



A Research Agenda for Microclimate Ecology in Human-Modified Tropical Forests

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Logging and habitat fragmentation impact tropical forest ecosystems in numerous ways, perhaps the most striking of which is by altering the temperature, humidity, and light environment of the forest—its microclimate. Because local-scale microclimatic conditions directly influence the physiology, demography and behavior of most species, many of the impacts of land-use intensification on the biodiversity and ecosystem functioning of tropical forests have been attributed to changes in microclimate. However, the actual pathways through which altered microclimatic conditions reshape the ecology of these human-modified ecosystems remain largely unexplored. To bridge this knowledge gap, here we outline an agenda for future microclimate research in human-modified tropical ecosystems. We focus specifically on three main themes: the role of microclimate in shaping (i) species distributions, (ii) species interactions, and (iii) ecosystem functioning in tropical forests. In doing so we aim to highlight how a renewed focus on microclimate can help us not only better understand the ecology of human-modified tropical ecosystems, but also guide efforts to manage and protect them.

Keywords: ecosystem functioning, habitat loss and fragmentation, logging, microrefugia, remote sensing, species distribution modeling, species interactions, thermal corridors

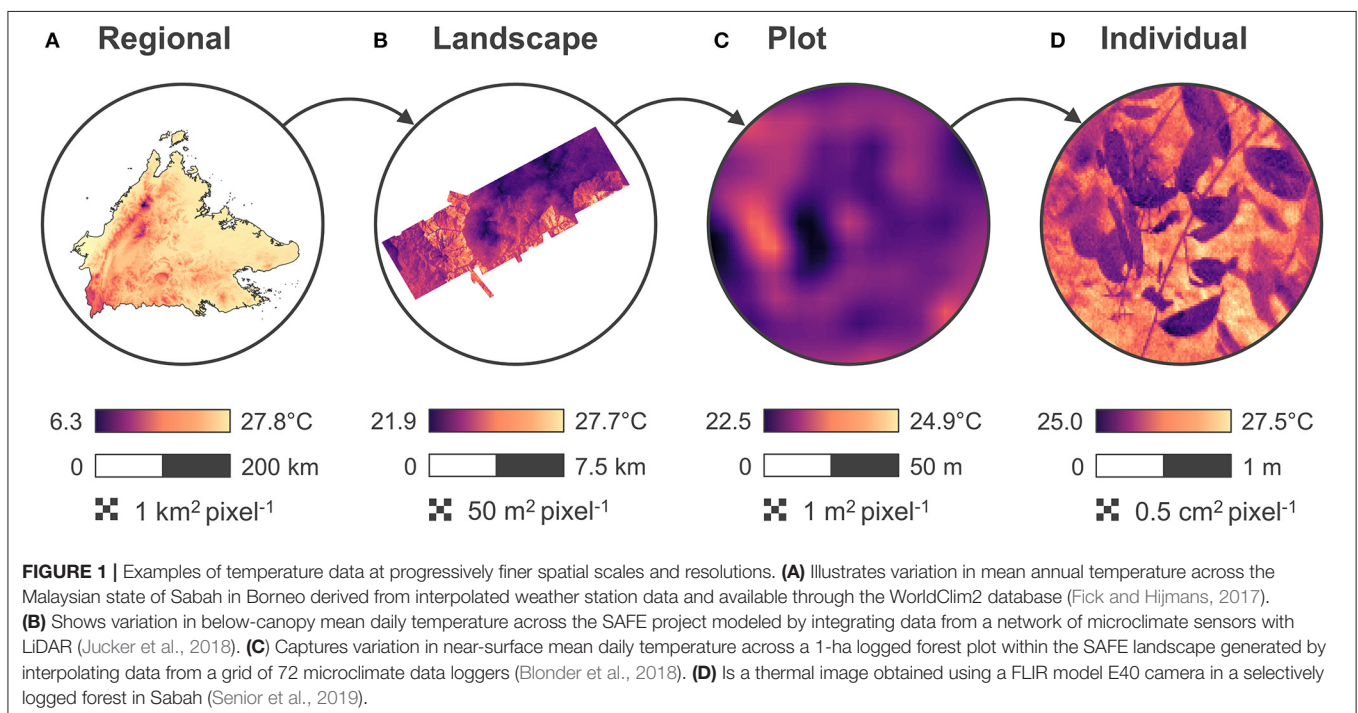
INTRODUCTION

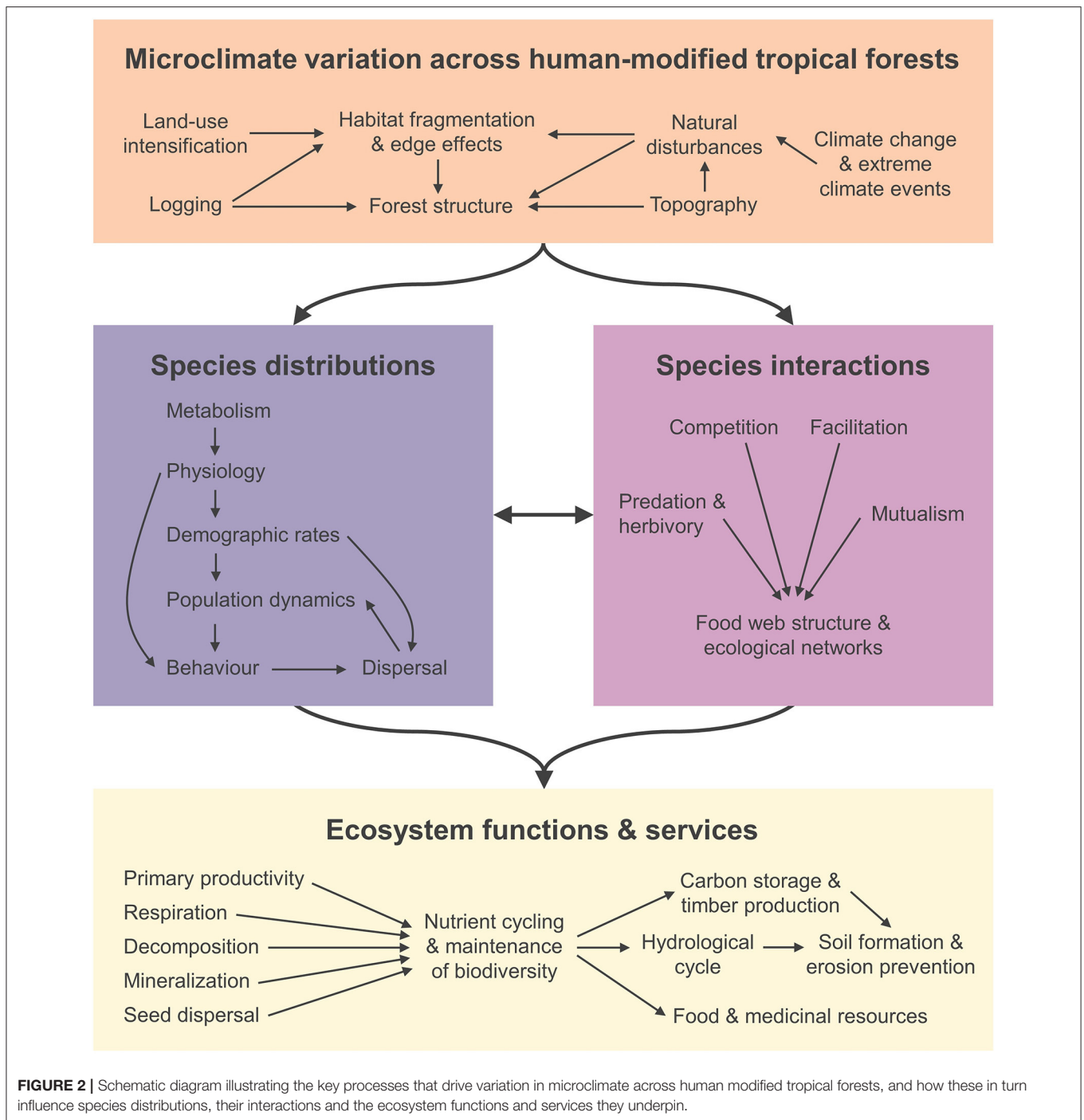
More than half of the world's remaining tropical forests have been logged or otherwise impacted by human activities (Lewis et al., 2015). These human-modified tropical forests differ from their old-growth counterparts in a number of important ways (Ewers et al., 2015; Pfeifer et al., 2017; Riutta et al., 2018), as the impacts of logging and land clearing go well beyond the simple removal of biomass. For instance, logging often results in soil compaction and erosion (Putz et al., 2008), while the selective removal of tree species can directly alter the stoichiometry and function of the entire ecosystem (Riutta et al., 2018; Both et al., 2019; Swinfield et al., 2019). But perhaps the most pervasive impact of logging is that by opening and thinning the canopy, it increases solar radiation and air flow in the understorey and decreases evapotranspiration—thereby altering the forest's microclimate (Breshears, 2006; Hardwick et al., 2015; Senior et al., 2017). As a result, not only do logged forests tend to be warmer, drier and brighter than old-growth ones (Hardwick et al., 2015; Fauset et al., 2017; Senior et al., 2017), but microclimatic conditions in these human-modified ecosystems are also more spatially and temporally heterogeneous (Hardwick et al., 2015; Blonder et al., 2018).

