not consistently related to body size overall, with responses among guilds ranging from negative but inconsistent LRR-body size relationships (Insectivore-Degradation) to positive but inconsistent relationships (Frugivore-Degradation) (**Figure 4A**). Among birds, body size was either unrelated, or weakly negatively related, to species' responses across disturbance types and across most dietary guilds, with the exception of herbivore/granivore and carnivore species which showed a negative but inconsistent LRR-body size relationship under the hunting category (**Figure 4B**). The full set of model estimated slope parameters and 95% CIs is provided in **Table S5**.

Declines of mammal species in hunted forests were consistent across conservation threat status categories. Forest conversion was associated with consistent declines of VU and NT species, but inconsistent declines in LC species (**Figure 5A**). Mammal species responses to forest degradation did not show a consistent relationship with any conservation threat category (**Figure 5A**). By contrast, forest degradation and conversion were consistently associated with large declines of threatened bird species (CR, EN, VU, NT). LC species experienced smaller consistent declines due to forest conversion, but positive if inconsistent effects of hunting and forest degradation (**Figure 5B**). The full set of model estimated parameters and 95% CIs is provided in **Table S6**.

DISCUSSION

Our findings suggest that hunting, forest degradation and conversion have marked but varied defaunation impacts on mammal and bird communities of relatively intact tropical forests. For mammal abundances, all three disturbance types exerted a negative effect, while the response in birds was more mixed. Hunting had stronger negative impacts than forest degradation or conversion on mammal abundances across all

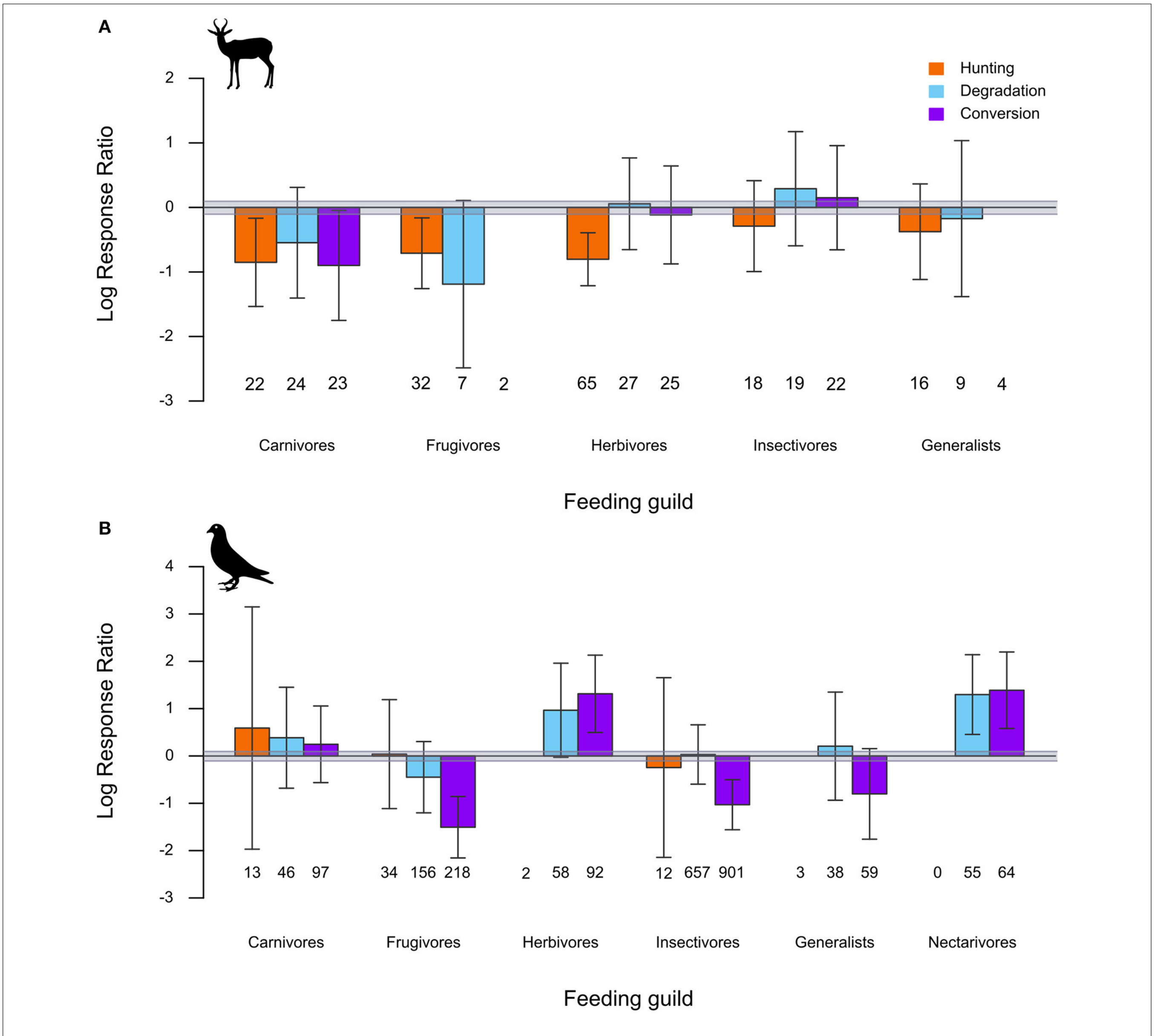


FIGURE 3 | Estimated average effect sizes and 95% CIs from linear mixed-effects models of **(A)** mammal and **(B)** bird species guild-wise LRRs in comparisons of hunted, degraded, and converted forests to relatively undisturbed forests. The "Herbivores" category also includes granivores. Numbers below each bar represent the number of species of that particular category included in the analysis. Categories comprising fewer than five species in the dataset (e.g., Frugivore mammals in Forest conversion comparisons; Nectarivore mammals) are not depicted. The gray band depicts a ≤10% difference in species' abundance between disturbed and undisturbed habitats.

species, with declines evident across the spectrum of high to low conservation priority species in hunted forests. However, given that species groups targeted by hunters (e.g., primates) were overrepresented in our hunting dataset, actual impacts of hunting at the level of mammal communities across targeted and non-targeted groups (e.g., small insectivores) may be weaker, and potentially differ less overall from the impacts of forest degradation or conversion. By contrast, forest conversion was most strongly associated with declines in bird species' abundances (high and low conservation priority species), while hunting—despite underrepresentation of non-targeted species (e.g., passerines)—and forest degradation were associated with weak increases in bird species' abundance, driven by the positive responses of low conservation priority (according to the IUCN) species in hunted and degraded forests. These findings suggest that while interventions aimed at reducing hunting pressure may be important for conserving mammals, incentive schemes for reducing forest degradation and promoting wildlife friendly farming might be equally if not more important for averting declines of bird species in the tropics.

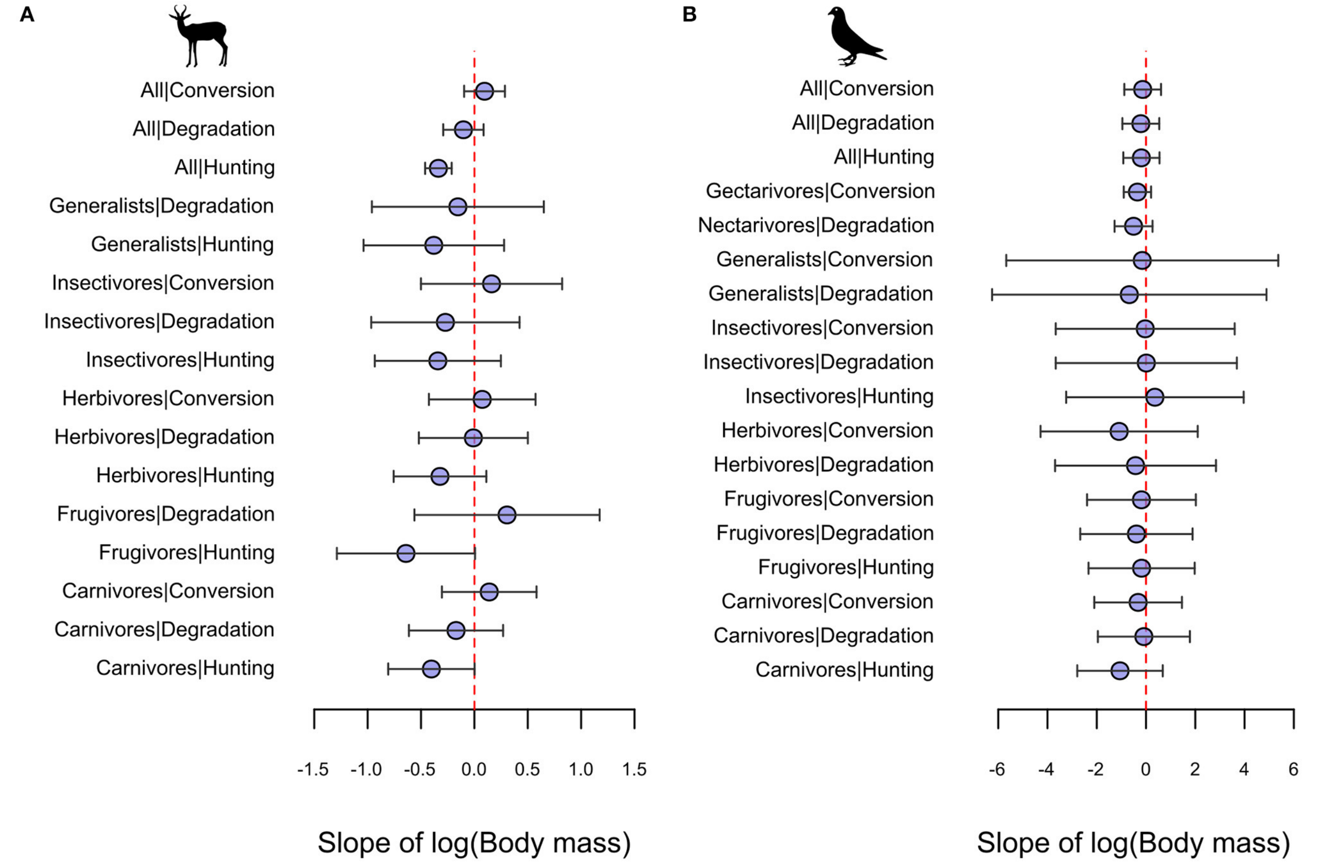


FIGURE 4 | Estimated slopes and 95% CIs of LRR-body size relationships from linear mixed-effects models for **(A)** mammal and **(B)** bird species across different diet guild|disturbance type combinations. Categories comprising fewer than five species in the dataset (e.g., Frugivore mammals in Forest conversion comparisons; Nectarivore mammals) are not depicted.

The effects of hunting, forest degradation, and conversion on birds and mammals differed with respect to species' body sizes and dietary guilds. Mammal species across all dietary guilds showed strong (in carnivores, frugivores, and herbivores) to weak (insectivores and generalists) reductions in abundance in hunted forests, while responses to forest degradation and conversion were more variable, ranging from strong declines (carnivores in converted habitats) to weak declines (carnivores in degraded forests) and increases (insectivores in degraded and converted forests). Hunting also had stronger negative impacts on large-bodied than smaller-bodied mammal species, possibly reflecting hunters' preference for larger wildlife (Fa et al., 2002; Young et al., 2016), while the impacts of forest degradation and conversion on mammals were less consistently related to body size. Among birds, while hunting impacts on species' abundance ranged from weakly positive (carnivores) to weakly negative (insectivores) and unknown (herbivores/granivores, generalists and nectarivores, due to a lack of data) across dietary guilds, responses to forest degradation and conversion were stronger in both directions across different guilds. For example, frugivores (conversion and degradation) and insectivores (conversion) showed marked declines in converted habitats, possibly due to reductions in food resources in degraded and non-forest habitats relative to intact forests (Gray et al., 2007; Naniwadekar et al., 2015), or due to the inability of certain species (e.g., understorey insectivores) to disperse across non-forest habitats (Şekercioğlu et al., 2002). Likewise, increases in the abundances of herbivore/granivore and nectarivore species in degraded and converted habitats relative to intact forests are possibly related to greater food availability in modified habitats [e.g., flowering trees in coffee plantations—Faria et al. (2006)], and a greater ability of birds in these guilds to disperse across open or disturbed habitats (Lees and Peres, 2009; Şekercioğlu, 2012). Collectively, notwithstanding gaps in current literature and understanding of hunting impacts on smaller-bodied species, our results suggest that defaunation drivers can vary in their impacts on, and result in communities comprising distinct combinations of, dietary guild, size class and conservation status groups of tropical forest mammals and birds.

A central question of both academic and applied relevance pertaining to the Anthropocene defaunation is of how the consequent losses of animal-mediated interactions and processes modify the structure, composition and functioning of the tropical forest ecosystem (Muller-Landau, 2007; Wright et al., 2007; Osuri et al., 2016). Our findings on the contrasting responses

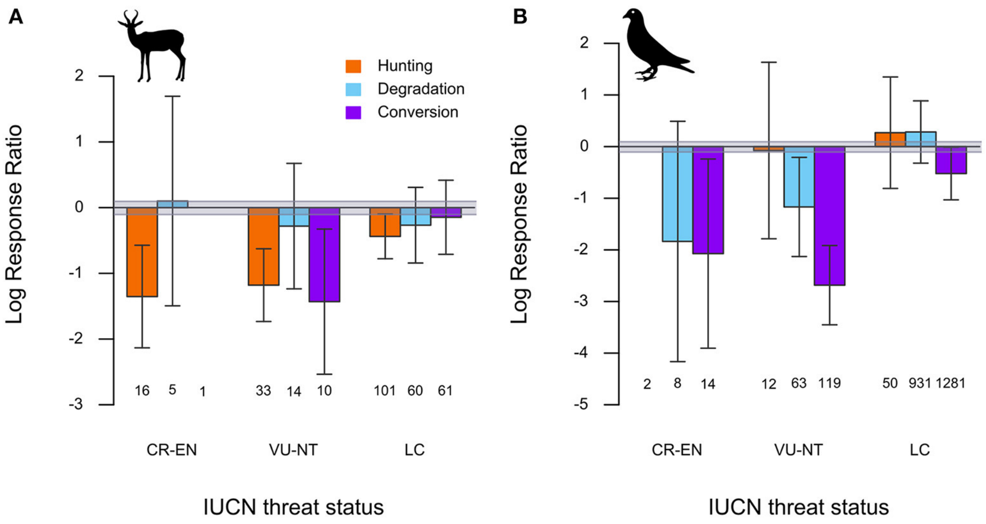


FIGURE 5 | Estimated average effect sizes and 95% CIs from linear mixed-effects models of **(A)** mammal and **(B)** bird species LRRs of different IUCN threat status groups in comparisons of hunted, degraded, and converted forests to relatively undisturbed forests. Groups include Critically Endangered and Endangered (CR-EN), Vulnerable and Near Threatened (VU-NT) and Least Concern (LC). Numbers below each bar represent the number of species of that particular category included in the analysis. Categories comprising fewer than five species in the dataset (CR-EN mammals in Forest conversion comparisons) are not depicted. The gray band depicts a ≤10% difference in species' abundance between disturbed and undisturbed habitats.

of different diet and body-size species groups to hunting, forest degradation and conversion suggest that such knock-on effects of defaunation on ecosystem processes, functions, and services might also vary across defaunation drivers. For example, our results suggest that while abundances of frugivores are reduced by both hunting (mammals) and forest modification (mammals and birds), mammalian herbivores and granivores decline more strongly in hunted than in modified forests (**Figure 3**). Seed dispersal by frugivores, and seed, seedling, and sapling predation by granivores and herbivores, are known to influence the regeneration of tropical trees (Wright, 2003; Paine et al., 2016; Terborgh et al., 2018). Thus, variation in the response of these guilds to different defaunation drivers could drive distinct trajectories of tree community composition, and consequently, result in distinct outcomes in terms of key ecosystem functions such as carbon storage (Culot et al., 2017). Given the long time periods—typically decades to centuries—that shifts in animal-mediated interactions and processes might take to manifest at the ecosystem level, vegetation-, and other types of models have emerged as an important tool for understanding and attempting to predict longer term ecosystem-level consequences of defaunation (Berzaghi et al., 2018; Schmitz et al., 2018). Our results suggest that incorporating disturbance-specific defaunation parameters and scenarios could improve the ability of such models to distinguish the ecosystem-level impacts of different drivers of faunal loss.

