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Range-wide trends in tiger conservation landscapes, 2001 - 2020

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Of all the ways human beings have modified the planet over the last 10,000 years, habitat loss is the most important for other species. To address this most critical threat to biodiversity, governments, non-governmental actors, and the public need to know, in near real-time, where and when habitat loss is occurring. Here we present an integrated habitat modelling system at the range-wide scale for the tiger (*Panthera tigris*) to measure and monitor changes in tiger habitat at range-wide, national, biome, and landscape scales, as often as the underlying inputs change. We find that after nearly 150 years of decline, effective potential habitat for the tiger seems to have stabilized at around 16% of its indigenous extent (1.817 million km^2). As of the 1st of January 2020, there were 63 Tiger Conservation Landscapes in the world, covering 911,920 km^2 shared across ten of the 30 modern countries which once harbored tiger populations. Over the last 20 years, the total area of Tiger Conservation Landscapes (TCLs) declined from 1.025 million km^2 in 2001, a range-wide loss of 11%, with the greatest losses in Southeast Asia and southern China. Meanwhile, we documented expansions of modelled TCL area in India, Nepal, Bhutan, northern China, and southeastern Russia. We find significant potential for restoring tigers to existing habitats, identified here in 226 Restoration Landscapes. If these habitats had sufficient prey and were tigers able to find them, the occupied land base for tigers might increase by 50%. Our analytical system, incorporating Earth observations, *in situ* biological data, and a conservation-oriented modelling framework, provides the information the countries need to protect tigers and enhance habitat, including dynamic, spatially explicit maps and results, updated as often as the underlying data change. Our work builds on nearly 30 years of tiger conservation research and provides an accessible way for countries to measure progress and report outcomes. This work serves as a model for objective, range-wide, habitat monitoring as countries work to achieve the goals laid out in the Sustainable Development Goals, the 30×30 Agenda, and the Kunming-Montreal Global Biodiversity Framework.

KEYWORDS

big cats, data sharing, habitat trend, species monitoring, google earth engine, species conservation landscapes (SCL), sustainable development goals (SDG), convention on biological diversity (CBD)

1 Introduction

Of all the ways human beings have modified the planet over the last 10,000 years, habitat loss is the most important for other species (Tracewski et al., 2016; IPBES, 2019; Powers and Jetz, 2019; Leisher et al., 2022). Habitat describes where a species can find the resources to complete its life cycle (Hall et al., 1997). Loss of habitat diminishes the ability of populations to persist (Fahrig, 2019; Staude et al., 2020). There are several ways in which habitat loss occurs: whole-scale ecosystem conversion, degradation of existing habitat, fragmentation of habitat, and defaunation. These different forms of habitat loss can trigger cascading consequences for other species and ecosystem functions, including the ecosystem services on which human beings rely (Dirzo et al., 2014; Emer et al., 2020; Moreno-Mateos et al., 2020; Williams et al., 2020; Mahmood et al., 2021).

To address this critical threat to biodiversity, governments, non-governmental actors, and the public need to know where and when habitat loss is occurring. They need this information, not at the pace of scientific publications, which, for all the advances made in speeding peer review and digitizing the publication process in recent years, remains a ponderous, laborious, and, therefore, painfully slow procedure. Rather conservationists and civil society need information in as close to real-time as possible to measure losses, count gains, and react consequentially. The development of the global Internet provides a mechanism to share detailed data broadly and quickly at the requisite temporal and spatial scales.

In recent decades, government agencies such as the US National Aeronautics and Space Administration (NASA) and the European Space Agency (ESA) have made timely, high-resolution, landscape-level information from satellite sensors more accessible and affordable than ever before, fulfilling a desire for information about environmental issues and stimulating significant technological advancements in satellite engineering (Turner et al., 2015; Reddy et al., 2019; Vaz et al., 2020). Each year scientists propose new algorithms to combine and transform these data streams into validated, reliable data products that either measure directly, or provide proxies of, essential habitat elements (e.g. Pettorelli et al., 2014; Fernández et al., 2020). Increasingly those algorithms reside on distributed computer arrays such as Microsoft's Planetary Computer (Microsoft, 2022) and Google Earth Engine (Google, 2022) that enable rapid computation and Internet sharing, which in turn enables fast iteration, learning, and improvement (e.g. Jones et al., 2022; Shirk et al., 2022).

The definition of habitat obviously depends on the life history of the organism in question (Hall et al., 1997); habitat is not the same for whales, wallabies, or tigers. Here we build a model appropriate for habitat of the tiger (*Panthera tigris*), which could be extended readily to other species with appropriate re-parameterization. Tigers are the world's largest living cat species, a highly evolved, obligate carnivore whose ancestors inhabited Eurasia some 62 million years ago (Mazák, 1981; Mazák et al., 2011). Tiger habitat consists of areas with cover for hunting and raising cubs, sufficient availability of prey biomass, preferentially medium- and large-sized ungulates, and freedom from persecution by humans, the tiger's main competitor (Gittleman and Harvey, 1982; Karanth and Sunquist, 1992; Smith, 1993; Miquelle et al., 1999a; Darimont et al., 2023). Before humans entered Asia, the tiger's habitat was shaped mainly by the climate, as manifested through shifts in vegetation, prey base, and sea and ice levels (Cooper et al., 2016). The indigenous range of the tiger at the time of first impact by human society shows the species living from the Black Sea to the Pacific Ocean and from the southern margins of the boreal forest in Siberia to the tropical rainforests of Bali (Sanderson et al., in press). In political terms, thirty modern nation-states once had suitable habitat with resident tiger populations; as of this writing, only ten do.