These changes in microclimate have clear implications for the ecology of tropical forest ecosystems. Local-scale microclimatic conditions directly influence the physiology, demography, behavior and—ultimately—the distribution of a broad range of taxonomic groups in forests (Chen et al., 1999; Clarke, 2017). Because of this, many of the impacts of logging and habitat fragmentation on the biodiversity and ecosystem functioning of

tropical forests have been attributed to changes in microclimate (Ewers et al., 2015). However, due to a lack of data in most cases this link between microclimate and ecosystem change has been assumed rather than directly observed. It is only with recent advances in environmental sensors and remote sensing that mapping microclimate at ecologically relevant scales has become a reality (Bramer et al., 2018; Jucker et al., 2018; Wild et al., 2019; Zellweger et al., 2019b; **Figure 1**). These new data streams provide an exciting opportunity to study the microclimate ecology of human-modified tropical forests.

Here, we explore the role of microclimate in regulating the ecology of human-modified tropical forests—from the lives of individual organisms to biogeochemical cycling at an ecosystem scale (**Figure 2**). Specifically, we outline how a microclimate-centered view can help us better understand the impacts of logging and habitat fragmentation on (i) the physiology, demography, behavior, and distribution of species; (ii) how species interact within and across taxonomic groups and trophic levels; and (iii) ecosystem functioning in human-modified tropical forests. In developing these ideas we primarily draw on examples from ongoing work at the Stability of Altered Forest Ecosystems (SAFE) project (Ewers et al., 2011)—a landscape-scale experiment designed to test how logging impacts the biodiversity and ecosystem functioning of Borneo's tropical forests. Our aim is to set an agenda for future research in the emerging field of microclimate ecology, with applications both in the tropics and beyond. We also explore how this new research field can inform efforts to better manage, conserve, and restore human-modified tropical landscapes.





SPECIES DISTRIBUTIONS AND POPULATION DYNAMICS

A common assumption in species distribution modeling is that a lack of climate data at the “appropriate” spatial resolution limits our ability to make robust predictions about how species will respond to global change (Lenoir et al., 2017; Lembrechts et al., 2019b). This makes intuitive sense: in most cases the

best climate data available are interpolated surfaces with a 1 km² resolution that not only miss much of the fine-scale climate variability found within tropical landscapes, but are also unrepresentative of buffered habitats such as forests (Jucker et al., 2018; De Frenne et al., 2019). Yet only a handful of studies have actually compared the performance of models fit with microclimate and coarse-resolution climate data (Lembrechts et al., 2019a,b), nor is it clear what the

“appropriate” spatio-temporal resolution of these microclimate data should be.

An initial priority is therefore to explore at what spatial scale microclimate data can prove most informative for distribution modeling (e.g., regional, landscape, plot, individual; **Figure 1**), and how this varies among species with contrasting life history traits (Potter et al., 2013; Scheffers et al., 2014). Similarly, we also need to tease apart which elements of microclimate are most important for predicting species distributions and develop clear guidelines and protocols for measuring them in standardized ways (Bramer et al., 2018). Given the role of temperature in regulating metabolism, as well as the fact that it can be measured accurately and cheaply, much emphasis has been placed on describing understorey air temperature heterogeneity in forests. But for some organisms microclimatic axes other than air temperature—such as surface temperature, humidity, vapor pressure deficit, soil moisture, solar radiation, or wind—may well prove more important in determining growth, reproduction and survival. Similarly, for many species microclimate extremes and temporal fluctuations—rather than mean values—may better predict their distribution (Mod et al., 2016). However, the challenge with teasing apart the relative importance of these various microclimatic axes is that temperature, relative humidity, soil moisture, and light levels will all tend to co-vary along disturbance gradients. Consequently, experimental setups that allow these different elements of microclimate to be manipulated independently are urgently needed (Cavaleri et al., 2015; De Frenne et al., 2015). These same experimental platforms would also provide a way to tease apart the effects of microclimate on species distributions from those of other drivers of environmental disturbance that are also associated with logging and habitat fragmentation.