While our meta-analysis uncovered broad patterns of variation in defaunation impacts across different anthropogenic drivers, empirical studies are needed in order to overcome existing biases in the literature and thereby to quantify the differences in faunal responses to different drivers more accurately. For example, most studies on hunting do not report community-wide responses but rather focus on particular target and non-target species, while studies on forest degradation and conversion frequently report community-wide responses. For this reason, differences between disturbance types on mammals should be interpreted cautiously, particularly for carnivore, frugivore, and herbivore guilds, which show size-dependent responses to disturbance. For birds, on the other hand, it is worth noting that forest conversion and degradation show stronger and more consistent effects than hunting in spite of the potential bias. Such biases could be overcome by future studies that assess community-wide faunal responses using consistent methodologies across disturbance types. A number of biases also exist in the geographic coverage of studies of faunal responses to different defaunation drivers—most notably, empirical studies on the effects of hunting are highly underrepresented in Southeast Asia, even as hunting is recognized as a major threat to mammals and birds in this region (Harrison et al., 2016).

Collectively, our findings highlight that the major regional-scale anthropogenic threats to intact tropical forests are associated with distinct types of defaunation, in terms of their impacts on different functional and conservation status groups of mammal and bird species, and consequently, in terms of their potential impacts on forest ecosystem functions and services. Other distinct combinations of species and ecosystem responses could potentially arise from interactions between disturbance types, such as logging and hunting, which frequently co-occur in the tropics (Wilkie et al., 2000; Peres, 2001; Laurance and Useche, 2009), and from interactions of regional drivers with global drivers such as climate change (Young et al., 2016). Incorporating this heterogeneity in species' and community responses to different drivers into defaunation theory and models, and efforts to address key gaps in species and geographic coverage, are important for better understanding, predicting and mitigating the pervasive declines of mammals and bird species, and their cascading impacts on the tropical forest ecosystem.

DATA AVAILABILITY STATEMENT

Data were accessed from published articles and publicly available datasets (see References, **Table S1**, and **Supplementary References**). Derived datasets and R scripts used for analysis and graphics are available on request from the authors.

AUTHOR CONTRIBUTIONS

AO, UM, RN, and VV designed the study, performed literature searches and collated the data, with inputs from SN. AO and VV performed the analysis with inputs from all authors. All authors contributed to writing the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2019.00087/full#supplementary-material

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The State of Conservation in North America's Boreal Forest: Issues and Opportunities

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The North American Boreal Forest biome has been recognized as containing some of the highest proportions of intact, primary forest left on Earth. Over 6 million km^2 of the Boreal Forest biome is found in Canada (5.5 million km^2) and the United States (0.74 million km^2) across 10 provinces and territories and one United States state (Alaska). All of it is within the traditional territories of hundreds of Indigenous governments, many of whom are now asserting their rights to make decisions about its future and current land-use including for conservation and development. The biome is considered to be 80% intact and between 8 and 13% formally protected. The North American Boreal Forest biome's intactness has allowed it to retain many globally significant conservation features including long-distance mammal and fish migrations, healthy populations of large predators, one to three billion nesting birds, some of the world's largest lakes and North America's longest undammed rivers, massive stores of carbon and ecological functionality. The biome's forests, minerals, and hydropower potential are also recognized as economic opportunities so that the industrial footprint is rapidly increasing, sometimes without careful land-use planning decisions. Indigenous, federal, state, provincial and territorial governments and conservation organizations have strived over recent decades to recognize the conservation opportunity inherent in such a still-intact landscape, resulting in implementation of some of the world's largest land conservation set-asides. Indigenous governments, in particular, have been at the forefront in developing and implementing world-leading, modern land-use plans that achieve land conservation at massive scales. Supporting efforts to ensure that a high proportion of North America's Boreal Forest biome is protected and remains as intact habitat with unimpeded ecosystem processes should be a priority of the global conservation community. Federal, state, and provincial/territorial governments should support Indigenous protected area proposals, vastly increase financial support for Indigenous government land conservation and stewardship activities, and should develop new protected area co-management models with Indigenous governments. Governments should also be strongly advocating for raising the global Convention on Biological Diversity protected area goal to at least 30% by 2030.

Keywords: boreal forest, forest conservation, intact forest, indigenous guardians, indigenous-led conservation, indigenous protected and conserved areas, primary forest, protected areas

INTRODUCTION

With the advent of GIS capabilities and the availability of complete global coverage of remote sensing products over the last two decades, identification of the biomes of the world with the least large-scale human impacts has become possible. Notwithstanding the various methodological and definitional questions around how to define and map such areas (Potapov et al., 2017; Venier et al., 2018; Watson et al., 2018) there has been broad consensus that there are five regions of the world that encompass the largest areal extent of forest habitat that has not been subject to large-scale industrial logging, roadbuilding, mining, or other modern industrial land-use impacts. First identified in 1997 (Bryant et al., 1997) and termed "frontier forests" these forest areas have subsequently been mapped under different criteria and terms including "wilderness," "intact forest" and "primary forest" in a number of other publications and analyses (Sanderson et al., 2002; Mittermeir et al., 2003; Potapov et al., 2008, 2017; Hansen et al., 2013; Mackey et al., 2014; Watson et al., 2016, 2018; Dinerstein et al., 2017). These five regions–the forests of New Guinea and Borneo, the Congo Basin, the Amazon Basin, the Russian Boreal Forest, and the North American Boreal Forest (**Figure 1**) – have all seen major losses in forest area since their original identification in 1997 (Hansen et al., 2013; Haddad et al., 2015; Venter et al., 2016; Watson et al., 2016).

Increasingly, terrestrial protected areas work in these and other regions around the world has focused on increasing protected areas coverage (Dinerstein et al., 2017, 2018; Watson et al., 2018). The first goal that many governments and non-governmental organizations have focused on is reaching the Convention on Biodiversity Target 11 goal of 17% of each nation protected as outlined in the so-called Aichi treaty (Environment and Climate Change Canada, 2016; Canadian Parks and Wilderness Society, 2018; Indigenous Circle of Experts, 2018). Academics and conservation practitioners have also increased awareness for the need to increase protected areas goals to much higher levels in order to achieve the goal of maintaining biodiversity and ecosystem services (Noss et al., 2012; International Boreal Conservation Science Panel, 2013; Wilson, 2016). These higher-level goals are being achieved in certain landscapes as a result of the leadership of Indigenous peoples and often through reconciliation processes that result in strong Indigenous self-government (Indigenous Circle of Experts, 2018; Zurba et al., 2019).

CONSERVATION VALUES OF THE NORTH AMERICAN BOREAL FOREST BIOME THAT MAKE IT A GLOBAL PRIORITY FOR CONSERVATION

North America's Boreal Forest biome (**Figure 2**) is one of the most intact of these global forested ecosystems (Lee et al., 2003, 2006; Andrew et al., 2012, 2014; Dinerstein et al., 2017; Venier et al., 2018). The biome is estimated to harbor 25% of the world's remaining intact forests (Aksenov et al., 2002; Lee et al., 2003, 2006). Spanning from Newfoundland and Labrador in the east and across Canada to interior Alaska, it encompasses 6.27 million km^2. Within its boundaries are some of the largest peatlands, lakes, and rivers in the world (Schindler and Lee, 2010; Wells et al., 2010) and a significant amount of the world's terrestrial carbon (Carlson et al., 2009, 2010; Tarnocai et al., 2009).

North American Boreal Forest biome peatlands include a wetland that is considered one of the largest in the world, the Hudson Bay-James Bay Lowlands that extend over 370,000 km^2 (Abraham and Keddy, 2005; Webster et al., 2015). Along with being enormous storehouses of carbon, these wetlands store and filter massive amounts of freshwater (Schindler and Lee, 2010; Wells et al., 2010). Canada's portion of the Boreal Forest biome is thought to hold a minimum of 208 billion tons of carbon in its trees and other plants, soils, peatlands, as well as under permafrost (Carlson et al., 2009). The biome's natural capital is worth an estimated $703 billion annually (Anielski and Wilson, 2009). Ecosystem goods and services are relatively unimpaired across the region due to its large degree of intactness.

The highest densities of trees on earth occur in the global boreal forest biomes and are estimated to support 24% of the world's individual trees (Crowther et al., 2015). Using Crowther et al.'s (2015) boreal tree density average applied to the North American Boreal Forest biome suggests that the biome holds as many as 500 billion individual trees representing 16% of the world's total number of individual trees. Many plants species are largely confined to the North American Boreal Forest biome or at least reach their greatest abundance and distributional extent within the biome. This includes many coniferous tree species which are considered characteristic of the North American Boreal Forest biome including *Picea glauca*, *Picea mariana*, *Larix laricina*, *Abies balsamea*, *Pinus banksiana*, *Pinus contorta* var. *latifolia*, and *Abies lasiocarpa* but also characteristic deciduous tree species like *Populus tremuloides*, *Populus balsamifera*, and *Betula papyrifera* (Brandt, 2009).

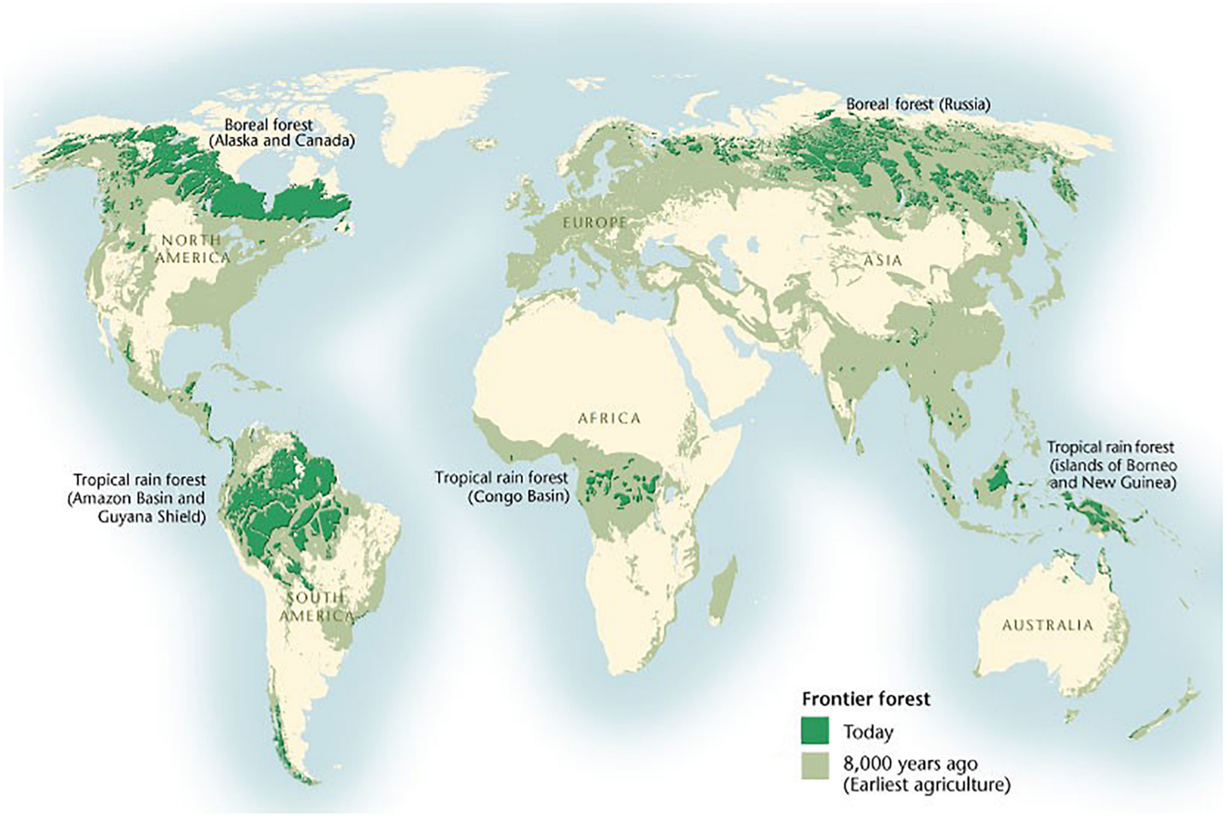

FIGURE 1 | The largest intact forest regions on earth are primarily confined to five regions: the forests of New Guinea and Borneo, the Congo Basin, the Amazon Basin, the Russian Boreal Forest, and the North American Boreal Forest. Map courtesy of Canadian Geographic.

The North American Boreal Forest biome encompasses millions of lakes and ponds (Wells et al., 2010) and Canada's Boreal Forest holds more available freshwater than any other single country on earth (Minns et al., 2008). Freshwater outflows from the North American Boreal Forest biome to marine systems play an important role in driving large-scale ocean currents, moving nutrients, impacting weather patterns and the productivity of marine fisheries across the globe (Aagaard and Carmack, 1989; Woo et al., 2008; Wells et al., 2010). Within the biome are four of the world's ten largest lakes. This includes Great Bear Lake in the Northwest Territories, one of the world's most pristine (**Figure 3**). Many large lakes here support healthy, age-structured fish populations that includes a significant proportion of larger and older fish that often become scarce under heavy fishing pressure. The largest known individuals of species like lake trout, brook trout, and Arctic grayling have been documented from these lakes (Wells et al., 2010). North America's Boreal Forest biome is rich also in free-flowing, undammed rivers (**Figure 4**) – more than now occur in the remainder of North America (Dynesius and Nilsson, 1994; Webster et al., 2015). Dams, pollution and water over-subscription have imperiled river biodiversity across much of the world, but rivers in North America's Boreal Forest biome are among the remaining strongholds for populations of many anadromous fish species (Wells et al., 2010). Pacific salmon continue to migrate up the Stikine, Nass, and Skeena rivers into the Sacred Headwaters of northern B.C. and the Yukon River through Alaska to the Yukon. Anadromous fish ascend the Mackenzie River southward from the Arctic over 1,000 km, some reaching to tributaries in B.C. and Alberta. Atlantic salmon runs along the Atlantic Coast of North America have been lost or are endangered in the United States and southern Canada (Limburg and Waldman, 2009). Yet healthy populations still ascend rivers in the boreal regions of Quebec and Newfoundland and Labrador.

North America's Boreal Forest biome is also home to both Old and New World evolutionary lineages of caribou (Polfus et al., 2017) and migratory and non-migratory lineages of wolves (Musiani et al., 2007) that persist together in the biome. Unfortunately, all populations and forms of caribou that occur in Canada (woodland, mountain, barren-ground) are now listed as Endangered, Threatened, or of Special Concern by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC, 2019) with major harvest restrictions now in place on caribou throughout Canada.

Within the biome are some of Earth's only remaining unfettered large mammal migrations – those particularly of herds of migratory tundra caribou (*Rangifer tarandus*) that can traverse 500–1500 km in an annual migration between boreal forest wintering ranges and tundra summer calving grounds (Hummel and Ray, 2008; Wilcove, 2008; Joly et al., 2019). The Porcupine

FIGURE 2 | The North American Boreal Forest biome as defined in Brandt (2009). The biome is estimated to harbor 25% of the world's remaining intact forests.

Caribou Herd in western Canada and Alaska travels over 1300 km each year as do the Bathurst and Beverly herds of western Canada and the Leaf River Herd of Quebec (Gurarie et al., 2019; Joly et al., 2019). The Western Arctic Caribou Herd of Alaska and the Qamanirjuaq Herd of Canada travel at least 1200 km each year (Joly et al., 2019). Loss of migration corridors threatens many herbivore species across the globe as habitat modification reduces the ability of animals to move across large tracts of intact landscape (Wilcove, 2008; Ripple et al., 2015).