Tigers are an endangered species in part because tigers have lost enormous areas of habitat (Goodrich et al., 2022). By one measure (Dinerstein et al., 2007), over 93% of tiger range is now empty of tigers; by another (Walston et al., 2010), nearly 99% of range had been lost, if one counts as viable tiger habitat only the places that are under conservation management and where tigers are known to raise cubs. The main mechanisms of range loss are direct habitat destruction, including physical conversion and fragmentation of suitable vegetation (Joshi et al., 2016; Poor et al., 2019) and the less visible, but no less deadly, depletion of prey populations (Karanth et al., 2004; Miquelle et al., 2015; Miquelle et al., 1999b; Jornburom et al., 2020.) Active persecution by humans has also depleted tiger numbers, including poaching for the illegal trade in tiger parts (Linkie et al., 2018; Villalva and Moracho, 2019; Skidmore, 2021); human-wildlife conflict (Lubis et al., 2020; Gulati et al., 2021); and the long-term consequences of once rampant sport hunting (Pikunov, 2014; Mandala, 2018). Unsustainable hunting of all wildlife, for example, with snares, can drive tigers extinct in otherwise high-quality habitat (O'Kelly et al., 2012; Gray et al., 2018; Figel et al., 2021).

The main mechanisms for conserving tigers, therefore, are halting habitat loss and degradation, preventing persecution, mitigating conflict, and restoring tigers and prey animal communities, all of which require a thorough understanding of habitat conditions and trends (Yang et al., 2019; Lubis et al., 2020; Ten et al., 2021; Adhiasto et al., 2023). Protected areas and Indigenous lands where natural ecosystems are actively managed on behalf of wild plants and animals are critical because they provide the legal and cultural enforcement mechanisms to limit damaging human activities (Soh et al., 2014; Sunarto et al., 2015; Karanth et al., 2020; Nijhawan and Mihu, 2020). Dynamic maps of habitat facilitate overlays with protected areas (UNEP-WCMC and IUCN, 2022), key biodiversity areas (KBA Partnership, 2023), and other spatial data reflecting safe-havens. Fortunately for tigers, their natural fecundity, ability to disperse long distances, and symbolic, spiritual, and ecological importance to human cultures across Asia contribute to the possibility of recovery (WCS Thailand, 2020; Jhala et al., 2021).

Concerns about habitat loss drove the first iteration of the Tiger Conservation Landscape analysis in the 1990s (Dinerstein et al., 1997). That analysis set the model of integrating satellite-derived observations with *in situ* knowledge of tiger populations to map large contiguous blocks of habitat (TCLs) and assess them with regard to ecological representation. In a second iteration, Sanderson et al. (2006) introduced the human footprint (Sanderson et al., 2002) into the analysis as a measure of human pressure, conducted extensive sensitivity testing, and reanalyzed TCLs using higher resolution satellite imagery and a renewed assessment of tiger distribution in the field and *in situ* knowledge of tiger populations (Sanderson et al., 2010). Subsequently, these maps have been cited in many analyses and planning efforts to save tiger habitat, plan surveys, and safeguard tigers (e.g. Dinerstein et al., 2007; Forrest et al., 2011; Global Tiger Initiative Secretariat, 2012; Joshi et al., 2016; Harihar et al., 2018; Sanderson et al., 2019; Sabu et al., 2022; Vasudeva et al., 2022).

This paper describes the third iteration of systematic improvements to the Tiger Conservation Landscape approach (abbreviated hereafter TCL 3.0; Figure 1; Table 1). As with previous iterations, TCL 3.0 integrates satellite-derived Earth Observation data with field-based observations of tigers in a well-defined and easy-to-understand spatial modelling framework to estimate how occupied and available habitat has changed annually between 2001 and 2020 using the Google Earth Engine (Gorelick et al., 2017). The primary analytical measure is "effective potential habitat", meaning habitat with appropriate, tiger-specific, structural characteristics derived from remote sensing and sufficiently low levels of human influence based on a new analysis of the human footprint (Sanderson et al., 2022). We delineate landscapes as interconnected blocks of effective potential habitat, larger than a minimum patch size (which varies by ecoregion, Dinerstein et al., 2017) and minimal connectivity distances across non-habitat.