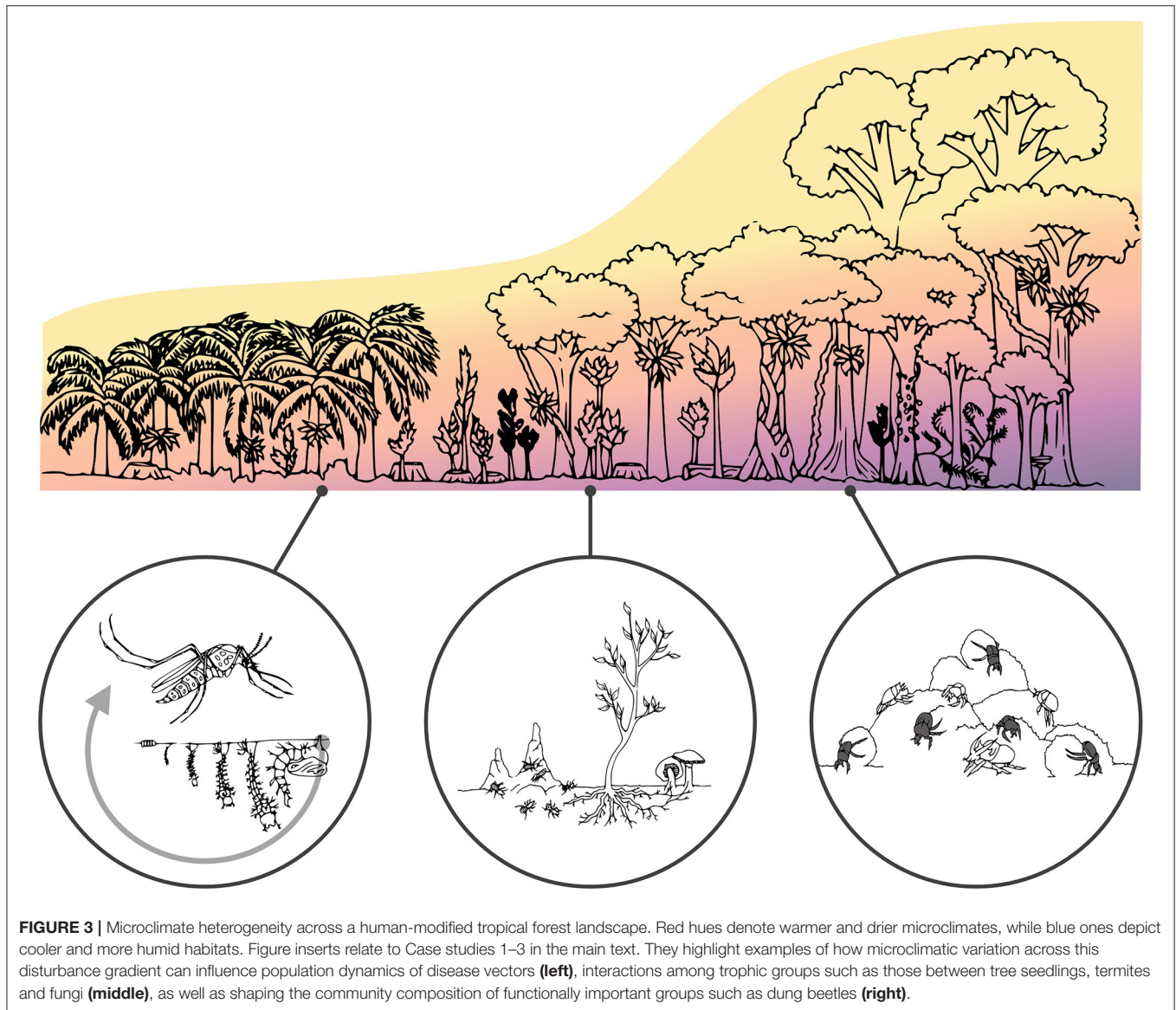
Moving beyond purely correlational models, better microclimate data would also facilitate the development of population dynamics models that can provide a mechanistic framework for predicting species responses to forest degradation (Merow et al., 2014; Swab et al., 2015; Zurell et al., 2016). While this comes with the added challenge of having to build a detailed picture of how microclimate influences demography, there is growing interest in characterizing species’ thermal niches—the thermal boundaries within which individuals can persist and populations grow (Gvoždík, 2018). Similarly, fine-scale microclimate data also provides an opportunity to determine species performances directly via energy budgets (Kearney and Porter, 2009). The SAFE project is an ideal testbed for this work, as physiological and behavioral responses to temperature have already been characterized for a number of functionally important invertebrate groups, including ants, termites, dung beetles, leeches and mosquitos (Drinkwater et al., 2019; Gregory et al., 2019; Woon et al., 2019; see Case study 1). Moreover, these data can be coupled with existing long-term microclimate records and high-resolution landscape maps of understorey temperature and vapor pressure deficit (Hardwick et al., 2015; Blonder et al., 2018; Jucker et al., 2018).