The North American Boreal Forest biome supports significant populations of large carnivores that have been lost from much of their southern range including wolves, grizzly bears, and wolverine (Laliberte and Ripple, 2004; Cardillo et al., 2006; Bradshaw et al., 2009). One of the southernmost populations of polar bears in the world occurs in the Boreal Forest biome in the Hudson Bay and James Bay region where the bears have the unusual habit of maternity denning in the ground (rather than in snow) sometimes hundreds of kilometers inland (Peacock et al., 2010).

Within the North American Boreal Forest biome are a variety of range-restricted mammal species including the Ungava collared lemming (found only in northern Ungava peninsula), Richardson's collared lemming, singing vole (found only in parts of Alaska, Yukon and the Northwest Territories), Dall's sheep, collared pika, and the American wood bison (Bowers et al., 2004). A subspecies of freshwater harbor seal is separated from the sea and found only in Quebec's Tursujuq National Park (Smith, 1996, 1997; COSEWIC, 2007).

A great abundance of invertebrates, especially insects, occur only or primarily in peatlands and other wetlands and lakes, rivers and streams of North America's Boreal Forest biome. This includes species of chironomid flies, lepidopterans, dragonflies, and beetles (Spitzer and Danks, 2006). Species of dragonfly whose range is primarily within the biome include the Boreal Snaketail, Quebec Emerald, Hudsonian Emerald, Kennedy's Emerald, Boreal Whiteface, Lake Darner, and Zigzag Darner (Cannings and Cannings, 1994; Dunkle, 2000).

Butterflies that are wetland-dependent and that have most of their range confined to the North American Boreal Forest biome include the Bog Fritillary, Titania Fritillary, Disa Alpine, Jutta Arctic, and Cranberry Blue (Opler and Malikul, 1992). Peatlands of the biome support unusual species, like the sphagnum bog cricket (*Neonemobius palustris*), bog katydid (*Metrioptera sphagnorum),* the pitcher plant mosquito (*Wyeomyia smithii*),

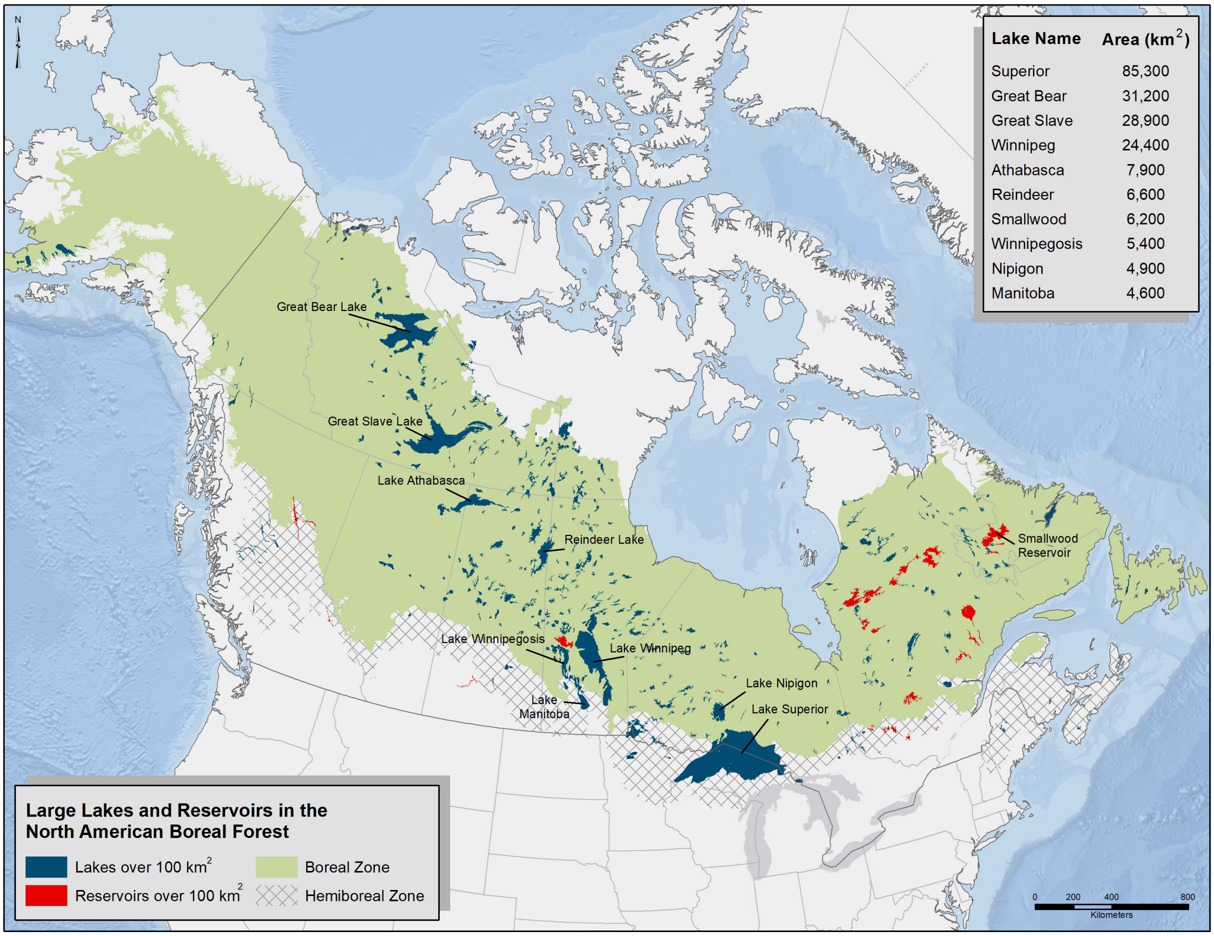

FIGURE 3 | North America's Boreal Forest biome contains millions of lakes, including Lake Superior, Great Bear Lake and Great Slave Lake, which rank amongst the world's largest in both surface area and overall volume.

and the pitcher plant midge (*Metriocnemus knabi*) (Capinera et al., 2004; Spitzer and Danks, 2006).

The North American Boreal Forest biome supports billions of songbirds, millions of waterfowl and shorebirds, and is the last stronghold for globally endangered species like the Whooping Crane (Wells and Blancher, 2011). The intactness of the North American Boreal Forest biome is a critical reason it has remained one of the world's most important breeding reservoirs for migratory birds, supporting an estimated 1–3 billion nesting birds each summer including billions of songbirds and millions of waterfowl and shorebirds (Wells, 2011; Wells and Blancher, 2011). The biome is the last stronghold for the globally endangered Whooping Crane which nests in or near Wood Buffalo National Park straddling the border between Alberta and the Northwest Territories (Wells and Blancher, 2011). Each fall, the biome annually "exports" some 3–5 billion birds once the young have hatched and migrated to populate their wintering ranges, from southern Canada and the United States south through Mexico, the Caribbean, Central America and South America (Robertson et al., 2011; Wells and Blancher, 2011; Wells et al., 2014). At least 96 species are estimated to have at least half of their North American breeding distribution within the biome and 151 to have at least 25% of their breeding distribution in the biome (Wells and Blancher, 2011). Wetlands within Alaska's portion of the Boreal Forest biome have long been known as an important stronghold for the original wild populations of Trumpeter Swan and these same wetlands are hosting increased densities of nesting waterfowl in recent decades, perhaps three times as many as in the 1950's (Petrie and Reid, 2009).

Sadly, there are a growing number of Boreal bird species in steep decline with six species considered globally threatened under IUCN Red List and eight Near Threatened. Boreal-dependent birds like the Rusty Blackbird, the Olive-sided Flycatcher, and Canada Warbler have shown declines in abundance of more than 50% over the last half-century. All three are now on Canada's list of Threatened or Special Concern species and Olive-sided Flycatcher appears on Audubon Alaska's Redlist (Warnock, 2017). Boreal-breeding waterbirds are also featured on that list, including the eastern populations of Barrow's Goldeneye and Harlequin Duck, the western populations of Horned Grebe, and Yellow Rail, Hudsonian Godwit and Red-necked Phalarope (Wells et al., 2014). The

Major Rivers	Length (km)
Yukon	2,714
Churchill	2,067
Mackenzie	1,662
Peace	1,236
Liard	1,089
Athabasca	1,094
North Saskatchewan	1,070
Dubawnt	1,060
South Saskatchewan	970
Thelon	951

FIGURE 4 | The North American Boreal Forest biome encompasses most of the continent's remaining, large undammed rivers, which maintain globally significant water, nutrient, and migratory fish movements between terrestrial and ocean ecosystems.

candidate species for future inclusion on that list include a number of shorebirds that are dependent on Boreal wetlands for breeding, including Lesser Yellowlegs, Semipalmated Sandpiper, Short-billed Dowitcher, Stilt Sandpiper, and Pectoral Sandpiper (COSEWIC, 2019). Many other Boreal-breeding species have seen steep declines in the last 50 years, including Black Scoter (listed at Near Threatened on the IUCN Red List), Surf, and White-winged Scoters, Lesser Scaup, Long-tailed Duck (listed as Vulnerable on the IUCN Red List), Blackpoll Warbler, and even well-loved backyard feeder birds like White-throated Sparrow and Dark-eyed Junco (Wells, 2007; Slattery et al., 2011; Sauer et al., 2015; Wells et al., 2016, 2018). Many of the species in steep decline on Alaska's Watchlist are found seasonally within Alaska's Boreal Forest biome (Warnock, 2017).

GOVERNANCE AND POLICY CONTEXT OF THE CANADIAN BOREAL FOREST

Virtually all of North America's Boreal Forest biome is considered (at least by non-Indigenous governments) to be under the dominion of federal, provincial and territorial governments as so-called "crown land" in Canada (Bone, 2000). Decisions about the management of that land have historically largely been under the control of provincial and territorial governments (Frideres and Rowe, 2010) in Canada. Indigenous governments, on the other hand, consider their traditional territories within the region to be sovereign lands for which they should have complete authority or co-authority with federal, provincial, and territorial governments. In some regions, these lands were never under a historic treaty and some areas of Canada remain without even a modern-day treaty (Bone, 2000). In other regions, there are historic treaties that are sometimes invoked by federal, provincial or territorial governments to suggest that all Indigenous land management rights were extinguished (Long, 2010). Recent legal cases have challenged the latter view and have been supported, at least in part, by court rulings including at the Canadian Supreme Court (Ariss and Cutfeet, 2012).

Provincial and territorial governments as opposed to the federal government, in the Canadian confederation system, hold the rights to make decisions about the use of crown lands. One of the types of land uses granted by provinces and territories that encompasses much of the southern half of the Boreal Forest biome is for industrial scale logging (International Boreal Conservation Science Panel, 2013). Often long-term land tenures to single logging companies cover vast areas, larger than some United States states. These tenures give those companies the rights to harvest logs and build roads, bridges and other infrastructure in order to do so. Mining companies and oil and gas companies can similarly license claims for areas of the boreal forest for exploration (Wells et al., 2010). If exploration has indicated a substantial mineral deposit, then those companies can apply for the right to develop mines or oil extraction facilities. Hydropower corporations in Canada are largely all public-private corporations. These entities must also be granted rights to develop dams, roads, transmission line corridors and other infrastructure within Boreal Forest lands. Historically, Indigenous peoples were rarely consulted on the management of their lands including the granting of rights to resource extraction companies to operate on their traditional territories (Ariss and Cutfeet, 2012; Indigenous Circle of Experts, 2018) or the designation of protected areas (Indigenous Circle of Experts, 2018). In the last two decades, more engagement and consultation of Indigenous governments and communities has begun taking place. But the degree of authority in land use decisions that any particular Indigenous government or community has over the use of its traditional territory varies greatly across Canada depending especially on the views of the provincial or territorial government and bureaucratic leadership and the level of pressure exerted by resource extraction industries in that region.

GOVERNANCE AND POLICY CONTEXT OF THE ALASKA BOREAL FOREST

The Alaska portion of the Boreal Forest biome is managed by the federal government (51%), Native Corporations (24%), state and local governments (25%), and private landowners (0.4%). Federal lands in the Alaska Boreal Forest biome are primarily managed by the Bureau of Land Management. The Bureau of Land Management is governed by a multiple-use mandate, seeking to balance a host of resources. This is outlined in federal statute 43 U.S.C. §1732(a) which states: "Multiple use means the management of the public lands and their various resource values so that they are utilized in the combination that will best meet the present and future needs of the American people," and includes "the use of some land for less than all of the resources." The resources to be managed specifically include, but are not limited to "recreation, range, timber, minerals, watershed, wildlife and fish, and natural scenic, scientific and historical values." In addition, the Bureau of Land Management is required to "give priority to the designation and protection of Areas of Critical Environmental Concern," which are areas that receive special management "to protect and prevent irreparable damage to important historic, cultural, or scenic values, fish and wildlife resources or other natural systems or processes. . ." (Federal Land Policy and Management Act, 43 U.S.C. § § 1712[b][3], 1702[a]).

Management for the Bureau of Land Management Boreal Forest lands in Alaska is defined in Resource Management Plans that govern land use for decades at a time. These Resource Management Plans are based on ongoing inventories of existing resources and identify which lands will be managed as Areas of Critical Environmental Concern or for other special purposes, as well as which lands will be available for oil and gas leasing and which lands will be recommended for withdrawal from mining (Federal Land Policy and Management Act, 43 U.S.C. §§1711, 1712). Based on its perception of the multiple use mandate, the Bureau of Land Management is generally reluctant to set aside lands for protection or to close them to leasing or other forms or development. For example, the Kobuk-Seward Record of Decision and Approved Resource Management Plans did not close any of the 11.9 million acres under consideration to oil and gas leasing (Bureau of Land Management, 2016). Nonetheless, many existing Resource Management Plans in Alaska do contain some Areas of Critical Environmental Concern that protect cultural and subsistence values for Tribes (e.g., Bureau of Land Management, 2008a; Bureau of Land Management, 2008b). In addition, much of the Boreal Forest lands, close to 50 million acres, were withdrawn from mining and leasing pursuant to the Alaska Native Claims Settlement Act, subject to later actions by the Bureau of Land Management and the Department of the Interior to revoke those withdrawals (Alaska Native Claims Settlement Act, 43 U.S.C. § 1616[d][1]).

INDIGENOUS LEADERSHIP IN BOREAL FOREST LAND-USE PLANNING AND LAND CONSERVATION

In recent years in Canada, Indigenous governments have increasingly been asserting more decision-making authority over their lands (Ariss and Cutfeet, 2012). One of the ways that this has been accomplished has been by Indigenous nations developing leading edge comprehensive land-use plans for their traditional lands (International Boreal Conservation Science Panel, 2013). These plans consolidate the Indigenous government's vision for the future of their lands and include protected lands as well as lands that may be available for resource development under the oversight of Indigenous governments through their laws, policies and regulations.

In some areas, these plans have led Indigenous governments to declare certain areas as off limits to resource development activities sometimes through a declaration of an Indigenous protected or conserved area (Ariss and Cutfeet, 2012; Indigenous Circle of Experts, 2018). Conflicts have arisen when a provincial or territorial government ignores the declaration and grants permits for private industry to operate within the area designated by the Indigenous government as off-limits to such activity. Those conflicts can result in actual on-the-ground standoffs with Indigenous blockades of access roads and/or may begin a string of protracted legal battles that can be financially debilitating for the Indigenous government (Ariss and Cutfeet, 2012).

THE CHALLENGE FOR NON-GOVERNMENTAL CONSERVATION ORGANIZATIONS

For non-governmental conservation organizations (NGCO), the political landscape is a complicated one within which to operate. In essence, both Indigenous and provincial or territorial governments control or strongly influence land use decisions across the Boreal Forest biome. NGCOs must develop and maintain supportive partnerships with many distinct and independent Indigenous governments and with provincial or territorial government officials to understand the intricacies of reinforcing Indigenous-led conservation actions and not overstep the Indigenous government's leadership.

CURRENT CONSERVATION STATUS OF THE NORTH AMERICAN BOREAL FOREST BIOME

Large tracts of North American Boreal Forest ecosystems remain intact not by design, but rather as the outcome of the inaccessibility of access (Andrew et al., 2012). The historical and current difficulty in accessing these lands has also made it one of the last industrial development frontiers on earth. The area protected is estimated to be only between 8 (Andrew et al., 2014) and 12.7% (Lee and Cheng, 2010; Carlson et al., 2015) and development and land-use management decisions are underway at an increased rate. Yet estimates do not yet reflect gains made in the last 2 years in creating new, large-scale protected areas in Canada's Boreal Forest region.