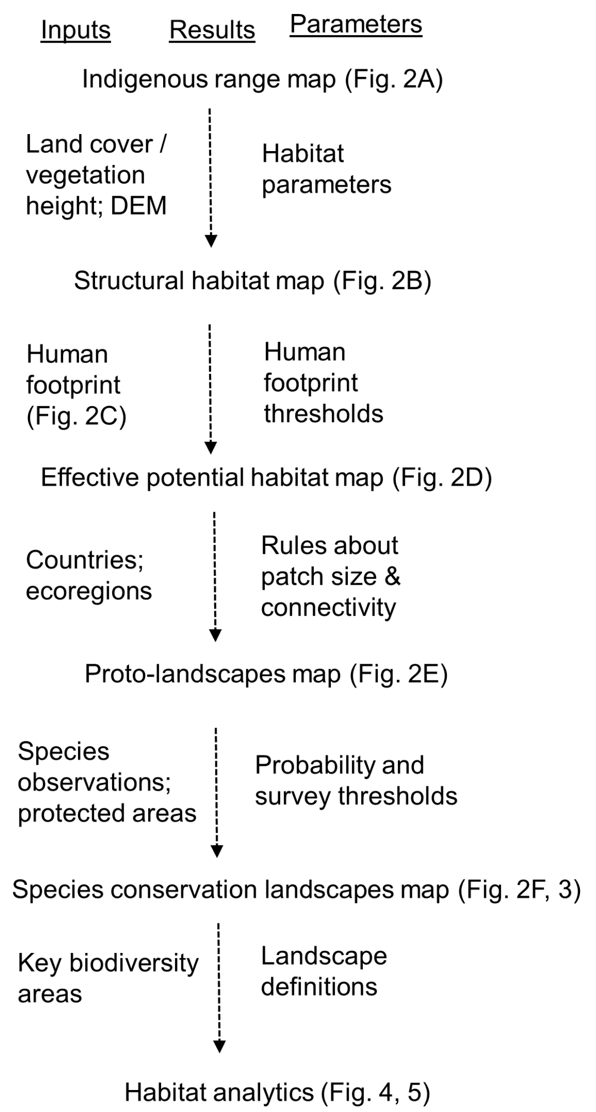

FIGURE 1
Schematic of analysis of the Species Conservation Landscapes including inputs and parameters.

TABLE 1 Definition of species conservation habitat and landscape metrics with conservation interpretations for the tiger (*Panthera tigris*).

Habitat metric	Definition	Conservation interpretation
Indigenous resident range	Areas where the species lived **before significant impact from human beings**	Areas where the species once existed; the area of interest for range-wide conservation activities
Structural habitat	Areas within the indigenous range with **appropriate habitat** as determined by land cover type, elevation, and vegetation height	Localities that could harbor the species assuming adequate prey base and no threats
Effective potential habitat	Areas of structural habitat with **sufficiently low human influence index** values to increase probability of species persistence	Localities most likely to harbor the species because threats from human activity are lower; these areas are further analyzed at landscape scale
Species conservation landscapes	An interconnected region of effective potential habitat patches with **sufficient area to maintain at least a minimal population**[1] and the **species is known to have occurred recently**[2].	Critical areas to be conserved and expanded, including prey populations
Restoration landscapes	An interconnected region of effective potential habitat with **sufficient area to maintain at least a minimal population** and where the **species is NOT known to have occurred recently** or presumed to be extirpated.	Areas for restoration, either through active reintroduction efforts or restoration of connectivity; meanwhile it is important to protect habitat and build prey populations
Survey landscapes	An interconnected region of effective potential habitat with **sufficient area to maintain at least a minimal population** and the **species occurrence is uncertain recently**.	Areas to be surveyed for the species; meanwhile it is important to protect habitat and build prey populations
Species fragments	Same as conservation landscapes, except below the sufficient area size[1]	Areas to be connected to larger blocks of habitat through lowering human influence, improving connectivity and expanding habitat; such fragments, while insufficient in themselves, may form "stepping stones" or transient habitat connecting landscapes
Restoration fragments	Same as restoration landscapes, except below the sufficient area size	
Survey fragments	Same as survey landscapes, except below the sufficient area size	
Occupied habitat	Areas of effective potential habitat where the species have been observed recently[2]	Localities that are known to harbor the species

[1]for tigers, the minimum landscape size is an area greater than what's needed for five, non-overlapping, female home ranges. Estimated female home ranges are allowed to vary across the range depending on biome; see Table S3
[2]for tigers, recently is defined within five years of the analysis date.

We now recognize six categories of habitat area (Table 1): Tiger Conservation Landscapes (TCLs), where tigers are found; Restoration Landscapes, where tigers are known or presumed to have been extirpated; and Survey Landscapes, where the status is unclear; and Tiger Fragments, Restoration Fragments, and Survey Fragments (respectively), where patches fall below the minimum patch size.

Our approach is related to, but different from, traditional habitat suitability index (HSI) approaches (e.g. Guisan et al., 2017). Habitat suitability models primarily aim to describe where a species might live, comparable to what we identify as "structural habitat" in our method (see below). While valuable, conservation action requires knowing much more than where a species might be; we also need to know what to do. Here we differentiate landscapes in specific terms that by definition suggest different sorts of conservation actions (Table 1). HSI models typically take observations as independent data to find dependencies among landscape factors (both biological and anthropogenic), usually through application of a statistical model. Here we model the habitat from first principles (e.g. land cover, then human footprint, then patch size and connectivity). Only later in the process do observations enter to classify the landscapes by type. The result is that for areas where tigers are no longer present, we can suggest why they have been extirpated, by measuring physical loss of structural habitat, trends in human influence (and implied conflict), and/or changes in patch size and fragmentation. Landscape classification suggests to conservation authorities where to address efforts and what kinds of efforts to ensure the long-term survival of tigers at range-wide, country-wide, and local scales.