A key challenge is to identify which elements of an individual’s microclimatic tolerance profile are most important for shaping population demography, as well as understanding if there

are trade-offs in the way different vital rates (e.g., fecundity and mortality) are influenced by microclimate (Walsh et al., 2019). There is also a clear need to explore how and why thermal niches vary among species (e.g., ecto vs. endotherms; sessile vs. mobile; closely and distantly related phylogenetic and functional groups) (Dell et al., 2011), as well as within them (e.g., differences between life stages or sexes) (Bennett et al., 2019). Related to this, we need to understand what physiological and behavioral strategies species adopt to cope with or evade unfavorable microclimates. For instance, mobile species might shift from diurnal to nocturnal activity to escape warmer temperatures (Davison et al., 2019; Levy et al., 2019), while sessile organisms such as plants can thermoregulate by increasing transpiration and adjusting leaf angles (Fauset et al., 2017). Alternatively, some species may be able to rapidly acclimate and/or adapt to novel microclimates, as was recently shown for a poison frog in Costa Rica that exhibits higher preferred body temperatures in forests that have been logged (Rivera-Ordóñez et al., 2019). Characterizing the traits that are favored by, or confer adaptability to, warmer microclimates may allow us to predict community responses to logging and forest fragmentation without relying on extensive species distribution data (Frishkoff et al., 2015; Bishop et al., 2016).

Case Study 1: Impacts of Land-Use Intensification on Mosquitoes and Vector-Borne Diseases

More than 80% of the human population is at risk of vector-borne disease (World Health Organisation., 2017). Climate is a key driver of disease dynamics, however the relationship between climate and disease transmission remains unclear (Kilpatrick and Randolph, 2012). Most models used to predict the effects of climate on transmission focus on temperature (Franklinos et al., 2019), using data collected at coarse spatio-temporal scales (Craig et al., 1999; Hoshen and Morse, 2004). As small-bodied ectotherms, insect vectors such as mosquitoes are instead more likely to respond to fine-scale temperature variations (Paaijmans et al., 2013; Beck-Johnson et al., 2017). Identifying what elements of microclimate shape insect vector life history is therefore critical to predicting population dynamics and developing vector control strategies. In field experiments spanning three years, Gregory et al. (2019) found that changes in temperature driven by tropical forest conversion to oil palm plantations dramatically altered larval development rates in the mosquito *Aedes albopictus*, which is the vector of dengue and chikungunya viruses (**Figure 3**). However, this response was mediated by the El Niño Southern Oscillation (ENSO) event of 2015–16. During non-ENSO years larval development rates were faster in oil palm plantations, where daytime temperatures were higher than those in logged forests. Increased temperatures during the ENSO event led to faster development rates in both land-use types. However, this increase was much more pronounced in logged forests, where development rates during the ENSO event were as fast as those observed in oil palm plantations. This suggests that in oil palm plantations, temperatures during the ENSO event may have exceeded the thermal development optimum of *A. albopictus*.



This work highlights how changes in climate and land-use can interact to shape vector demography and, ultimately, vector-borne disease incidence (MacDonald and Mordecai, 2019).

SPECIES INTERACTIONS

Because microclimate influences how species are distributed, their demographic rates and how they behave, it also plays an important role in structuring the complex network of interactions between species. These interactions, including competition, predation, herbivory, parasitism and mutualism, ultimately shape the biodiversity and functioning of ecosystems (Nakamura et al., 2017). So while some species may be able to tolerate a much greater range of microclimatic environments than others, these interactions mean that altered microclimate regimes of logged and degraded forests can impact them

indirectly (Ewers et al., 2015; Kemp, 2018). The challenge with unpacking these direct and indirect effects of microclimate on species interactions is their sheer complexity, particularly when working in hyper-diverse tropical ecosystems (Novotny et al., 2010; Gripenberg et al., 2019). A review of how species interactions are affected by different global change drivers revealed substantial variation in the magnitude and direction of responses (Tylianakis et al., 2008). Because of this complexity, little progress has been made on understanding the cascading effects of microclimate heterogeneity and change across tropical food webs.