The overall areal extent of the North American Boreal Forest biome considered intact or relatively free of industrial anthropogenic impacts (including forestry, mining, oil and gas, hydropower, and infrastructure but not including climate change) has been estimated at 80–83% (Lee and Cheng, 2010; Lee et al., 2010; Andrew et al., 2012; Powers et al., 2013; Smith and Cheng, 2016). An area of contention in global analyses of areal extent of intact forest is whether areas impacted by forest fires should be considered as part of the anthropogenic footprint (Venier et al., 2018). Most forest fires in the North American Boreal Forest biome have historically been considered to be lightning-caused (Veraverbeke et al., 2017) and part of the long-term ecological history of the biome (Brandt et al., 2013; Venier et al., 2018). Very large forest fires have historically occurred across much of the North American Boreal Forest biome. In recent decades, the size and frequency of fires has increased, especially in the Alaskan and western Canada portions of the biome, perhaps to a level that has not occurred in the last 10,000 years (Kelly et al., 2013).

In contrast, in the Russian Boreal Forest biome most forest fires are generally considered to be human caused. Most experts now agree that the area burned in forest fires in the North American Boreal Forest should not be considered part of the anthropogenic footprint since most large fires are in remote areas lacking industrial infrastructure and these burned over areas will regrow and remain intact. However, because of the inclusion of areas burned by forest fires, several global analyses have suggested that the North American Boreal Forest biome has lost forest cover in recent decades at exceptionally high rates (e.g., Hansen et al., 2013; Haddad et al., 2015). An estimated 399,000 km^2 of the Canadian portion of the North American Boreal Forest biome was impacted by forest fires between 1985 and 2010 (White et al., 2017), amounting to 9% of the Canadian portion of the biome. If this were considered part of the anthropogenic footprint, the area considered intact would be lowered to approximately 74%.

A 1987 study reported that, of the "frontier forests" of North American (most in the Boreal Forest biome), 26% were under moderate or high threat (Bryant et al., 1997). An expert review of the state of all of North America's ecoregions categorized two southern Boreal Forest ecoregions as in Critically Endangered condition, one as Endangered, and an additional seven Boreal Forest ecoregions as Vulnerable (Ricketts et al., 1999).

As these studies reflect, the loss and fragmentation of intact ecosystems of the North American Boreal Forest biome is increasing as industrial access infrastructure is established from south to north. This is clear from the fact that while northern portions of the biome like the Taiga Plains ecozone are substantially intact (78% of the ecozone consists of intact landscapes of 10,000 ha or larger), substantial disturbance has occurred in southern portions like the Boreal Plains ecozone which is only 36% intact (Lee et al., 2006). In the southern portion of the North American Boreal Forest biome, estimates of the amount of no-longer-intact habitat range up to 66% (Ricketts et al., 1999) encompassing 1.77 million km^2. Lee et al. (2006) demonstrated that less than fifteen percent of the 710,000 km^2 Boreal Plains ecozone (the portion of the southern Boreal ranging from the eastern foothills of the Canadian Rockies to south-central Manitoba) was in forested landscapes that were still large and intact. More than 4,000 km^2 of the southern Boreal Forest biome within Saskatchewan and Manitoba and over 24,000 km^2 of the Boreal Forest biome within Quebec was impacted between 1900 and 2000 by forestry, road-building, and other infrastructure development (Stanojevic et al., 2006a,b).

FOREST INDUSTRY IMPACTS IN THE NORTH AMERICAN BOREAL FOREST BIOME

Forestry practices differ across international boundaries within the North American Boreal Forest Biome but forestry clearly has impacted more area of the Boreal Forest biome than any other industrial activity. A third of the North American Boreal Forest biome is tenured (leased) for forestry in Canada (Carlson et al., 2015). As of 2003, an estimated 61% of the 1.6 million km^2 Canadian commercially managed portion of the North American Boreal Forest biome had been logged at least once – an area of over 1 million km^2 (Venier et al., 2014) or 16% of the entire biome (note that this does not include any portion of Alaskan boreal that was logged). Using Landsat time series, White et al. (2017) estimated that 104,000 km^2 were disturbed by harvest in boreal ecozones of Canada between 1985 and

2010 while 399,000 km^2 were impacted by wildfire during the same period. A remote sensing analysis in 2013 estimated that 240,000 km^2 of Canada's portion of the Boreal Forest biome showed visible forest cutblocks (Pasher et al., 2013; Webster et al., 2015). A number of declining and Canadian federally listed Boreal Forest dependent birds species show major overlap with the most heavily impacted southern portion of the Boreal Forest biome (Wells, 2011) as does the Canadian federally threatened Woodland Caribou (Environment Canada, 2008, 2011; International Boreal Conservation Science Panel, 2011).

In the eastern Canadian part of the North American Boreal Forest biome, the pace and scale of forest harvest has increased in recent decades. Combined with increased size and frequency of forest fires, this is diminishing the amount of older age forest on the landscape to critically low levels (Cyr et al., 2009; Venier et al., 2014; Gauthier et al., 2015; Bergeron et al., 2017). Similarly, only 16.5% of old growth was estimated to be remaining in the managed portion of the Boreal Forest biome in Ontario and only 10% in Alberta (Venier et al., 2014).

The Alaska portion of the Boreal Forest biome has experienced limited timber harvest that has been concentrated near communities with infrastructure. Less than 5% of the total timber harvested in Alaska comes from Boreal Forests (Wurtz et al., 2006). Forested boreal lands make up 47 million hectares of land (roughly the size of California) in interior Alaska. Most timber extraction occurs in mature stands of white spruce where volumes are highest, with much of this harvest being devoted to local wood product needs. During the late 1980's and early 1990's, many high-quality white spruce logs were exported to Pacific Rim countries from state and private lands in the Boreal Forest. However, changing global markets largely ended these exports and the likelihood of future log exports from Alaska's interior forests appears small. Timber harvest in Alaska's Boreal Forest remains low due to distance from markets, low population densities, and lack of accessible timber lands for harvest.

MINING AND OIL AND GAS INDUSTRY IMPACTS IN THE NORTH AMERICAN BOREAL FOREST BIOME

A variety of other types of industrial disturbances occur within the North American Boreal Forest biome. In the western Canada portion of the biome, oil and gas extraction and exploration are rapidly increasing. As many as 22,800 oil and gas wells were drilled in 2004 and there were 222,000 active and abandoned well sites as of 2011 (Brandt et al., 2013). There are now at least 441,000 km of pipelines and 1.7 million km of seismic lines (1.75–10 m wide cleared corridors for deploying equipment to search for oil and gas deposits) set primarily in the Alberta portion of the North American Boreal Forest biome (Lee and Boutin, 2006; Brandt et al., 2013; Dabros et al., 2018). The industrial footprint from the oil and gas industry in Canada's portion of the Boreal Forest biome as of 2003 was estimated at 460,000 km^2 or approximately 8% of Canada's portion of the biome (Anielski and Wilson, 2009). Habitat that would have supported an estimated 58,000–402,000 breeding birds has already been lost within Alberta's oil sands region (Timoney and Lee, 2009) and future accumulated losses have been estimated into the tens of millions (Wells et al., 2008).

Mining may be one of the most damaging of the natural resource extraction industries to both the environment and local communities. Effects include cumulative impacts, disruption of ecological and social systems, and lasting contamination. Because many of these impacts occur over decades or centuries, the ways that mining activities impact the broad ecological landscape and environment is often not widely acknowledged. Eighty percent of Canada's mines occur within the Boreal Forest biome (Wells et al., 2010). There were 108 mineral, metal, and coal mines in the Canadian portion of the North American Boreal Forest biome as of 2009 and 1300 or more abandoned mines (Brandt et al., 2013). Although there is no existing estimate of the impact to waterways of abandoned and active mines in Canada's portion of the Boreal Forest biome, at least 3,000 such sites are known to occur within 1 km of a stream, river, or lake into which they have the potential to leach contaminants (Wells et al., 2010).

The biggest anthropogenic challenges, other than climate change, for Alaska's Boreal Forest biome, come from proposed development projects that include infrastructure for large-scale mining operations and access to currently roadless landscapes. Some of these projects will threaten the ecological integrity of existing protected areas (Wilson et al., 2014). The proposed Ambler road would develop a 400 km route through western Alaska Boreal Forests, cross three major salmon-producing rivers (including two Wild and Scenic designated rivers), and bisect the southern portion of Gates of the Arctic National Park. The proposed road would allow access and spur development for at least twelve individual mines that would create the largest mining district in Alaska and one of the largest mining districts in the world's Boreal Forest biome (Guettabi et al., 2016). Global development scenarios suggest oil, gas, mining, and renewable energy development in Alaska will concentrate across regions of the Boreal Forest biome (Oakleaf et al., 2019). Four of Alaska's six largest operating mines and six of the seven largest, proposed mining projects occur within the Boreal Forest biome (Spengler, 2013).

HYDROPOWER PROJECT IMPACTS IN THE NORTH AMERICAN BOREAL FOREST BIOME

Large hydropower projects in Canada, many developed in the 1970s and 1980s, have inundated millions of hectares (Wells et al., 2010; Cheskey et al., 2011), especially in parts of the eastern Boreal Forest biome. For example, 1.1 million hectares of terrestrial habitat were lost to five reservoirs established in the La Grande River region of central Quebec (Gauthier and Aubry, 1996). According to Brandt et al. (2013) there were 713 large dams (>5 m in height) and another 290 smaller dams in Canada's portion of the Boreal Forest biome as of 2011. The total surface area of hydropower impoundments was estimated at 50,724 km^2. Most of this surface area was formerly terrestrial habitat (Wells et al., 2010; Lee et al., 2011).

Large, proposed hydropower projects in Alaska would bring significant changes to Alaska's Boreal Forest biome. The Susitna-Watana Hydroelectric project would destroy over 20 km of spawning habitat for Arctic grayling and impact 100 km of salmon spawning habitat. The dam created by the project would be the fifth largest concrete dam in the world. Proposed dams and both claimed and surveyed mining claims encompass a significant portion of Alaska's Boreal Forest, indicating the potential for large-scale industrial development in a currently intact ecological region larger than the size of California.

ROAD NETWORK AND AGRICULTURE IMPACTS IN THE NORTH AMERICAN BOREAL FOREST BIOME

Roads and associated infrastructure threaten the ecological integrity of large portions of North America's Boreal Forest biome. Between 1959 and 1970, over 6,000 km of new permanent roads were built in Canada, largely in the Boreal Forest biome (Bone, 1992). A vast network of hundreds of thousands of kilometers of logging roads still span Canada's southern Boreal Forest biome – at least 51,000 km (ten times the driving distance between Montreal and Vancouver) in Quebec alone. In addition, there are over 1,200 km of new or upgraded roads under consideration in Quebec's northern regions (Government of Quebec, 2011). In British Columbia, there are now over 600,000 km of resource roads with an estimated 10,000 km of new roads added every year (Forest Practices Board, 2015).

In Alaska's portion of the Boreal Forest biome, the 577 km Dalton Highway was built in 1974 to serve the oilfields on Alaska's Arctic coastline. It bisects Boreal Forest and has accelerated the degradation of permafrost in the region and shifted plant community composition due to the accumulation of road dust. The extent of the degradation footprint from the road extends 115 km^2 along the road corridor (Farmer, 1993; Connor and Harper, 2013). The Red Dog Mine haul road in northwestern Alaska has impacted birds, mammals and vegetation communities in the region through heavy metal contamination and road dust pollutants (Hasselbach et al., 2005; Neitlich et al., 2017). Even the Denali Park Road, which extends through Denali National Park and allows limited vehicle traffic, has shown degradation of wilderness characteristics within the national park along the road corridor (Burrows et al., 2016).

Land use conversion for agriculture is significant in some parts of the Boreal Forest biome. In the western Canadian Province of Saskatchewan, deforestation rates for agriculture can reach 1% per year (Hobson and Bayne, 2000). Parts of the biome in Alberta, Manitoba, and northeastern British Columbia have also experienced significant conversion to agriculture.

POLICY CHANGE IMPACTS IN ALASKA'S BOREAL FOREST

In Alaska, current government actions by the Department of Interior and the Bureau of Land Management are putting the ecological and subsistence functions of Alaska's Boreal Forest lands at even further risk. The Bureau of Land Management is preparing revised Resource Management Plans that govern millions of acres and proposes to remove all protections for Areas of Critical Environmental Concern while declining to designate any new Areas of Critical Environmental Concern, despite its statutory obligation. For instance, in the Bering Sea Western Interior Resource Management Plan, the Bureau of Land Management has proposed to remove Areas of Critical Environmental Concern protection from approximately 1.9 million acres (769,000 ha) and refused to give protection to an additional 4.2 million acres (1.7 million ha) that the agency found merited such protection (Bureau of Land Management, 2019). Further, the United States Department of the Interior has issued Public Land Orders revoking withdrawals on nearly 2 million acres (809,000 ha) of Boreal Forest lands (Rait, 2019; Rowland-Shea et al., 2019).

CLIMATE CHANGE IMPACTS IN NORTH AMERICA'S BOREAL FOREST BIOME

While large areas of the North American Boreal Forest biome are being rapidly transformed by industrial activities, the biome is also undergoing major impacts from climate change (Price et al., 2013; Gauthier et al., 2015; Wells et al., 2018). Books, reviews and thousands of pages of government reports are published annually on the changes underway and expected from climate change in the Boreal Forest biome. While these are important (and we summarize some of the major impacts below), we focus in this review on impacts from land-use change activities and policies and actions related to large landscape conservation.

Mean annual temperatures across the biome are projected to be higher by 4–5°C by 2100 with an increase in droughts significant enough to cause tree mortality in the western portion of the biome coupled with increased size and frequency of forest fires and the severity of tree-killing insect outbreaks (Price et al., 2013). Climate warming may initially increase boreal tree growth but after an average 2°C temperature increase is reached, tree growth is expected to decrease as a result of warming and drying (D'Orangeville et al., 2018). The areal extent of the North American Boreal Forest biome is predicted to shrink by 25% by the end of the century (Rehfeldt et al., 2012). More than half of birds dependent on forested habitats within the biome are projected to decline by 2100 as a result of less favorable climate conditions (Wells et al., 2018).

Climate change is also accelerating ecological changes across the Boreal Forest biome. In Alaska, over 50% of these forests have low biomass production due to underlying discontinuous permafrost that leads to stunted timber growth. White spruce is vulnerable to permafrost degradation and may be replaced by grasslands and deciduous trees. Black spruce recruitment is declining due to shortened fire-free periods of time. Drought stress, insects, and displacement of conifers by deciduous species are driving ecological regime shift through much of the Boreal Forest biome. Boreal Forests in Alaska are expected to resemble the mixed deciduous-conifer forests of southern Canada as early as 2040 (Mann et al., 2012) and in Canada there is evidence that deciduous species are already becoming more prominent in the southern extent of the Boreal Forest and that shift may be exacerbated by modern forestry practices (Cyr et al., 2009; Cadieux et al., 2020).

Several recent publications have outlined the regions within the Boreal Forest biome that are predicted to be important future climate change refugia for a variety of wildlife and plants and the factors that are important in determining what areas will show rapid change and what areas will show slower changes (Stralberg et al., 2018, 2020a,b).

A VISION FOR THE FUTURE OF THE NORTH AMERICAN BOREAL FOREST BIOME

The recognition of the increasing pressure for industrial resource development led a Canadian senate subcommittee in 1999 to describe the Canadian portion of the North American Boreal Forest biome as "under siege" (Sub-Committee on Boreal Forest of the Standing Senate Committee on Agriculture and Forestry, 1999). The senate subcommittee suggested that management of these lands was not living up to government commitments to sustainable management and ecosystem protection (e.g., Canada's Forest Accord and National Forest Strategies). A forward-thinking recommendation of the subcommittee was for the establishment of industrial footprint thresholds – an idea that has been proposed and debated in the context of protecting the remaining herds of Threatened Woodland Caribou in Canada's portion of the Boreal Forest biome (Environment Canada, 2008, 2011; Festa-Blanchet et al., 2011; International Boreal Conservation Science Panel, 2011). Significantly, the senate subcommittee pointed out that recognition and protection of Indigenous rights and participatory land-use planning were critical to the region's future.