Using our conservation-centered approach, here we summarize the current state of wild tiger habitat and discuss trends in habitat change over the last 20 years. We close with a few comments about how this approach to habitat mapping can be used for national-level reporting for international conventions and by countries to ensure the lasting existence of wild tigers on Earth.

2 Materials and methods

2.1 Study area

We analyzed tiger habitat annually, on January 1st of each year from 2001 – 2020, within the "likely resident indigenous range" of the tiger as defined in Sanderson et al. (in press) (Figure 2A). The indigenous range mapping indicates which ecoregions, or parts of ecoregions, were most likely to have resident tigers before human beings became a significant factor shaping the distribution of the

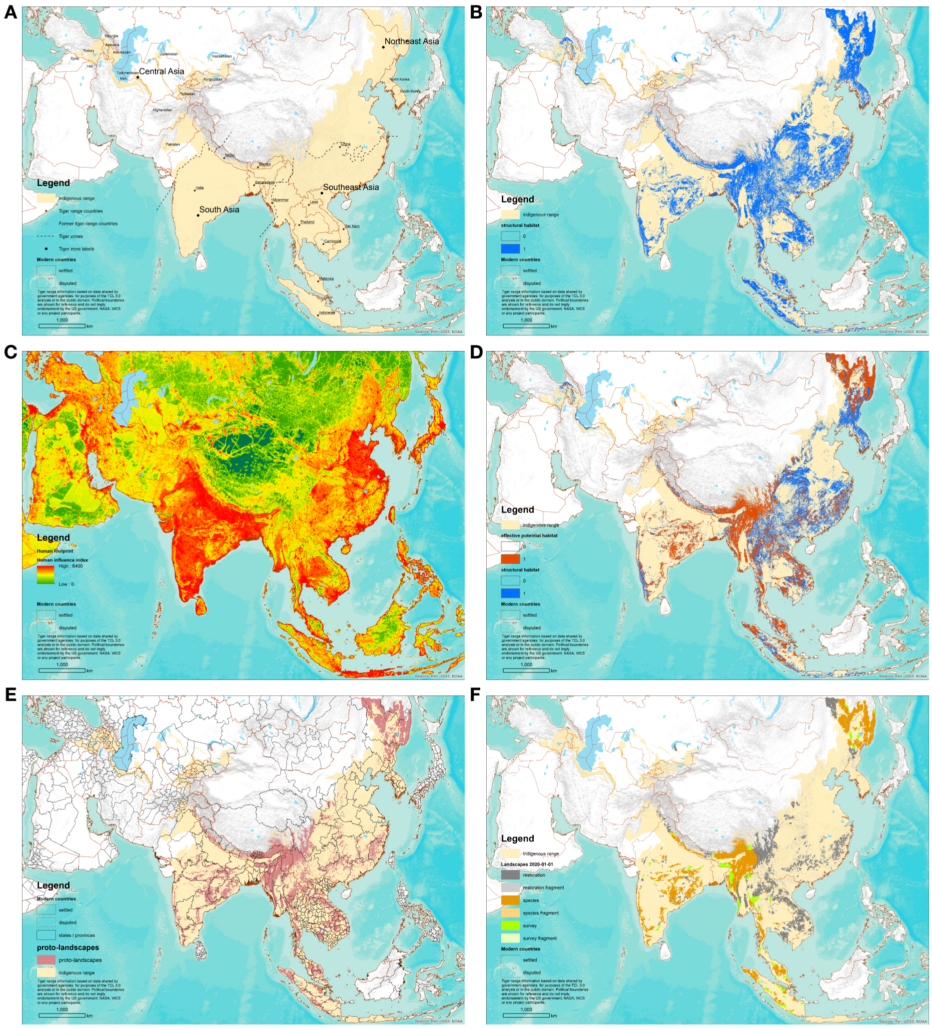

FIGURE 2
Species Conservation Landscape Mapping process, with application to tigers (*Panthera tigris*) for 1 January 2020. **(A)** Map of the likely resident indigenous range, with zone boundaries (dotted lines). **(B)** Map of structural habitat as revealed by land cover, elevation, and vegetation height. **(C)** Map of human footprint (Sanderson et al., in press). **(D)** Map of effective potential habitat (orange) overlaid structural habitat (blue). Areas of structural habitat above the human footprint threshold for each zone show as blue. **(E)** Map of proto-landscapes overlaid state or province boundaries for each current or former range state. **(F)** Map of six categories of Tiger Conservation Landscapes on 1 January 2020.

species (Sanderson et al., 2019). This definition is consistent with how the indigenous range is defined by the IUCN Green Status Assessment process (Akçakaya et al., 2018; see also Stephenson et al., 2019). Within the study area, raster analyses were made over the 300 m grid cells coincident with the ESA CCI Landcover data (European Space Agency, 2017) used for the structural habitat mapping (see below). Previous TCL mappings used a base resolution of 1 km cells, so our landscapes are approximately 3x better resolved than earlier efforts.

We divided the study area into four zones along ecoregional boundaries, representing major differences in tiger biology and status: South Asia, Southeast Asia, Northeast Asia, and Central Asia (Figure 2A). These zones were used to create a grid-based system for mapping species observations as areas of analysis for the human footprint (Sanderson et al., 2022) thresholds, and for assigning minimum patch sizes, as described below.