One way to address this knowledge gap is to reduce the complexity of the problem by leveraging natural microcosms or working with functionally important taxonomic groups (see **Case study 2**). Bird's nest ferns (*Asplenium* spp.) are a classic example of the former. By modifying their own microclimate

through rainwater retention and evaporative cooling, these epiphytes can colonize and grow in a variety of environments, including old-growth forest understoreys, the high-canopy, logged forests, and even oil palm plantations. In doing so they support a large diversity and biomass of invertebrates that would not otherwise persist in these environments (Ellwood and Foster, 2004). The communities that inhabit these “*islands in the sky*” can be easily manipulated, making them excellent natural laboratories for studying how microclimate influences species interactions (Ellwood et al., 2009; Phillips et al., 2019). Using this model system, Phillips et al. (2019) revealed that by buffering ambient temperatures by several degrees, bird’s nest ferns provide a key habitat for centipedes to build nests where their eggs are sheltered from daily fluctuations in air temperature and humidity that occur in the canopy. As a result, while adult centipedes show strong signs of spatial segregation and avoidance while foraging, a range of centipede species were found to share the same nest sites. So instead of competing for nests—as one might expect based on their typical behavior—centipedes are altering the way they interact with one another in order to access sites that are climatically suitable for egg-laying. Similarly, warming experiments conducted on artificially assembled communities have been used to explore how changes in competitive ability driven by microclimate impact dung beetle assemblages and the ecosystem functions they perform (Slade and Roslin, 2016). However, without incorporating the full breadth of antagonistic and synergistic processes that occur across trophic levels (e.g., Raine et al., 2018b), the outcomes of these experiments may not always reflect those observed in nature. It is therefore critical to pair manipulative experiments with larger-scale observational studies and models that together link pattern with process.

An alternative to working with simplified model systems is to explore how microclimate constrains entire ecological networks. While this is a relatively new field of research, there are some promising early results. For instance, Ohler et al. (2019) were able to identify a clear microclimate fingerprint in the spatial arrangement of alpine plant communities, which in turn shaped the composition and diversity of pollinators and their interactions with plants. Recent technological and computation advances (e.g., metabarcoding, acoustic monitoring, camera trapping, network analytics) are now opening the door to testing these same ideas in the tropics (Evans et al., 2016; Wearn et al., 2017; Burivalova et al., 2018). The development of new and ever-cheaper DNA sequencing approaches has enabled increasingly complex food webs to be resolved in detail (Creedy et al., 2019; Gripenberg et al., 2019). Others, instead, have used filming to reconstruct ant interaction networks and understand how they are impacted by forest disturbance, a proxy for microclimate (Gray et al., 2018). We can use these well-resolved interaction networks to explore how vulnerable they are to the loss of certain species, including ones that are most sensitive to changes in microclimate (Schleuning et al., 2016). This could be done in conjunction with existing and emerging climate manipulation experiments in the tropics (Cavaleri et al., 2015), which would provide a more robust platform

for teasing apart microclimatic effects on species interactions from those of other drivers of global change associated with logging. By doing so we could begin building a clearer picture of how microclimatic constraints on species distributions, physiology, demography, and behavior come together to shape the biodiversity and ecosystem functioning of human-modified tropical forests.