A coalition of Indigenous governments, conservation non-governmental organizations, and forward-thinking industry soon came together after this to form the Boreal Leadership Council (BLC). The BLC has promoted a vision for maintaining the special ecological and cultural values of the Boreal Forest biome within Canada (Carlson et al., 2015). They published this collaborative vision in 2003, describing the idea of an approach to land-use within the biome that would balance conservation and industrial activities with a suggestion that half or more of the biome should be considered for some form of protected area status (Boreal Leadership Council, 2003; Carlson et al., 2015). The need to significantly raise targets for protected areas goals in order to represent all native ecosystems, maintain populations of native species in natural patterns of abundance, maintain ecological processes, and maintain resilience to climate change (Noss and Cooperrider, 1994: International Boreal Conservation Science Panel, 2013; Carlson et al., 2015) is now widely acknowledged and discussed by both scientists and policymakers (Schmiegelow et al., 2006; Noss et al., 2012; International Boreal Conservation Science Panel, 2013; Locke, 2013; Wilson, 2016; Dinerstein et al., 2017).

CONSERVATION SUCCESSES AND OPPORTUNITIES IN CANADA

Fortunately, large conservation gains have been and continue to be made in North America's Boreal Forest biome through innovative, collaborative efforts of Indigenous, provincial, territorial, and federal governments and NGCO. Over 450,000 km^2 of protected areas have been formalized in Canada's portion of the Boreal Forest biome since 2000 and 400,000 km^2 of forest tenures had been certified through the Forest Stewardship Council (Carlson et al., 2015). In partnership with provinces and territories, the Canadian federal government has embarked on an ambitious effort to reach its Convention on Biodiversity-Aichi obligation of protecting at least 17% of its terrestrial landscape by 2020 (Wulder et al., 2018) through, among other things, establishing a $500 million Nature Fund, including a $175 million Target 1 Challenge Fund. A significant proportion of Challenge Fund support has been used to assist Indigenous and provincial/territorial governments in developing protected areas proposals. Because of its relative intactness, lands in the Boreal Forest biome of Canada make up the vast proportion of these proposals.

CONSERVATION OPPORTUNITIES IN ALASKA

In Alaska, National Wildlife Refuges, and National Parks and Preserves make up the current protected areas of the Boreal Forest biome. Over 12 million hectares within the Boreal Forest biome were protected under the Alaska National Interest Lands Conservation Act in 1980. These land protections included subsistence rights for Indigenous Peoples within Alaska, but did not convey management or ownership to Indigenous Peoples. In fact, Alaska's 229 Federally recognized Tribes do not have equal land rights to those of Native Corporations, or state and federal government. Even with the current political structure, Indigenous Peoples have engaged in land use management planning efforts to establish Areas of Critical Environmental Concern and other types of protected areas within management plans. In Alaska, species-based co-management groups govern specific wildlife populations, but they do not have authority over land management decisions. For example, the Western Arctic Caribou Herd Working Group makes management recommendations for the Western Arctic Caribou Herd and the Alaska Migratory Bird Co-Management Council makes recommendations to inform state and federal wildlife guidelines for migratory birds. However, the conservation of species must include the conservation of species' habitats, and thus, the co-management models that have been built by species-specific co-management boards should be expanded to include land units for conservation. Although these efforts have not resulted in permanent protection for specific places, the opportunity exists to build new collaborations and secure protections for Alaska's Boreal Forest biome that are consistent with the requests of Indigenous governments and communities across the region.

INDIGENOUS-LED CONSERVATION

Indigenous governments across the Boreal Forest biome of Canada are leading in many of the most modern, cutting edge land and wildlife management plans and models in the world (International Boreal Conservation Science Panel, 2013; Wells et al., 2013; Carlson et al., 2015). Land-use plans developed by Indigenous governments cover vast regions involving hundreds of thousands of hectares of habitat (Wells et al., 2014). The recommendations for protected areas and sustainable development zones in these landscape plans are some of the most significant conservation efforts ongoing in North America and the world. In 2018, the Canadian federal government announced $175 million in new funds (Target 1 Challenge Funds as mentioned above) to support new protected areas proposals, including those led by Indigenous governments. New Indigenous land-use plans and protected areas proposals (often termed Indigenous Protected and Conserved Areas) for areas within the Boreal Forest biome continue to be announced and developed.

EXAMPLE INDIGENOUS LARGE-SCALE LAND-USE PLANS AND PROTECTED AND CONSERVED AREAS PROPOSALS

The Łutsël K'e Dene First Nation in the Northwest Territories is implementing a conservation plan for their traditional territory. On August 21st 2019, the Łutsël K'e Dene First Nation signed an agreement with the Parks Canada Agency and the Government of the Northwest Territories to permanently protect 26,376 km^2 of boreal lands. The entire area, called Thaidene Nëné, is an Indigenous Protected and Conserved Area. Parts of it are also designated as a national park, territorial park and wildlife conservation area (S. Nitah, personal communication).

The Dehcho First Nation in the southwestern part of the Northwest Territories finalized a sophisticated land-use plan in 2006 for their more than 200,000 km^2 traditional territory (Dehcho Land Use Planning Committee, 2006). While negotiations with the Government of the Northwest Territories and the Canadian federal government are still ongoing, the original Dehcho plan called for more than 100,000 km^2 of protected lands (International Boreal Conservation Science Panel, 2013; Wells et al., 2013). In October 2018, Dehcho leaders and federal government representatives held a signing ceremony to designate the Edéhzhíe Dehcho Protected Area and National Wildlife Area. Spanning 14,249 km^2 of Boreal Forest, Edéhzhíe marked the first Indigenous protected and conserved area established since Canada laid out its pathway process to protect at least 17% of lands and freshwaters by 2020.

The Sahtúgot'ine Dene in the Northwest Territories proposed and established the Tsá Tué Biosphere Reserve in 2016. The Biosphere Reserve encompassed more than 90,000 km^2 of area including Great Bear Lake (one of the world's largest and most pristine) and its watershed. More recently the Sahtúgot'ine Dene have proposed creating an Indigenous protected and conserved area in their traditional territory.

In Yukon, the Peel River Watershed Land Use Plan which was developed through a many-year process involving a number of First Nations as well as conservation organizations and the Yukon Government, was approved in 2019 requiring 55,000 km^2 of new protected areas be formally established in coming years (Government of Yukon, 2019).

In Manitoba and Ontario, several First Nations that developed and implemented land-use plans for their traditional territories, worked with the governments of Manitoba and Ontario to be granted World Heritage status under the name of Pimachiowin Aki (the Land that Gives Life). They protected 29,040 km^2 of intact forest within the southern portions of the Boreal Forest biome in eastern edge of Manitoba and western Ontario (Davidson-Hunt et al., 2012; Wells et al., 2013). In northern Manitoba, the Sayisi Dene First Nation has proposed protection of the entire 50,000 km^2 of the Seal River watershed, a 260 km free-flowing river whose watershed is free of any large-scale industrial development. Other Indigenous governments and NGCOs are working toward creating a marine protected area at the mouth of the Seal River to protect important beluga calving habitat and other marine protected areas in western Hudson Bay (Labun and Debicki, 2018).

In Ontario the Moose Cree First Nation has submitted a proposal to protect an additional 5,080 km^2 of the North French River watershed (of which 1,583 km^2 is currently protected) that flows north into James Bay (Canadian Parks and Wilderness Society, 2018).

In Quebec, the Cree Nation has completed a comprehensive protected areas proposal (Cree Nation Government, 2015) with community proposals for more than twenty large, new protected areas together totaling about 80,000 km^2 in extent (Cree Nation Government, 2019b). A new agreement was signed in 2019 between the Cree Nation and the Canadian federal government to launch a feasibility assessment for considering a new national marine conservation area in Eastern James Bay (Cree Nation Government, 2019a). A marine protected area had been proposed in 2009 off the central east coast of James Bay by the Wemindji First Nation (Mulrennan and Scott, 2019).

The Innu Nation in Labrador developed a Forest Ecosystem Strategy Plan that directs that more than 50% of the 71,000-km^2 agreement area be protected for ecological or cultural values – an area of 35,000 km^2 (Forsyth et al., 2003; Wells et al., 2014).

Although technically north of the Boreal Forest biome in Alaska, there is an opportunity for a new United States model of co-management or Indigenous leadership in protected area management for the Arctic National Wildlife Refuge (Arctic Refuge). The Arctic Refuge was established in 1960 and expanded in 1980 in Alaska. Adjacent to the Arctic Refuge are Ivvavik National Park and Vuntut National Park in Canada. The Porcupine Caribou Management Board, which includes Alaska Native Tribes, Canada First Nations, federal, state and provincial governments, was established in 1987 to fulfill the international treaty obligations to protect the Porcupine Caribou Herd within these protected areas. These landscapes have been proposed as an international Arctic Wilderness area with an emphasis of continuing to protect a land base for the Gwich'in and Inupiat cultures (Miller, 1995) and to protect the ecological integrity of habitats and migration corridors for the Porcupine Caribou Herd. Adoption of such a new co-management model in Alaska could be an important step toward establishment of other new co-managed protected areas within Alaska's Boreal Forest biome.

INDIGENOUS GUARDIAN PROGRAMS

Increasingly, Indigenous governments across the North American Boreal Forest biome region are also developing programs to train and equip Indigenous people from their own nations to serve as on-the-ground guardians. Indigenous guardians fulfill a wide range of duties including land and people management, biological monitoring, safety and enforcement, and education within their traditional territories and protected areas using both Indigenous knowledge and western science. Often termed "Indigenous ranger" programs in Australia, such efforts already employ about 840 full time equivalent Indigenous people managing protected areas in Australia (Woinnarski et al., 2014) and the Australian government has committed another $700 million to support rangers until 2028. One of the earliest modern examples of this approach in Canada was initiated by the Haida Gwaii in 1981 under the name of the Haida Watchmen Program (M. Richardson, personal communication). Since that time, the program has expanded to other First Nations and is now collectively called the Guardian Watchmen Program (Coastal First Nations–Great Bear Initiative, 2018). There are now about 60 Indigenous Guardian programs operating across Canada. The Łutsël K'e Dene First Nation, for instance, established the Ni hat'ni Dene (the "Dene Watching the Land") program in 2008 that trains and employs young people from the community in Indigenous knowledge, scientific monitoring and visitor education and safety duties (Łutsël K'e Dene First Nation, 2018). In 2017, the Canadian Federal government committed $25 million to help support existing and establish more such guardian programs. By the end of 2020, more than 70 existing and new programs will have received financial support for guardian programs.

CONSERVATION RECOMMENDATIONS FOR NORTH AMERICA'S BOREAL FOREST BIOME

- Land-use decisions across the North American Boreal Forest biome will determine its ecological future. Those decisions must be led by Indigenous governments and communities. This is consistent with Free Prior and Informed Consent (FPIC) principles that state that Indigenous peoples have the right to determine and develop priorities and strategies for the development or use of lands and waters or other resources within their traditional territories (Boreal Leadership Council, 2012).
- Federal, provincial and territorial governments should make large-scale, multi-year investments in providing financial resources for Indigenous governments and communities to train and hire Indigenous land-use planners, managers, and on-the-land guardians. Such programs can fill existing gaps in ecological data particularly in remote northern regions where data are most sparse.
- Federal, provincial and territorial governments should make large-scale, multi-year investments in providing financial resources for Indigenous governments and communities for the planning, development, and management of Indigenous protected and conserved areas. This will be essential for Canada to meet both its current and any future conservation commitments, including the Government of Canada's 2019 Speech from the Throne commitment to protect 25% of lands and waters by 2025.
- To maintain the full complement of all plant and animal species and associated ecological processes, at least 50 percent of the North American Boreal Forest biome should be within a network of protected areas free of large-scale industrial disturbance, including from forestry, mining and exploration activity, oil and gas extraction and exploration, agriculture and hydropower production (International Boreal Conservation Science Panel, 2013; Wells et al., 2014). Industrial development that does occur must be carried out at the highest sustainability standards and only with Indigenous government consent and oversight.
- The protected area networks must include very large landscapes – ideally on the order of 10,000–30,000+ km^2 (2.5–7+ million acres) in size – connected to allow wildlife populations to survive and to ensure the full range of habitat diversity and ecosystem functions that will serve as biodiversity reservoirs in the face of climate change (International Boreal Conservation Science Panel, 2011).
- Conservation of lands must accommodate Indigenous traditional uses of the land and should be managed or co-managed by Indigenous governments and guardians. In all conservation areas, there should be protection of traditional values and uses, including hunting, trapping, gathering plants for food, materials, medicines and spiritual and ceremonial practices.
- Planning must take into account the cumulative impacts of development over meaningful time periods (i.e., decades to a century). This is necessary to ensure that the full consequences of land use are understood and addressed. Given the unprecedented speed of climate change impacts to ecological systems, especially in northern regions, the viability of wildlife populations is dependent on managing land use to maintain large, intact habitat areas and landscape connectivity.
- While Alaska has examples of species-specific co-management plans, such a co-management model must be applied to Indigenous protected areas or ecosystem-based plans that can be implemented through Indigenous resource management, such as the approach originally envisioned for the Arctic National Wildlife Refuge.
- In Alaska, the foregoing recommendations generally apply. However, they will also need to be implemented in a manner that addresses the challenges of current

land ownership and management within the state. The federal agencies, as well as the State of Alaska, can and should use their management flexibility to enter into co-management arrangements for landscapes and set up Indigenous guardian programs, similar to those employed in Canada. They should undertake an effort to identify the best places for management with Indigenous governments and communities immediately. The opportunity to protect large, intact Boreal Forest landscapes in Alaska will require coordination among diverse stakeholders, investment in Indigenous governments and communities, and recognition of the issues that have resulted from the history of colonization across the United States.

CONCLUSION

The North American Boreal Forest biome is one of the last, large intact landscapes remaining on Earth. The intactness of the biome has allowed it to retain globally significant conservation values and features and ecological functions. As the human industrial footprint and climate change impacts continue to degrade ecosystems and increase the loss of biodiversity on the planet, the protection of the North American Boreal Forest biome becomes even more essential. Maintaining its massive terrestrial carbon storehouse is critical to preventing further carbon from being released into the atmosphere (Bradshaw et al., 2009; Carlson et al., 2009; Bradshaw and Warkentin, 2015). The biome will also become increasingly important as a place of refuge for species forced northward by inhospitable climate further south (Stralberg et al., 2015, Stralberg et al., 2017). Further, the best insurance for maintaining resilience of plant and animal communities to climate change will be the maintenance of intact ecosystems and robust populations (Wells et al., 2018). Species that must shift ranges northward to survive will have their best opportunity to so do when unimpeded by fragmented habitat full of human-made barriers. Careful land-use planning now that conserves very large parts of the North American Boreal Forest biome will provide the best likelihood of survival for countless species, including humans. The most significant land-use planning and conservation proposals underway across the biome are led by Indigenous governments. Governments, non-governmental organizations, academics and indeed the public at large, should be finding ways to support and encourage Indigenous-led land-use planning, Indigenous guardians and Indigenous protected and conserved areas.