2.2 Extirpation masks

We also developed maps of ecoregions or parts of ecoregions where tigers had been declared extirpated, including broad swaths of the Black Sea region, Central Asia, Indochina, and central China, for each year from 2001 – 2020 (Sanderson et al., in press). For extirpated areas, we assigned the approximate date of extirpation and provided supporting references.

2.3 Species observations

We systematically reviewed the literature to identify peer-reviewed studies, government and non-governmental organization reports, and in some cases, newspaper accounts to develop a temporally and spatially explicit observational database from 1995

– 2021 for tigers. Observations include any information of direct observations of the species, including systematic surveys, that document whether or not the species was detected. We also included surveys for other mammal species (e.g. small cats, wild cattle) using techniques that would likely have detected and reported tigers, especially in parts of the range and/or time periods where or when no tiger-specific studies were available.

We began by searching Google Scholar and Web of Science using keywords "tiger(s)" OR "*Panthera tigris*" and "survey" OR "field" in journals focused on ecology, environmental science, and conservation. Next, we filtered the extensive literature by reviewing titles and abstracts and, where necessary, article contents, keeping only papers that provided first-hand observational data on tigers or where second-hand summaries provided access to otherwise unpublished information. We also contacted tiger biologists and conservation officers working in tiger range countries to share information and identify sources our review might have missed, including non-English language sources and experts (Table S1). Finally, for a few localities where scientific accounts were unavailable because of censorship or lack of data sharing, we supplemented scientific observations with accounts of human-wildlife conflict drawn from a search of newspaper and magazine accounts, confirming observations through independent sources and/or photographic evidence. We maintained all the bibliographic details in a read-only, public bibliography: https://www.zotero.org/groups/2516009/tiger_conservation/library. A full list of sources is provided in Table S2.

The four types of data were:

- Camera trap studies (full details): Camera trap studies were represented with a deployment table, including information on location, deployment and pick-up dates, and a corresponding observation table, including dates of positive detections, sex and age class (adult or juvenile) of the tigers observed.
- Camera trap studies (summary): Camera trap studies where the full details were unavailable, but the dates of study, study area, observed density, and measures of variation in that density (standard error or confidence intervals; see Moy, 2021) were available, we created observations in a modified version of the *ad hoc* template.
- Sign surveys: Sign surveys were handled with a survey table describing the locations and replication of the surveys, and an observation table, describing which replicates had positive detections.
- *Ad hoc* observations: All other observations were summarized in "*ad hoc*" observation tables, which gave the date and location of positive detections of tigers, with no measures of the search effort.

Observations were located by coordinates, if available, or by matching to a standardized grid reference, if not. We created an overlay of grid cells that varied in size in different zones of tiger range, depending on a summary of tiger home range information (Table S3). In South Asia, we used cells with a grid side of 4 km (area of 16 km^2); in Southeast Asia, including Sumatra, we used 16 km cells (area of 256 km^2); and in Northeast and Central Asia, we used 32 km cells (area of 1024 km^2). If precise coordinate data were unavailable in the paper or from the study authors, we georeferenced map figures and extracted spatial locations according to the overlying grid cells.

Observations were dated to the day of the observation when possible, and if not to an observation period, with a start and end date. If survey dates were given in months (e.g. March 2004 – October 2004), we used the first and last days of the corresponding months. Where observations were in years, we used the first and last days of the corresponding years.

All observations were tagged with the observer's name, institution, email address, and reference. For multi-authored studies, we identified the observer as the survey leader, where given, or the corresponding author's name, where not. We agreed, as a matter of security for the safety of tigers and to respect the research interests of the investigators, not to reshare the point locality information used for the analysis. They do not appear on the website or in this paper.

2.4 Structural habitat

As ambush hunters, tigers need vegetative cover to stalk and kill prey (Sunarto et al., 2012). They also use thick vegetation to hide their cubs during weaning (Smith et al., 1998). We used land use/land cover data developed by the European Space Agency to identify land cover classes that are possibly tiger habitat and vegetation height product derived from NASA's Landsat sensor (Potapov et al., 2019). Both datasets were rescaled to a common 300 m grid. For tigers, structural habitat was defined land use/land cover classes where tigers are typically found – essential habitat types with sufficient cover for tigers to hunt and raise cubs (Table S4). For mixed mosaic classes, we add another criterion, including areas with at least 5 meters of vegetation height (Figure 2B). For the Northeast Asia zone, we excluded areas 1000 meters above sea level; elsewhere we applied an elevation threshold of 3350 meters, though note that rarely tigers have been observed at higher elevations in the Himalayas (Adhikarimayum and Gopi, 2018; Shrestha et al., 2021).

2.5 Effective potential habitat

Factors invisible to satellite sensors impact where tigers can live (Redford, 1992; Harrison, 2011). Tigers are illegally hunted or killed in many parts of the range after human/wildlife conflict (Nyhus and Tilson, 2004; Karanth and Gopal, 2005; Musavi et al., 2006; Lubis et al., 2020). Tigers may also be depleted by the lack of prey caused by indirect competition with human hunters (Miquelle et al., 1999b; Karanth et al., 2004; Johnson et al., 2006). Because we lack range-wide, spatially and temporally explicit data on prey depletion and human disturbance, we use a proxy: the human influence index, or informally, the human footprint (Sanderson et al., 2002; Venter et al., 2016; Sanderson et al., 2022). The human influence index is a unitless, weighted sum based on human population density, infrastructure, accessibility, and power consumption on a 0 – 60 scale (Figure 2C). The result is a gradient map of human impacts that have been widely correlated to human disturbances and range collapse in large mammals (Yackulic et al., 2011; Di Marco et al., 2018; Tucker et al., 2018).