Case Study 2: of Tree Seedling, Termites, Fungi, and Drought

Understanding the processes that shape the survival and growth of tree seedlings is critical to forecasting the structure, composition, and function of tomorrow’s forests. Microclimatic conditions related to solar radiation, air temperature, vapor pressure deficit, and soil moisture all play a direct role in modulating plant ecophysiology and metabolism (Ashton and Gunatilleke, 1995; Will et al., 2013). But they can also affect seedling survival and growth indirectly, by altering competitive, facilitative, and mutualistic interactions with other species (Figure 3). For instance, mycorrhizal fungi can promote seedling growth and survival by increasing access to soil nutrients and moisture, and by conferring resistance to pests and pathogens (Brunner et al., 2015; Corrales et al., 2018). These fungal communities are themselves shaped by their surrounding microclimate. In Borneo, lowland forests are dominated by dipterocarps which, unlike most other tropical tree lineages, form associations exclusively with ectomycorrhizal fungi (Brearley, 2012). While these fungi have been shown to increase soil water uptake in inoculated seedlings (Brearley, 2011), there is evidence suggesting that they are susceptible to high soil temperatures (Smits, 1994), meaning they could be much less prevalent in warmer logged and degraded forests. Similarly, recent work by Ashton et al. (2019) showed that termites can alleviate the effects of drought on seedlings, as they increase soil moisture by transporting water upwards through the soil profile. However, termites are among the taxonomic groups worst affected by logging (Ewers et al., 2015; Tuma et al., 2019), with strong declines in diversity and abundance thought to be driven by the warmer and drier microclimate of degraded forests (Jucker et al., 2018). As a result, seedlings in logged forests could lose two key allies in their search for water: ectomycorrhizal fungi and termites. This may have contributed to their lower survival during the 2015–16 El Niño drought compared to their counterparts in Borneo’s old-growth forests (Qie et al., 2019). Further work is needed to test this hypothesis, but the implications for forest regeneration could be substantial. In particular, there is a risk that if seedlings in degraded secondary forests struggle to recruit due to unfavorable microclimatic conditions, heavily logged forests could find themselves in a state of arrested succession from which recovery is much slower (Jucker et al., 2018). This microclimate “trap” is likely to be further exacerbated by climate change and would lead to an increased risk of fire, which in turn could set in motion a positive feedback loop that pushes these ecosystems toward a more open, savanna-like state (Silvério et al., 2013).

ECOSYSTEM FUNCTIONING

Through its influence on all aspects of organismal biology and on the structure and composition of ecological communities, microclimate inevitably also plays a role in shaping a range of ecosystem-level processes. These include processes associated with nutrient cycling, such as net primary productivity, decomposition, respiration, and nutrient mineralization. However, we lack a quantitative understanding of how important microclimate is in regulating these processes relative to other factors such as soils, canopy structure, and disturbance history (Bradford et al., 2014; Keiser and Bradford, 2017; Chen et al., 2018; Pau et al., 2018). Nor do we know to what degree microclimatic influences on ecosystem functioning are direct (e.g., constraining net carbon assimilation rates by plants, determining canopy transpiration rates, regulating activity of decomposers) or indirect (e.g., shaping community composition and interaction networks). Addressing these uncertainties would allow the development of more realistic ecosystem models of human-modified tropical forests and a better understanding of the likely impacts of global change on these systems.

Manipulative experiments that alter microclimatic conditions while controlling for other potentially confounding effects provide one way forward. Microclimate can be manipulated either actively (e.g., rainfall exclusion, heating, shading; Cavaleri et al., 2015) or passively (e.g., through transplant experiments across microclimate gradients associated with canopy cover or microtopography; Jucker et al., 2018). Taking wood decomposition and soil faunal activity as an example, experiments such as these can be used to identify the primary microclimatic controls of wood decay (Crockatt and Bebbler, 2015), compare these effects to those of other local-scale drivers (Bradford et al., 2014) and understand how they are mediated by changes in the decomposer community and by wood traits (Weedon et al., 2009; Riutta et al., 2016; Cheesman et al., 2018). The challenge with these experimental approaches is balancing realism and scale with costs.

An alternative approach to scaling-up the effects of microclimate on ecosystem functioning is to combine distribution, abundance, and functional trait data of functionally important taxonomic groups with regional microclimate maps and measures of ecosystem functioning (see **Case study 3**). Along with dung beetles, termites would be a good candidate group for this work, as they contribute disproportionately to decomposition and soil bioturbation in tropical forests (Griffiths et al., 2019; Tuma et al., 2019) and appear to be strongly susceptible to changes in microclimate that result from logging (Ewers et al., 2015). This approach could be used to test the extent to which changes in community composition and diversity driven by microclimate impact ecosystem functioning (Slade et al., 2019; Tuma et al., 2019). The challenge, however, lies in the inherent complexity of scaling species abundances and interactions, particularly when working in data-poor regions. What remains unclear is whether we even need to account for this level of complexity, or if instead we could simply measure and model broad scale patterns in ecosystem functioning directly. High spatial and spectral resolution remote sensing

imagery would be one way to up-scale data from localized experiments. Using litter decomposition as an example, key components of this process could be estimated accurately using airborne LiDAR and hyperspectral imagery (Krishna and Mohan, 2017), including microclimate (Jucker et al., 2018), litter quantity (Detto et al., 2015), litter quality (Asner et al., 2015), and solar radiation (Zellweger et al., 2019a).