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Older Eastern White Pine Trees and Stands Accumulate Carbon for Many Decades and Maximize Cumulative Carbon

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Pre-settlement New England was heavily forested, with trees exceeding 2 m in diameter. The forests have regrown since farm abandonment, representing what is arguably the most successful regional reforestation on record and identified recently in the "Global Safety Net." Temperate "old-growth" forest and remnant stands demonstrate that native tree species can live several hundred years and continue to add to forest biomass and structural and ecological complexity. Forests globally are an essential natural climate solution that accumulate carbon and reduce annual increases in atmospheric CO_2 by approximately 30%. Some studies emphasize young, fast-growing trees and forests while others highlight carbon storage and accumulation in old trees and intact forests. We addressed this directly within New England with long-term, accurate field measurements and volume modeling of individual trees and two stands of eastern white pines (*Pinaceae*: *Pinus strobus*) and compared our results to models developed by the U.S. Forest Service. Within this sample and species, our major findings complement and clarify previous findings and are threefold: (1) beyond 80 years, an intact eastern white pine forest can accumulate carbon above-ground in living trees at a high rate and double the carbon stored in this compartment in subsequent years; (2) large trees dominate above-ground carbon and can continue to accumulate carbon; (3) productive stands can continue to accumulate high amounts of carbon in live trees for well over 150 years. Because the next decades are critical in addressing the climate emergency, and most New England forests are less than 100 years old, a major implication of this work is that maintaining and accumulating carbon in some existing forests—proforestation—is a powerful regional climate solution. Furthermore, older and old-growth trees and forests are rare, complex, highly dynamic and biodiverse: dedication of some forests to proforestation will produce large carbon-dense trees and also protect ecosystem integrity, special habitats, and native biodiversity long-term. In sum, strategic policies to grow and protect suitable existing forests in New England will optimize a proven, low cost, natural climate solution that also protects and restores biodiversity across the landscape.

Keywords: proforestation, intact forest, ecological resilience, carbon accumulation, chronoseqeuence, old-growth and second-growth forest, tree volume, ecological integrity

INTRODUCTION

A global priority for the climate has long been reducing ongoing emissions of heat-trapping greenhouse gases (GHGs) produced by burning carbon-based fuels. While this is essential, it is not sufficient for halting the rise in global temperatures. It is necessary to also simultaneously increase carbon dioxide (CO_2) removal (CDR) and keep carbon stored within natural systems. Clearing and harvesting forests, draining and developing wetlands, and degrading soils account for one-third of all the CO_2 added to the atmosphere by humans since the beginning of the industrial revolution (Simmons and Matthews, 2016). Together, these ongoing actions continue to add approximately 1.6 PgC/year (1 Pg equals 1 Gt or 10^{15} grams or 1 billion metric tons; Friedlingstein et al., 2020). Burning wood for heat and electricity adds additional CO_2, and current forest management practices limit the potential of this natural solution to accumulate carbon above and below ground and keep it out of the atmosphere (Sterman et al., 2018).

Two recent Intergovernmental Panel on Climate Change (IPCC) reports identify the urgent and unprecedented imperative to simultaneously and rapidly reduce Carbon Dioxide Emissions and achieve additional Carbon Dioxide Removal (CDR) from the atmosphere (Intergovernmental Panel on Climate Change, 2018, 2019). These reports identify forests as playing a major role in accumulating carbon out of the atmosphere. However, for CDR the focus is primarily on afforestation (planting new forests) and reforestation (regrowing forests) and ignores the more rapid climate mitigation and adaptation benefits of additional growth by existing forests, termed "proforestation" (Moomaw et al., 2019).

Even achieving the goal of "zero net carbon" will only "probably" limit global average temperatures to 1.5°C (Intergovernmental Panel on Climate Change, 2018) above the pre-industrial global temperature and a significant increase above the current level (~1.2°C). This additional temperature increase will result in greater disruption to the climate system and will accelerate ecological decline. To avoid ever more serious consequences of a changed climate, the goal must be to become net carbon *negative* as soon as possible. Growing suitable existing forests is an effective and low cost means for reducing the atmospheric stock of carbon as others have noted (Fargione et al., 2018; Hudiburg et al., 2019; Moomaw et al., 2019; Mildrexler et al., 2020) and will be demonstrated by the findings reported in this paper. Natural regeneration of forests has recently been found to accumulate more carbon in the first 30 years than managed reforestation (Cook-Patton et al., 2020).

A second and perhaps even more urgent priority is the strong protection of intact biodiverse natural systems (Watson et al., 2018), as verified in the Global Assessment Report on Biodiversity and Ecosystem Services (Intergovernmental Science-Policy on Biodiversity and Ecosystem Services, 2019) and the recent "Global Deal for Nature"(Dinerstein et al., 2019). A global review with a dual focus on carbon and biodiversity identified regions that are part of a "Global Safety Net" (Dinerstein et al., 2020), and the safety net must be now be translated to local levels. This joint climate/biodiversity priority was also highlighted in the peer-reviewed declaration of a Climate Emergency signed by over 13,000 scientists in late 2019 and which highlighted proforestation as a global climate solution (Ripple et al., 2020).

There is scientific consensus that we can substantially close the gap between CO_2 emissions and removals by maximizing a range of nature-based solutions (Griscom et al., 2017; Fargione et al., 2018). Regarding biodiversity, the beneficial role of protected areas in supporting species abundance and diversity was confirmed in a global meta-analysis (Coetzee et al., 2014), and the benefit of protecting intact ecosystems was quantified by comparing the probability of extinction in the six major global regions. On average, "wilderness" reduces the rate of species' extinction by half due to higher rates of species loss in unprotected areas (Di Marco et al., 2019); the quantified benefit of wilderness in preventing extinction is even higher in regions, including the Eastern United States. Biodiverse intact forests can simultaneously provide long-term protection to natural processes and biodiversity, reduce extinction, and provide pathways for migration while accumulating atmospheric carbon moderating local and global temperature increases (Friedlingstein et al., 2020). Taken together, it is practical and possible to act immediately to protect ecosystems and prevent extinction while we maintain increased CDR rates and store and accumulate additional carbon in forests and forest soils.

Forest conservation studies tend to focus on high-biodiversity tropical forests (Mitchard, 2018), yet temperate forests are also biodiverse (Hilmers et al., 2018), benefit human health and well-being in highly populated areas (Karjalainen et al., 2010), and provide many essential ecosystem services (United States Forest Service, 2021). They also have a large additional potential for CDR that has been underestimated by 32% (Cook-Patton et al., 2020). New England Acadian Forests are the only region in the lower 48 United States identified as part of the "Global Safety Net" as a Tier 1 climate stabilization area (Dinerstein et al., 2020). Current forest CDR in the United States reduces annual net nation-wide greenhouse gas emissions by 11.6% (United States Environmental Protection, and Agency, 2018), with the potential for much more (Keeton et al., 2011; Moomaw et al., 2019). Houghton and Nassikas (2018) estimate the current gross carbon sink in forests recovering from harvests and in abandoned agriculture to be −4.4 PgC/year (negative means removal) globally, consistent with the IPCC 1.5°C report that identified forests as key to increasing accumulation rates. This potential carbon sink from recovering forests is nearly as large as the gap between anthropogenic emissions and removal rates, 5.1 PgC/year (Friedlingstein et al., 2020).

In the context of resource production and forest management, some forest carbon is stored in lasting wood products, and responsible forestry can provide a reliable wood supply from a semi-natural forest. However, multiple analyses have found that more carbon associated with timber harvests is lost to the atmosphere than is stored in the harvested wood products (Nunery and Keeton, 2010; Harris et al., 2016). For example, just 19% of the original carbon stock in Oregon forests in 1900 is in long lived wood products; approximately 16% is in landfills, and the remaining 65% is in the atmosphere as carbon dioxide (Hudiburg et al., 2019). Updated models indicate that the product substitution benefits of wood products are overestimated between 2 and 100-fold (Harmon, 2019) and any near-term carbon benefit relies on product subsitution (Hudiburg et al., 2019; Leturcq, 2020). Biogenic emissions from harvesting in the United States are estimated to be 640 MtC/year or 85% of total forestry emissions, exceeding the commercial and residential building sectors, and fossil fuel emissions from harvesting add an additional 17% CO_2 to the atmosphere above biogenic emissions (Harris et al., 2016).

Strategic planning for responsible resource production can both mitigate these emissions and ensure a protected network of intact natural areas. For example, the US Climate Alliance underestimates the importance of "net carbon accumulation" in forests (United States Climate Alliance, 2021). Forests do accumulate net carbon now, but carbon above and below ground is far below historic levels and far below its potential (Law et al., 2018; Hudiburg et al., 2019). A critical and explicit goal is to increase and optimize carbon accumulation by utilizing some forests for responsible resource production as needed and protecting other forests for climate protection, long-term full biodiversity, science, and human health and well-being.

At a global level, if deforestation were halted, and existing secondary forests allowed to continue growing, a network of these intact forests would protect the highest number of species from extinction (Di Marco et al., 2019; World Wildlife Federation, 2020) and it is estimated that they could accumulate ∼120 PgC in the 84 years between 2016 and 2100 (Houghton and Nassikas, 2018). This is equivalent to about 12 years of current global fossil fuel carbon emissions. These global numbers are conservative as outlined in recent analyses (Cook-Patton et al., 2020) and they do not factor in the enhanced regional CDR potential and high cumulative carbon that can be achieved with proforestation in such carbon-dense temperate forests of the Pacific Northwest (Law et al., 2018) and New England (Nunery and Keeton, 2010; Keeton et al., 2011; Moomaw et al., 2019; Dinerstein et al., 2020).

Because these global and regional projections can be difficult to translate locally, particularly over time, we focused on a detailed analysis of individual trees and stands in New England. Historically, between 80 and 90% of the New England landscape was heavily forested, and early chroniclers describe pre-settlement forests with many large, mature trees reaching 1–1.5 m in diameter (Whitney, 1996). Fast-growing riparian species like sycamores and cottonwoods could reach or exceed 2 m. Today, New England trees of this size are mostly found as isolated individuals in open areas, parks, and old estates. Old-growth forests (primary forests) and remnants are currently less than 0.2% of northern New England's landscape, and less than 0.03% in Southern New England. Ongoing attempts to document their value and identify their locations is underway (Davis, 1996; Kershner and Leverett, 2004; Ruddat, 2020). Secondary forests in New England consist mostly of smaller, relatively young trees (on average less than 100 years old). The U.S. Forest Service estimates that fewer than 7% of the nation's forests exceed 100 years in age.

Our goal in this study was to measure carbon directly in individual trees and in an "average" vs. an older stand of eastern white pine (*Pinaceae: Pinus strobus*) in New England. Most forest carbon studies focus on large geographical areas, and utilize "net" carbon data gathered from LIDAR (Light Detection And Ranging) and satellite technology, as well as statistical modeling based on the US Forest Service methods. Upon examining these options we note that carbon estimates from different tools and models can lead to disparate results at the level of individual trees—and these errors can be extrapolated to stands (Leverett et al., 2020). Therefore, we capitalized on the extensive tree-measuring protocols and experience of the Native Tree Society (NTS) to conduct highly accurate direct field measurements and measure volume precisely in younger vs. older trees growing in stands (Native Tree Society, 2021). We used direct measurements to evaluate volume-biomass models from multiple sources and developed a hybrid—termed FIA-COLE—to capitalize on the strengths of each model. We calculated the live above-ground carbon (in metric tons) in individual eastern white pines and individuals of other species in pine stands using conservative assumptions and direct measurements in pines up to 190 years old.

MATERIALS AND METHODS

This paper centers primarily on (1) individual eastern white pines (*Pinaceae*: *Pinus strobus*), (2) a representative older pine stand in Western Massachusetts, named the *Trees of Peace (TOP*: located in Mohawk Trail State Forest, Charlemont, MA), and (3) a nearby younger pine stand (∼230 m center to center from the *TOP*). Both stands regenerated naturally from pasture and they share abiotic conditions such as a similar elevation, soil type (Hinkley loamy), temperature and precipitation. The younger stand is slightly downslope, and neither shows evidence of major recent disturbance. In 1989 the *TOP* lost 6 trees in a storm. Currently the *TOP* has 76 pines covering 0.6–0.7 ha.

While not discussed in detail herein, we have also collected and analyzed data from NTS measurements in 38 other sites with white pines in the Eastern United States. Since 1990, NTS has taken thousands of on-site direct measurements of individual trees in dozens of stands of eastern white pines (see examples **Supplement 1**). Measurements are published on the society's website (Native Tree Society, 2021) and comprehensive measurement protocols were adopted from those developed by NTS (Leverett et al., 2020) and incorporated into the American Forests Tree Measuring Guidelines Handbook (Leverett and Bertolette, 2014). A brief description of the measurement methods and models is provided in "Height and Diameter Direct Measurement Methodology," **Supplement 2** and in Leverett et al. (2020). Here, in all cases, the best mathematical processes were applied, e.g., the sine instead of the tangent height method and the best statistical models.

In the pine stands, a point-centered plot was established with a radius of 35.89 m, covering 0.403 hectares (subsequently referred to as 0.4 ha), with the goal of evaluating a standard acre (radius: 117.75 ft), and thus relevant to forestry conventions in the U.S. Within the *TOP*, 44 mature white pine stems were tallied along with 20 hardwoods and eastern hemlocks greater than 10 cm in diameter at breast height (DBH, 4′ 5″ or 1.37 m from the ground). The measured acre had 50 pines in July 1989 when six trees were lost in a wind event. The pines are ∼160 years old; the hardwoods and hemlocks are estimated to be between 80 and 100 years old.

Height and Diameter Direct Measurement Methodology

We quantified the volume of the trunk and limbs of each tree from heights and diameters measured with laser-based hypsometers, monoculars with range-finding reticles, traditional diameter tapes, and calipers (described in detail in Leverett et al., 2020). Each instrument was calibrated and independently tested for accuracy over a wide range of distances and conditions (see **Supplement 2** for an example). Absolute accuracies of the two main infrared lasers were verified as ±2.5 cm for distance, surpassing the manufacturer's stated accuracy of ±4.0 cm. The tilt sensors were accurate to ±0.1°, meeting the manufacturer's stated accuracy. The combination of these distance and angle error ranges, along with the most accurate trigonometric methods noted above (sine vs. tangent method), gave us height accuracies to within 10–15 cm on the most distant targets being measured and approximately half that on the closest targets. We distinguished the rated and/or tested accuracy of a particular sensor of an instrument (such as an infrared laser or tilt sensor) from the results of a measurement that utilized multiple sensors.

Tree heights were measured directly for each pine with a visible top, using the sine method (**Supplement 2**) whenever possible rather than the traditional tangent method. Our preference for the sine method is supported by NTS, the US Forest Service (Bragg et al., 2011) and American Forests (Leverett and Bertolette, 2014). The more traditional tangent method often over/under-estimates heights by treating the sprig being measured (interpreted as the top), as if it were located vertically over the end of the baseline. The heights of 38 white pines in the *TOP* with visible tops were measured directly using the sine method.

Use of a Form Factor and FIA-COLE in Determining Pine Volume

To compute trunk volume directly from the base to the absolute top of a tree, diameters at base and breast height were measured with conventional calibrated tapes according to the procedures established and published by NTS. Diameters aloft were measured with the combination of laser range-finders and high performance monoculars with range-finding reticles. A miniature surveying device, the LTI Trupoint 300, was also used. Its Class II, phase-based laser is rated at an accuracy of ±1.0 mm to clear targets and its tilt sensor is accurate to ±0.1 degrees. In the *TOP*, we computed the volume of each pine's trunk and limbs using diameter at breast height, full tree height, trunk form, and limb factors. (See **Supplement 3** for a discussion on the development of the form factor and its importance in measuring volume, with comparisons to other methods of measurement).

Detailed measurements of 39 sample trees established an average form factor (see NTS measurements in **Supplement 3, Table S3.2**). The volume of each sample tree was determined by dividing the trunk into adjacent sections, with the length of each section guided by observed changes in trunk taper and/or visibility. Each section was modeled as the frustum of a regular geometric solid (neiloid, cone, paraboloid; see **Supplement 3** and Leverett et al., 2020, for formulas). The form factor for each pine was computed by adding its section volumes to obtain total trunk volume and then dividing the result by the product of the pine's height and breast-high cross-sectional area. This produced an average factor that would fit the pines growing in a stand. We applied the average form factor to all pines included in the *TOP* as one determination of trunk volume.

For comparison to our direct volume measurements, we applied a hybrid volume-biomass model to compute trunk volumes for pines in the *TOP*. This hybrid allowed us to make use of the extensive analysis of the US Forest Service Forest Inventory and Analysis (FIA) program and database (which determines volume and biomass through the use of allometric equations; United States Forest Service, 2020) as well as the Carbon On-Line Estimator (COLE; National Council for Air Stream Improvement, 2020). This hybrid was termed FIA-COLE. See **Supplement 4** for a full explanation of the variables and equations for defining trunk volume. We finalized volumes for the pines in the *TOP* by averaging our direct measurements with those of FIA-COLE.