We recorded the human influence index values and zones where tigers have been observed between 2001 – 2020. Following methods developed by Sanderson et al. (2006), we randomly sampled the human influence index at the same number of locations within each zone. We repeated this analysis a thousand times for each year for each zone. Then, we calculated frequency histograms of human influence index values for the tiger detections and the random sample for each zone and subtracted them to show human influence values where tigers are more or less likely than random selections would suggest, equivalent to a chi-squared test (Nikulin, 1973). The lowest human influence value where the difference in frequency between the tiger and random distributions is zero, we call the "social tolerance threshold" (Figure S1).

To define effective potential habitat, we excluded areas of structural habitat where the human influence index value was greater than the social tolerance threshold for a given zone and year (Figure 2D). We applied the threshold from the Northeast Asia zone to the Central Asia zone.

2.6 Landscape delineation

We applied a two-step delineation process to group patches of effective potential habitat into landscapes. First, we found all patches of contiguous cells and tested them against core patch size specific to ecoregions (Table S3). A "core" patch size is defined as an area large enough to maintain at least five tigers, based on densities observed in the literature. "Stepping stone" patches were also recognized that were one-tenth the size of a core patch. These small patches are considered to provide temporary respites during movement, but the patches are not large enough to maintain a tiger for a breeding season. In a second step, we tested how patches were close enough to be considered potentially connected. If core patches lay within 4 km of each other, or were connected with "stepping stone" patches within 4 km, they were delineated as part of the same landscape (Figure 2E).

2.7 Landscape attribution

We attributed landscapes, or portions of landscapes, into one of six classes based on size, the presence of the species, and the survey effort applied to detect them, based on the observational data for the last five years. The classes are summarized in Table 1. We analyzed landscapes using underlying state/province boundaries of countries (administration level 1 as defined in the Global Administrative Database – see Anonymous, 2021). States/provinces represent potentially important political differences in management regime and cultural situations that might differentially impact portions of species conservation landscape (Figure 2E). Observations with coordinates were assigned with a point in polygon analysis. Observations located by grid cells were assigned based on the centroids of the grid cells to the overlapping landscape.

2.8 Probability of presence and level of survey effort

To integrate various survey data, estimate the effective amount of survey effort and account for variation in the size of landscape patches, we fit a multi-scale occupancy model (Nichols et al., 2008), in which the landscape patches were the coarser scale and grid cells were the finer scale (and whose dimensions were defined approximately based on average tiger home range size in that zone). In multi-scale occupancy models, occupancy at the finer scale is conditional on occupancy at the coarser scale – in other words, tigers can only occupy a grid cell within a landscape patch if the landscape patch is occupied; however, there can also be unoccupied grid cells within an occupied landscape patch. In this context, the finer scale occupancy would be equivalent to the probability of use. To fit the multiscale occupancy model, observations and effort associated with sign surveys and camera trap surveys with full details were attributed to grid cells nested within landscape patches. Occupancy at the coarser scale was a function of random effects for state/provinces, and fixed effects for area of state/province and proportion of the area protected. We standardized area of each subnational unit before fitting models. We used constant (e.g., no covariates) probability of detection for camera trap surveys and constant probability of detection for sign surveys.

Models were fit in JAGS (Plummer, 2003) run from Python using a Python interface to JAGS, PyJAGS (pyjags version 1.3.8) to analyze Bayesian hierarchical models. We chose a Bayesian framework because it allowed us incorporate the random effects detailed above more easily.

For each landscape patch, we estimated the unconditional probability that tigers were present in a landscape (given the landscape patch's potential effective habitat area, protected area status, state/province, and ecoregion). We also estimated the conditional probably that tigers were present given the observational data from the last five years (e.g. for the 2020 analysis, observational data applicable, based on the start and end dates of the study, from 2016 – 2020). If *ad hoc* or camera trap summary data indicated that a landscape patch was occupied and its conditional probability was less than 1 (i.e., no tigers were seen in the detailed camera trap data or sign survey data), the conditional probability was changed after model fitting to 1. We measured survey effort of landscape patches by taking the ratio of the conditional to the unconditional probability subtracted from 1.