Case Study 3: Dung Beetles and Nutrient Cycling in Human-Modified Tropical Forests

Dung beetles are a widely used indicator group, as they play a key role in driving numerous ecosystems functions—such as nutrient cycling and seed dispersal—and can be easily sampled using pitfall traps (Nichols et al., 2008). Across the SAFE landscape dung beetle diversity, abundance and traits have been extensively surveyed, as has their contribution to nutrient cycling through dung removal (Raine et al., 2018a). By combining these data with existing high-resolution microclimate maps of understorey temperature and vapor pressure deficit (Jucker et al., 2018), dung beetle abundance and community composition can be extrapolated across the oil palm–forest mosaic landscape. In this way one can explore how changes in the diversity and trait composition of dung beetle communities associated with microclimate gradients impact soil nutrient cycling across human-modified tropical landscapes (**Figure 3**). This research would add to the growing body of literature exploring whether biodiversity loss driven by land-use change leads to a collapse in ecosystem functioning, or if instead relatively species-poor communities of disturbance-resistant species are able to maintain high levels of ecosystem functioning (Slade et al., 2017, 2019; Tuma et al., 2019). It would also allow us to model the likely impacts of different land-use change scenarios on biodiversity and ecosystem functioning in tropical landscapes where the aim is to balance conservation with economic development. These models would enable ecologists and conservation scientist to inform policy and management decisions, such as those related to the importance of riparian buffer zones in oil palm plantations as ecological and microclimatic corridors (Luke et al., 2019).

GUIDING CONSERVATION AND RESTORATION EFFORTS IN HUMAN-MODIFIED TROPICAL FORESTS

In addition to advancing our understanding of the ecology of human-modified tropical forests, a renewed focus on microclimate would also benefit efforts to better manage, conserve and restore these ecosystems. Mapping horizontal, vertical, and temporal variation in microclimate at landscape and regional scales (e.g., Jucker et al., 2018) would help identify dispersal corridors that are climatically suitable for a range of taxonomic groups (Milanesi et al., 2017). This would allow microclimate ecology to be integrated into classical landscape ecology and metacommunity dynamics (Hesselbarth et al., 2019; Senior et al., 2019), and also guide efforts to restore and increase connectivity in fragmented landscapes (e.g., through

the rehabilitation of riparian buffer zones; Luke et al., 2019). It also provides an opportunity to assess the effectiveness of different forest and plantation management practices that aim to restore microclimate regimes by altering canopy structure and ecophysiology, such as natural regeneration, enrichment planting, and climber cutting (Rodríguez-Ronderos et al., 2016; Ichihashi et al., 2017; Guzmán et al., 2018). Moreover, this would also provide an opportunity to understand how different management interventions alter specific facets of microclimate (e.g., impact of liana cutting on transpiration) and whether these can be tailored to restore specific microclimatic conditions.

A further application would be to characterize the microclimate niche breadth of different forest and land-use types (i.e., the range of microclimatic conditions experienced within an area of interest) and map how this varies horizontally and vertically across entire landscapes (Scheffers et al., 2017; Blonder et al., 2018). This would facilitate identifying the distribution, abundance, and connectivity of microrefugia, which have been shown to play a critical role in enabling species to persist through extreme climate events (Scheffers et al., 2014). It would also provide a way to relate data from biodiversity surveys to microclimate and its heterogeneity. Such models would shed light on how microclimate contributes to structuring tropical forest biodiversity and would provide a tool to forecast the potential impacts of climate change and land-use intensification on these ecosystems. However, to realize the full potential of new microclimate data streams, we need to standardize how they are measured and pair them with sensors that capture the physiology, chemistry, growth, movement, interactions and genetics of organisms (e.g., camera traps, acoustic sensors, dendrometers, sap flow sensors, thermal imagery, eDNA readers; Porter et al., 2009). While the development of these biological sensors has lagged behind that of meteorological ones, the advent of low-cost, open-source hardware and software components is leveling the playing field (Pearce, 2012). Integrated biophysical

sensor networks—coupled with advances in remote sensing and computing—promise to revolutionize our understanding of the microclimate ecology of human-modified tropical forests.

AUTHOR CONTRIBUTIONS

TJ and DC conceived the idea for the paper. TJ led the writing with help from TDJ, FZ, and TS. TJ, TDJ, NG, JW, and ES developed the case studies. JP produced the drawings for **Figure 3**. All authors contributed substantially to revisions and worked together to define the structure and content of the paper.

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