For the total volume of the above-ground portion of a pine, we derived a factor for limbs, branches, and twigs as a proportion of the trunk volume using the FIA-COLE model (**Supplement 5**). That model includes all the branching in what is defined as the "top" in a biomass calculation and the limb factor for large trees is typically an additional 15–16%. We ran the model for each of the individuals in the *TOP* and calculated the volume. This was converted to biomass (density) and then to carbon mass using a conservative carbon mass fractional factor of 48%.

Analysis of Individual Pine Trees and a Representative Stand

In addition to the *TOP*, and older exemplary pines, we quantified above-ground carbon in younger trees and a representative stand. To determine an "average" pine at 50 years we defined two populations: (1) trees at 50 years that are still alive today, and (2) trees that were alive at 50 years but are missing today. This allowed us to compute an average trunk size for the missing trees and the associated carbon. We also measured white pines from young to older ages to estimate growth rates and volumes. The number of pines alive at 50 years but not alive today was determined from stand density data coming from both field counts and FIA (United States Forest Service, 2020).

We extensively studied an ∼80-year-old stand of pines adjacent to the *TOP* (**Supplement 6**) growing on a terrace located just downslope from the *TOP* in an area fairly well protected from wind and with similar abiotic conditions and adequate soil depth. This age is more representative of the average stand of eastern white pine in New England (60–80 years; United States Forest Service, 2019). We also considered the range of pines of known ages from stands within the vicinity and elsewhere. Where we could, we examined ring growth and height patterns for individual pines during their early years on a variety of sites in different geographical locations. In some cases, we examined stumps and measured the average ring width. In other cases, we measured trees and counted limb whorls to get age estimates.

We measured the tallest pine in the *TOP* over a long time-span (referred to as Pine #58, its research tag number). Pine #58 has been measured carefully and regularly over a period of 28 years. In 1992 the tree was 47.24 m tall and 2.93 m in circumference. Since then, it has been climbed 4 times, tape-drop-measured, and volume-determined. Pine #58 continues to grow and has enabled us to quantify the changes in carbon accumulation in a dominant tree over decades. See **Supplement 7** for a detailed measurement history of Pine #58.

Live tree above-ground volumes were converted to mass using standard wood density tables (United States Department of Agriculture, 2009). The air-dried density for white pine is 385.3 kg/m^3 (0.3853 metric tons/m^3). As noted above, we calculated the amount of carbon in each pine conservatively as 48% of total air-dried weight, whereby a cubic meter of white pine trunk or limbs holds 0.18494 metric tons of carbon (at least 50% is used more commonly; the percentage of carbon content in different species ranges from ∼47% to 52+% and there is evidence that pine is at the upper range (Nicodemus and Williams, 2004). Note that the carbon in a cubic meter of wood varies depending on the species and is usually greater in hardwoods (United States Department of Agriculture, 2009).

RESULTS

Our measurements indicate that individual eastern white pines can accumulate significant above-ground volume/carbon up to at least 190 years, that this volume/carbon accumulation in an individual tree can accelerate beyond 100 years, and that a stand of pines can double its above-ground live carbon between ∼80 and 160 years.

Analysis of Dominant Individuals and Averages for Stand-Grown Pines

As Pine #58 is the tallest and the largest tree (volume) in the Trees of Peace (*TOP),* its performance over time was analyzed in great detail. It started growing as part of a more tightly packed stand, but presently has ample space. Its circumference at breast height is 3.30 m, its height is 53.71 m, and its crown spread is approximately 15.5 m. Over a period of 26 years, beginning in 1992, Pine #58 has grown in circumference at an average rate of 1.39 cm per year and grown in height 23.71 cm per year. For a chronosequence, we assumed that Pine #58 grew a lot when it was young—an average of up to 61 cm per year in its first 50 years. Its trunk and limb volume was 23.33 m^3 at the end of the 2018 growing season (**Supplement 7**).

Figure 1 shows the increase in height, circumference and volume of Pine #58 within each 50-year interval up to 150 years and includes a photo of the tree. Its estimated age is ∼160 years, and we used a chronosequence to determine previous epochs. For dominant pines in stands on good sites, ring widths for the first 50 years average ∼0.6 cm and thus a 1.88 m circumference at 50 years. (Note that we measured one exceptional pine at 2.13 m in circumference.) Heights of stands at age 50 depend largely on site characteristics and expressed as site index (the average height of a stand at 50 years). The average index for white pine in Massachusetts is approximately 20 m (William Van Doren, Massachusetts Department of Conservation and Recreation, *pers. comm.*). For Pine #58 we calculated a much higher index to assume rapid early growth in the first 50 years. Based on these principles, the change in circumference and growth in height were greatest in the first 50 years, and decreased in the next two 50-year periods, confirming young pines "grow more rapidly" in terms of annual height and radial increases. However, volume growth, and thus carbon accumulation, continued to increase in the epochs studied here. This is primarily because volume increases linearly with height but increases as the square of the diameter (see **Figure 1** and **Supplement 8**).

As noted, we assumed Pine #58 had optimal rapid growth in the first 50 years. Even so, our analysis supports the conclusion that the pine accumulated the majority of its current carbon *after age 50* and at an increased rate during subsequent epochs. Pine #58 now stores 4.33 tC above ground and continues to grow. For comparison, the carbon stored in the trunk of the highest volume 50-year-old pine that we encountered (2.13 m circumference, 34.75 m height, and 0.4346 form factor) is 1.16 tC. Therefore, even in the best-case scenario Pine #58 would have acquired only a quarter of its current carbon by age 50. Note that the same crown area occupied by multiple younger trees cannot achieve the carbon in this larger tree (Leverett, unpublished observations).

Up to a point, the carbon advantage gained by the older trees accelerates with their increasing age and size, a finding that has been affirmed globally (Stephenson et al., 2014). **Figure 2** documents the average volume in individual pines in the stands at ∼80 and 160 years as well as several additional large pines. MSF Pine #1, the largest pine in Monroe State Forest, western Massachusetts, has a trunk volume of 35.9 m^3 at approximately 190 years (6.62 tC; **Figure 2**). Assuming its early years accumulated 1.16 tC at 50 years, which is the fastest growing 50-year old pine we measured in all sampled locations, the large pine added 5.46 tC between 50 and 190 years, or 1.95 tC per 50-year cycle after year 50. This is at least 1.68 times the rate of growth for the first 50 years. This compares to a 1.6 ratio for Pine

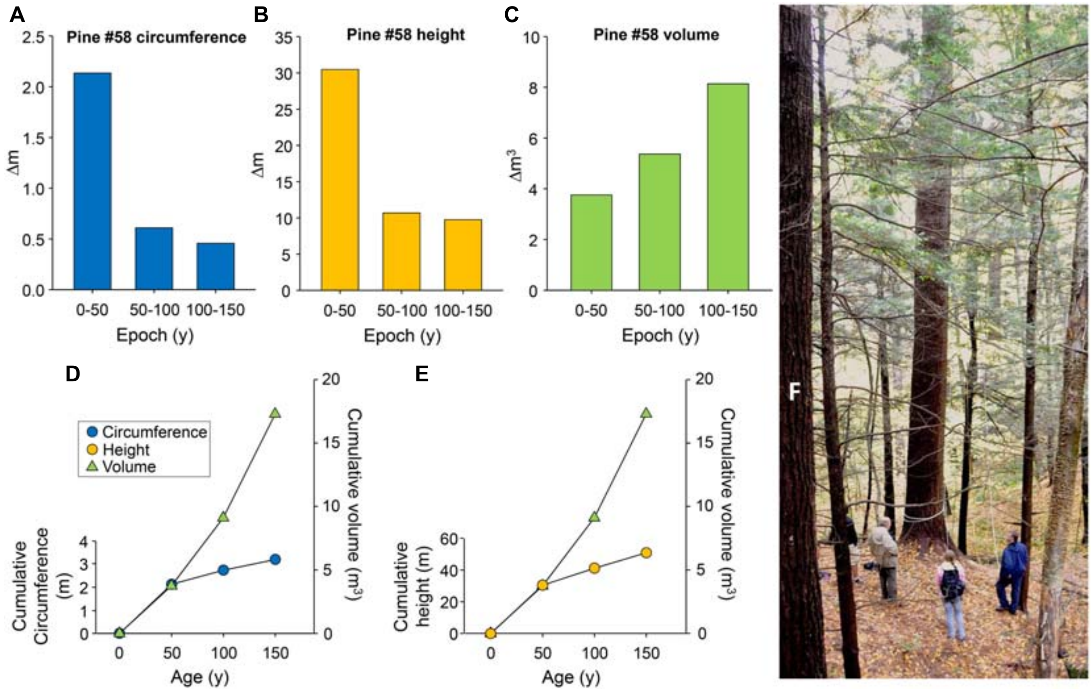

FIGURE 1 | Changes in circumference, height and volume of a stand-grown individual eastern white pine (Pine #58) in three 50-y intervals. *Upper panels* **(A)** Change in circumference during 0–50, 50–100, and 100–150 years. **(B)** Change in height between 0–50, 50–100, and 100–150 years. **(C)** Change in above-ground tree volume (trunk plus limbs) between 0–50, 50–100, and 100–150 years. *Lower panels* **(D)** Cumulative circumference at 50, 100, and 150 years compared to cumulative above-ground volume. **(E)** Cumulative height at 50, 100, and 150 years compared to cumulative above-ground volume. On each lower panel initial slopes were matched to reflect the rapid change in circumference and height during the first 50-years interval. Note that volume is a proxy for above-ground carbon. Values for circumference, height and volume of Pine #58 were determined by a combination of direct measurement and chronosequence and described in the text and in Supplement. **(F)** Pine #58 (center) being readied for climbing and measuring.

#58. In both cases ~75% of the carbon they accumulated occurred *after* their first 50 years even when assuming the most optimal growth observed during the first 50 years.

Stand Measurements at ~80 and 160 Years

Detailed measurements were taken in comparable pine stands at ~80 and 160 years *(TOP)*. As noted, the average tree in each stand is shown in **Figure 2**, and the distribution of tree sizes in the *TOP* is shown in **Figure 3A**. The largest pine in the *TOP* holds 4.33 tC and the smallest holds 0.53, an eightfold difference. A comparison of the stand density and above ground carbon at ~80 vs. ~160 yr are shown in **Figure 3B**.

Complete data for 76 individual pines in the *TOP* (the 0.4 ha primary plot plus additional trees in the stand) is provided in **Supplement 9**. Similar data were collected from 0.4 ha of the ~80-year old stand (**Supplement 6**). This age is more representative of the average stand of eastern white pine in New England. Average values for both stands are summarized in **Table 1**. As shown in **Figure 2**, we found an average of 0.66 tC per tree compared to 1.93 tC per tree in the *TOP*, a near tripling of carbon in the average individual pine in the older stand. We found a robust size distribution among the pines in the older stand (**Figure 3A**), as well as a lower stand density (fewer stems), and a higher level of carbon in the *TOP* (**Figure 3B**). Pines predominated both plots, and non-pine species added ~10% to the total above ground carbon in the *TOP* (**Figure 3B**).

We emphasize that all of our calculations are based on a conservative value for the carbon mass fractional factor in the pines (48%) and only include above-ground live tree-based carbon—they do not include more labile sources of additional carbon in needles, leaves and understory plants, or the accumulation of carbon in downed woody debris in older stands. Our measurements also do not include the large store of underground carbon (the root system is typically estimated as an additional 15–20% of the above-ground tree volume, and total soil organic carbon can be an additional 50% or more (Birdsey and Heath, 1995). Therefore, the total carbon is considerably higher. Nevertheless, the live trees in the older stand hold twice the carbon of the younger stand: the above-ground tree-based carbon measured directly in the primary acre in the 80 year old stand is 46.9 tC and the 160-year-old stand is 94.4 tC, translating to 117.2 and 236.0 tC per hectare, respectively. Approximately 10% of the tree-based carbon in the older stand is non-pine whereas non-pine live tree carbon in the younger stand is negligible (**Table 1**).

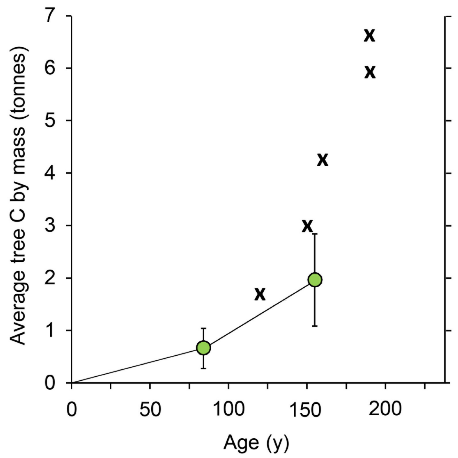

FIGURE 2 | Metric tons of above-ground carbon (tC) in an "average" eastern white pine in a measured research acre (green locants) and in five individual trees measured directly on site at three separate locations in Massachusetts. Average tC and standard deviation is based on pines in a stand at ~80 years (0.66 ± 0.38 tC) and ~160 years (1.93 ± 0.73 tC) as described in the text. Direct measurement of tC is shown for individual trees in western Massachusetts at these ages and locations (the centers of the X symbols indicate the data points): ~190 years: MSF #1 and #2, Monroe State Forest; ~160 years: Pine #58, Mohawk Trail State Forest; more details of Pine #58 shown in **Figure 1**; ~150 years: Totem, Northampton, MA; ~120 years: BB #2, Broad Brook, Florence, MA.

DISCUSSION

We found that above-ground carbon stored in individual eastern white pines (*Pinaceae: Pinus strobus*) and stands can continue to increase well beyond 150 years. A chronosequence coupled with decades of direct measurements of a dominant stand-grown individual pine in Massachusetts demonstrate that height and circumference increase rapidly during the first 50-year epoch with smaller increases in 50-year epochs thereafter. In contrast, volume (and therefore carbon) shows the smallest increment in the first 50 years and the biggest in the 50-yr epoch between 100 and 150 years. This superior carbon sequestration in older trees is consistent with recent reports of recent rapid sequestration of older oak trees in Massachusetts (Finzi et al., 2020) and the outsized forest accumulation in large trees (Stephenson et al., 2014; Mildrexler et al., 2020). Here, the largest pine measured in Massachusetts (by volume) achieved 6.62 tC at 190 years old, and we found very large pines at ages ranging up to 350 years at dozens of sites in the Eastern United States.

Using direct measurement of above-ground carbon in different-aged pine stands, we found that live tree carbon can continue to increase in a pine stand up to at least 160 years. We found twice as much above-ground live tree carbon in a measured research acre within the older vs. the younger stand. The live pines in the older stand also exhibited marked size diversity and the stand had a higher tree species diversity.

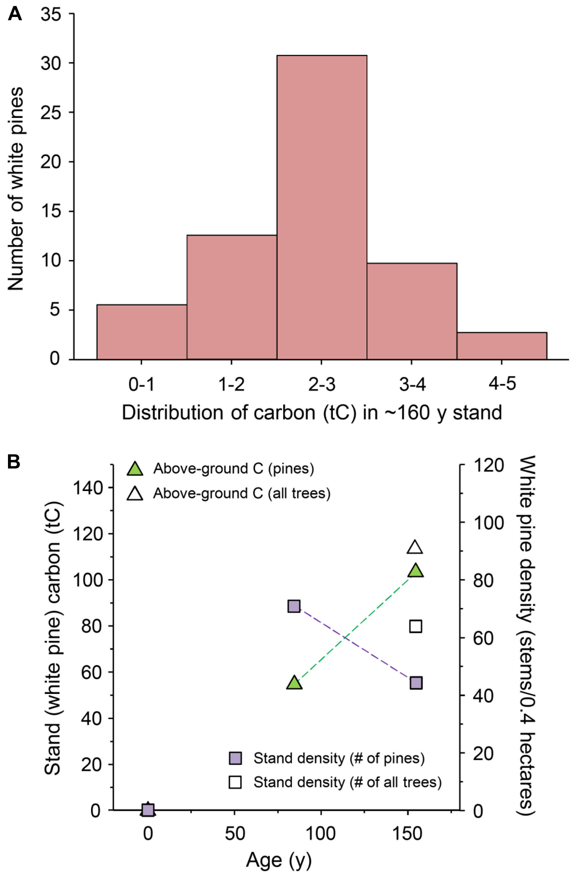

FIGURE 3 | Carbon distribution, stand density and cumulative carbon in predominantly eastern white pine stands at ~80 and 160 years. These two stands were regrown from land previously used as pasture (i.e., not recovering from a harvest at time zero). **(A)** Distribution of above-ground carbon (tC) among 76 eastern white pines of different sizes in the full *TOP* stand at ~160 years old. The majority contained 1–3 tC. **(B)** Stand density and above-ground carbon measured directly on site in a research acre of eastern white pine at ~80 and 160 years. Stand density (# of stems) declined while above-ground carbon increased. The older stand includes some non-pine species that added to the number of stems and total carbon (open locants).