Tiger conservation landscapes were defined as areas with a conditional probability of the presence of tigers of >=99%. Survey landscapes have a lower conditional probability (<99%) and a

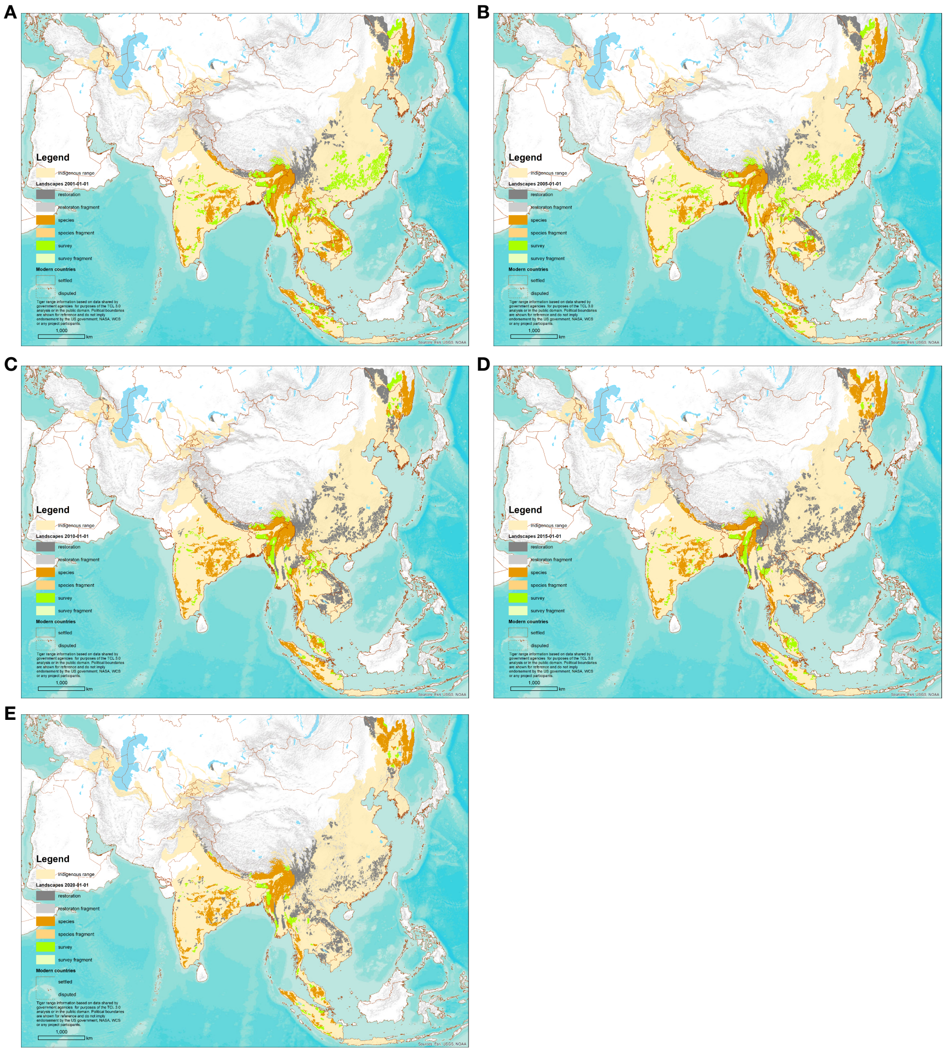

FIGURE 3
Map of Tiger Conservation Landscapes on five dates. Note: Figures 2F and 3E are the same. **(A)** 1 January 2001. **(B)** 1 January 2005. **(C)** 1 January 2010. **(D)** 1 January 2015. **(E)** 1 January 2020.

survey effort below 0.6. Restoration landscapes have a lower conditional probability and a survey effort greater than 0.6.

After classifying the landscapes into the six classes, contiguous landscapes of the same class were recombined to create the final landscape delineation, as shown in Figures 2F, 3.

2.9 Landscape summary

We created several automated summaries to make the information contained in these data more tractable to policymakers and on-the-ground managers (Figures 4, 5; Tables 2–4). Each landscape is analyzed against the World Database of Protected Areas (UNEP-WCMC and IUCN, 2022) to measure the extent of protection and the Key Biodiversity Areas (IUCN, 2016) to measure its importance for meeting Sustainable Development Goals (United Nations, 2015) and other biodiversity-related targets. This information is available for each country *via* the project website at act-green.org

2.10 Data processing

The steps above were implemented on Google Earth Engine (Gorelick et al., 2017) in a task-based architecture, implemented in Python (Python Software Foundation, 2022) and designed to be recalculated as often as the underlying data change. All areas are reported based on Google Earth Engine's area calculation procedure, which treats each pixel element as its true three-dimensional area, not dependent on any particular map projection. The open-source code is available at https://github.com/SpeciesConservationLandscapes.

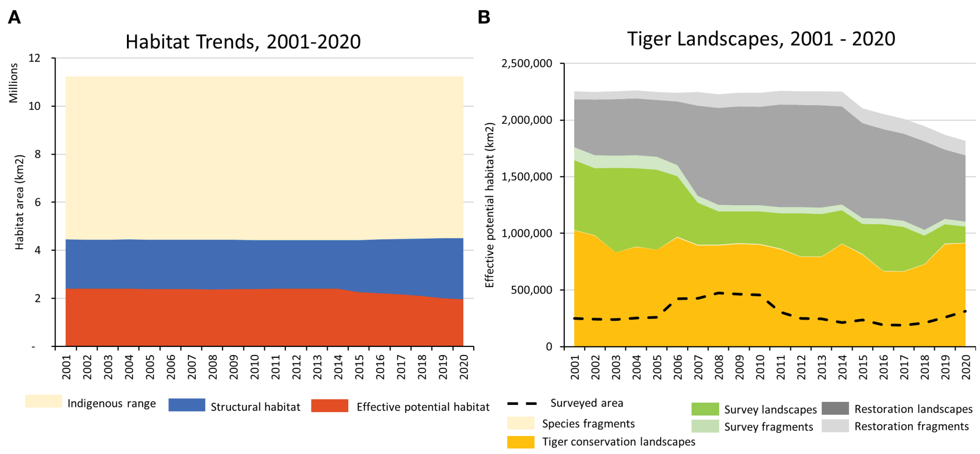

FIGURE 4
Range-wide trends. **(A)** Trends in structural habitat and effective potential habitat within the tiger's likely resident indigenous range, 2001 - 2020. **(B)** Trends in Tiger Conservation Landscapes, Survey Landscapes, and Restoration Landscapes, fragmented landscapes, and estimated surveyed area from 2001 – 2020.