The representative stands in this analysis approximate the average pine forest age in New England (~80 years old) and a comparable stand approximately twice that age. To determine the biomass and above ground carbon in living trees as a function of tree size and age, we have used a combination of direct measurements and a hybrid FIA-COLE (Forest Inventory and Analysis—Carbon On-Line Estimator) volume and biomass model to quantify individual trees and stands of eastern white pine. We found that individual trees continue accumulating carbon well past 150 years, and ~75% of the carbon in pines up to 190 years is gained after the first 50 years. Despite a lower stand density (fewer stems), total above-ground carbon is greatest in older stands and continues to increase past 150 years. The carbon per hectare quantified in these stands aligns with previous averages for the region and previous regional estimates that New England forests can accumulate between 2.3 and 4.2 times as much carbon as they now contain on productive sites (Keeton et al., 2011). The total carbon stored is much greater when below-ground carbon in roots, coarse woody debris, standing dead trees,

TABLE 1 | Summary of key measurements within a 160-year pine stand (*TOP*) and a comparable ∼80 year old stand (2018–2019 values).

Individual values	**∼160 year old 0.4 hectare**	
	Circumference at breast height (avg)	2.36 m
	Diameter at breast height (avg)	0.75 m
	Height (avg)	45.10 m
	Tree volume (trunk + limbs; avg)	10.47 m^3
	Above-ground carbon per tree (avg)	1.93 tC
	∼80 year old 0.4 hectare	
	Circumference at breast height (avg)	1.56 m
	Diameter at breast height (avg)	0.50 m
	Height (avg)	38.4 m
	Tree volume (trunk + limbs; avg)	3.58 m^3
	Above-ground carbon per tree (avg)	0.66 tC
Stand values	**Full stand at ∼160 years**	
	Number of pines	76
	Above-ground pine-based carbon	146.84 tC
	Above-ground non-pine carbon	14.90 tC
	Total above-ground tree carbon	161.74 tC
	Research acre ∼160 years (0.4 hectare)	
	Number of pines	44
	Above-ground pine-based carbon	85.8 tC
	Above-ground non-pine carbon	8.6 tC
	Total above-ground tree carbon	94.4 tC
	Research acre ∼80 years (0.4 hectare)	
	Number of pines	71
	Total above-ground pine-based carbon (*negligible non-pine carbon*)	46.86 tC

smaller plants and soils are included (Birdsey and Heath, 1995; Nunery and Keeton, 2010; Tomasso and Leighton, 2014).

Forest managers stress the high accumulation rates of younger forests as important in absorbing atmospheric CO_2. This is an important consideration for production forests as well as to help optimize between growing a wood resource and accumulating carbon. Younger individual trees do not accumulate absolute amounts of carbon more rapidly than larger more mature trees, and we did not find evidence for a significant benefit for a young stand compared to an older stand. We note this is a limited sample, and we did not estimate rates of accumulation below 80 years (**Table 1**).

Multi-use forests provide a source of wood products and can support recreation but active management practices limit forest carbon accumulation long-term. At a range of scales, chronic intervention eliminates the ability for that forest to host the full biodiversity of some of our rarest species of plants, animals, insects, fungi, lichens, reptiles and amphibians found in older and continuously forested areas (McMullin and Wiersma, 2019; Moose et al., 2019) as well as climate-sensitive birds that may benefit from mature or old-growth forests (Betts et al., 2017). These older unmanaged forests also have fewer invasive species (Riitters et al., 2018).

The pine stands studied here grew from abandoned sheep pasture, and therefore were unlikely to have been severely disturbed prior to natural regeneration. Site history influences growth and net carbon accumulation, especially in the early years, since disturbed soil can continue to lose carbon for more than a decade (Birdsey and Heath, 1995; Hamburg et al., 2019). We recognize that at some point the above-ground carbon in living trees will no longer increase as the live trees in the stand eventually will reach a steady state of death and renewal. Pines easily reach 200 years and some live 400 years; today the *TOP* is less than halfway to that age and the younger stand is only ∼25% of that lifespan. Previous work shows that pine stands continue to add above ground carbon beyond 200 years (Seymour, 2011, 2016), and even when above-ground live carbon reaches asymptote, total forest carbon continues to increase, even in some primary ("old-growth") forests (Mackey et al., 2015): after tree death or forest disturbance there is a new growth as well as transfer of live carbon to dead wood and woody debris, the litter layer, and into the soil. For example, 70 years after an old-growth (virgin) eastern hemlock (*Tsuga canadensis*) and eastern white pine stand blew down (the 1938 Hurricane in New England) that forest stored as much carbon as forests that were 250 years old (D'Amato et al., 2017).

There is no evidence of recent disturbance in either research plot herein. A major storm in 1989 blew over six large pines in the older research acre, reducing stand density by >10% and thereby reducing above-ground live-tree carbon. Downed wood due to death and disturbance contributes to total forest carbon and biodiversity. The older pine stand shows an increased prevalence and growth of trees of other species (including more carbon-dense hardwoods), and for multiple reasons it is unlikely it has reached maximal above-ground live carbon or total carbon. Rather, this forest appears to be transitioning into a phase where the structural diversity, species diversity and total carbon load will continue to rise. A goal for future research is a better understanding of tree and stand-level carbon accumulation and dynamics as well as many other ecological features in different forest types and in stands well beyond 150 years—a time when old-growth characteristics are starting to redevelop in eastern forests.

Public forests in New England are typically older than private forests (but still predominantly less than 100 years old), and provide the greatest possibility for future carbon-dense and biodiverse intact forests across the landscape. Native tree species can live for several hundred years (and in the case of eastern hemlock (*Tsuga canadensis*) and black gum (*Nyssa sylvatica*), up to and exceeding 500 years) (Whitney, 1996; Sperduto et al., 2000). Despite the shortage of old and old-growth forests (and their proven resilience to disturbance (D'Amato et al., 2017), and the increased prevalence of natural disturbances (e.g., insect outbreaks, windstorms) creating forest diversity and forest openings (Oswalt et al., 2019), a major focus across public land has been to make forests younger. These programs assert that these habitats prevent a suite of species from declining, that they accumulate carbon more rapidly, and that they are more resistant to disturbance than their older counterparts (Anwar, 2001). This approach downplays the rate of the natural development of niches for multiple species (Zlonis and Niemi, 2014) and the accumulation of biodiversity in temperate forests during natural forest succession (Hilmers et al., 2018). It also overlooks cumulative forest carbon (Moomaw et al., 2019) as well as the superior resilience of older forests to the stresses of climate change (Thom et al., 2019). Comparing details of age and location (tropical, temperate, boreal, etc.) are important, as is evaluating the term "young"—in some cases it is considered up to 140 years (Pugh et al., 2019).

Our findings are consistent with Stephenson et al. (2014) who found that absolute growth increases with tree size for most of 403 tropical and temperate tree species, and a study of 48 forest plots found that in older forests, regardless of geographical location, half of all above-ground biomass (and hence carbon), is stored in the largest 1% of trees as measured by diameter at breast height (Lutz et al., 2018). An increase in carbon density per hectare was found as the age of the stand increased in the Northeast U.S. (Keeton et al., 2011), and a recent study in China found that forests with older trees and greater species richness had twice the levels of carbon storage than did less diverse forests with younger trees (Liu et al., 2018). Earlier work demonstrated that intact old growth forests in the Pacific Northwest contained more than twice the amount of carbon as did those that were harvested on a fixed rotation basis (Harmon et al., 1990).

Globally, forests are capable of accumulating twice as much atmospheric carbon, and the current deficit is due to a combination of conversion and management (Erb et al., 2018). Continuing current management in the Northeast will result in a large difference between the potential for land-based carbon and the current trajectory (Duveneck and Thompson, 2019). Meanwhile, natural regeneration and reforestation is a superior climate solution compared to managed reforestation and tree planting (Cook-Patton et al., 2020). Proforestation—growing existing natural forests—complements and extends natural regeneration as an ongoing climate solution by leveraging the accumulation potential in forests that are already established (Moomaw et al., 2019). These strategies are outlined in the recent report on "ten golden rules" for restoring forests wherein the first rule is protect existing forest (Di Sacco et al., 2021). Proforestation recognizes implicitly that older forests and large trees are critical to a global strategy for carbon accumulation and biodiversity protection (Lindenmayer and Laurance, 2016). Rapidly moving large stocks of atmospheric carbon as CO_2 into forests and reducing emissions are both essential to limiting the increase in global temperatures, and protecting intact and connected habitat is essential in preventing extinction. These time-sensitive dual goals and the importance of traditional indigenous land use are explicitly recognized internationally in the Global Deal for Nature, the Global Safety Net, and the recent "Campaign for Nature" or "30 × 30"—i.e., protecting 30% of the planet's land and water by 2030 (Campaign for Nature, 2021), and in the ambitious coalition goal of "Nature Needs Half" (Nature Needs Half, 2021).

An important additional implication of our study is that the estimated potential additional carbon dioxide (CO_2) removal (CDR) achieved by future growth of secondary forests as reported by Houghton and Nassikas (2018) is likely an underestimate because it does not account for high ongoing accumulation rates as trees age in regions with relatively young (compared to tree lifespan) forests like those of the Northeast United States. The global study of natural forest carbon accumulation by Cook-Patton et al. (2020) and the synthesis of quantified carbon and biodiversity by Moomaw et al. (2019) provide evidence for the power of natural forest processes throughout their growth and development. These reports and the current site-specific findings support the high regional contribution of carbon accumulation in the coming decades by Northeastern temperate forests and their designation as a Tier 1 climate stabilization region (Dinerstein et al., 2020).

Whereas the IPCC clearly identified forests as essential for accumulating additional carbon for climate stability, it focused on production forests that are currently recovering from being harvested or on unforested areas where forests could be planted (afforestation). Bastin et al. (2019) proposes an afforestation project on 0.9 billion ha but acknowledges the relatively long time before large amounts of carbon would be stored. Global tree planting efforts are under way, but are presented too simplistically (Holl and Brancalion, 2020); for example, there is little data on how to plant an ecosystem, and tree planting efforts can suffer from numerous challenges, including high mortality (Cao et al., 2011). In contrast, growing existing forests is an established near-term strategy (Moomaw et al., 2019). Overall, afforestation and reforestation are valuable, but neither can keep as much carbon out of the atmosphere as proforestation in the next 50 years—the timeline when it is needed most to avoid irreversible consequences of a changed climate.

Although this study focused exclusively on above-ground live tree carbon accumulation, we emphasize that additional carbon exists and accumulates above and below ground. Other ecosystem services of proforestation also accrue, and the essential goal of protecting a "Global Safety Net" of nature extends explicitly beyond greenhouse gas emissions and mitigating the climate crisis (Dinerstein et al., 2020). Nevertheless, an accurate carbon-centric model of "business as usual" vs. proforestation must include comprehensive real-world carbon fluxes. Removing carbon from the forest releases carbon into the atmosphere, and in some cases a portion of the carbon is stored in wood and/or wood is substituting for other materials. Recent work shows that near-term carbon benefits associated with wood products and substitution have been overestimated based on outdated assumptions or neglecting or underestimating future accumulation (Harmon, 2019; Leturcq, 2020). Efforts should be made on consumption and conservation to ensure we protect primary forests and additional secondary forests where possible: carbon storage in forests is low-risk, high-capacity and practical—therefore preferable to experimental bioenergy with carbon capture and storage (BECCS) suggested by the IPCC report (Anderson and Peters, 2016; Intergovernmental Panel on Climate Change, 2018). Finally, letting existing secondary forests grow creates a network of nature that can provide equity, access to natural heritage, scientific discovery, and cumulative health benefits for people. Protecting and growing a network of suitable existing forests as a carbon sink in New England is cost-effective (Tomasso and Leighton, 2014) and does not compete directly with agriculture and other demands for land use.

The direct measurements at the tree and stand level in this paper are consistent with parameterized and other studies at larger scale in verifying that larger trees (Stephenson et al., 2014; Lutz et al., 2018) and stands of larger trees accumulate the most carbon over time compared to smaller trees (Mildrexler et al., 2020). They support the proforestation strategy of growing existing forests to achieve their natural capacity to accumulate carbon and achieve their ecological potential (Moomaw et al., 2019) to redress the balance of carbon lost to the atmosphere from global forests due to human activity (Hudiburg et al., 2019). The important implication of these findings is that the trees and the forests that we need most for carbon storage and CDR to help limit near-term climate change are the ones that are already established.

Currently, plantations and forests managed for forest products account for 71% of all forest area globally (Intergovernmental Panel on Climate Change, 2019), more than sufficient for resource production. Strategic decisions can enable some of these forests to be dedicated to climate protection and research, and the remaining 29% should be protected wherever possible. This would be a major step toward the goal of 30 × 30—with additional climate stabilization areas needed beyond that. Together 30 × 30 plus climate stabilization will move us toward long-term protection of "half-earth" (Wilson, 2016). High levels of carbon accumulation and biodiversity protection are integral to resiliency in a changing climate—including the resiliency achieved by protecting species networks and interactions, genetic diversity and the potential for specific adaptive epigenetic changes (Hanlon et al., 2019). These complexities are poorly understood—science and technology is evolving, and new techniques can discover new species (Schulz et al., 2018)—and any areas, even on public land, lack a detailed ecological inventory due to resource constraints or a focus on other priorities. Meanwhile, intensive biodiversity inventories have yielded many hundreds of new species—often small species such microbes, lichen, fungi, algae and insects; i.e., Smokies Species Tally (Discover Life in America, 2021). Much more research is needed, and essential ecological processes develop and diversify at timescales far beyond a human lifetime.

In sum, the current findings ground-truth the capacity for a representative New England eastern white pine stand to at least double its above-ground live tree carbon in the coming decades, confirming previous chronosequencing of pine stands in the region (Seymour, 2011). We did not attempt to quantify or estimate the flux in other carbon compartments above or below ground. With a small fraction of New England (∼3% overall, ∼1% in Southern New England) prioritized for proforestation and natural processes, protection of a suitable network of land from unneeded intervention is urgent, and public land is the most logical place to start: funding to ensure evidence-based intervention and additional data collection will generate policies that protect the long-term public trust. At the same time, systems to support local wood use and reuse are equally needed to ensure the highest and best use of this resource, protect local expertise and jobs, and reduce emissions associated with the forest industry; in some states it is the largest source of emissions (Law et al., 2018). Comprehensive education, information and compensation programs should be established to provide private landowners a range of options based on numerous ecosystem services, including maximal carbon and biodiversity accumulation, with the goal of optimizing natural solutions that address the Climate Emergency immediately (Ripple et al., 2020). Failing to protect natural systems erodes the wealth and well-being that is essential to meet this unprecedented challenge and avoid "a ghastly future" (Bradshaw et al., 2021).

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

RL chose site locations and individual trees, established measurement methods and protocols, did the on-site tree measuring, and performed the subsequent analysis. SM analyzed and organized the content and supplements, and participated in drafting and finalizing the text. WM framed the analysis in the context of other studies and the larger context of climate change, assisted with data analysis and presentation, and drafting and editing the text. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2021.620450/full#supplementary-material

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