2.11 Quality control

Each tiger observation study was reformatted into a data entry form compatible with the database schema. Another analyst (usually the senior author) separately reviewed each data entry form before inclusion in the database. Through extensive online consultations, we also reviewed the landscape outputs with tiger biologists and conservationists noted in Table S1. Our results are replicable by other scientists as our code is open-source, and we identify in detail the sources used (Table 2). Sensitivity testing of the model was conducted, as described in Sanderson et al. (2006).

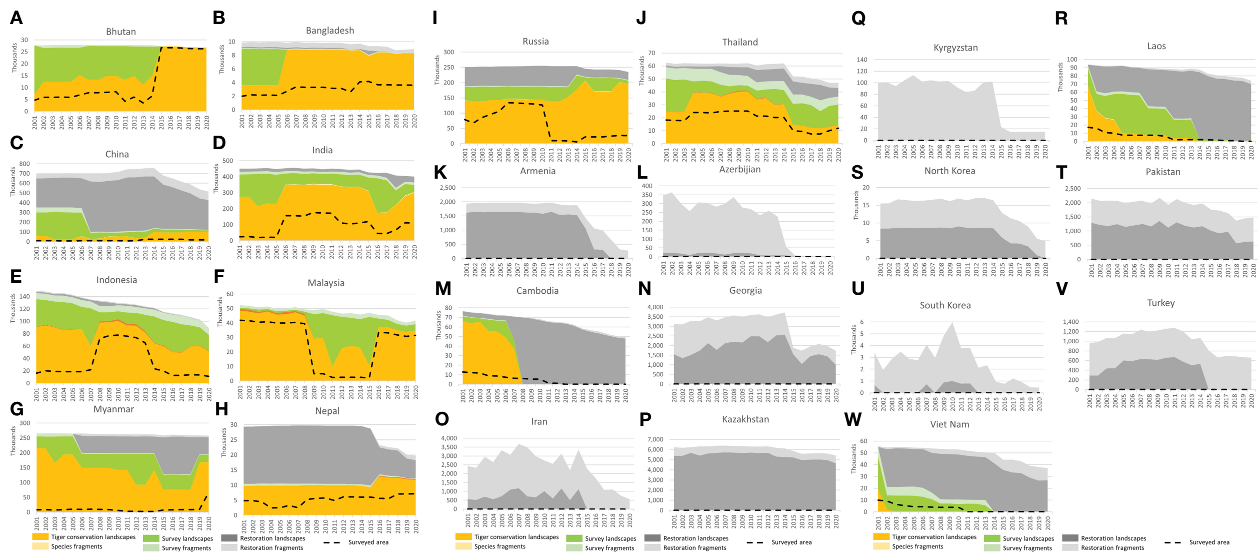

FIGURE 5
National level trends in Tiger Conservation Landscapes, Survey Landscapes, and Restoration Landscapes, fragmented landscapes, and estimated surveyed area from 2001 – 2020. The first 10 figures **(A–J)** show countries, where tigers lived in 2020. The remaining 13 figures **(K–W)** show former range states with some extant habitat, where tigers lived prior to 2020. The following six countries no longer have any effective potential habitat for the tiger: Afghanistan, Iraq, Syria, Tajikistan, Turkmenistan, and Uzbekistan, according to this analysis – see discussion. Note that y-axis values vary plot to plot. **(A)** Bhutan. **(B)** Bangladesh. **(C)** China. **(D)** India. **(E)** Indonesia. Fig. Malaysia. **(G)** Myanmar. **(H)** Nepal. **(I)** Russia. **(J)** Thailand. **(K)** Armenia. **(L)**. Azerbaijan. **(M)**. Cambodia. **(N)**. Georgia. **(O)**. Iran. **(P)**. Kazakhstan. **(Q)**. Kyrgyzstan. **(R)**. Laos. **(S)**. North Korea. **(T)**. Pakistan. **(U)**. South Korea. **(V)**.Turkey. **(W)**. Vietnam.

TABLE 2 Analysis of tiger conservation landscape types by country on 2020-01-01.

				Species Landscapes		Species Fragments		Survey Landscapes		Survey Frag-ments		Restoration Landscapes		Restoration Fragments	
Country	Area of likely resident indigenous range (km2)	Area of structural habitat (km2)	Area of effective potential habitat (km2)	% of eff. pot. hab.	#	% of eff. pot. hab.	#	% of eff. pot. hab.	#	% of eff. pot. hab.	#	% of eff. pot. hab.	#	% of eff. pot. hab.	#
Afghanistan	46,816	6,482	0												
Armenia	28,348	7,045	278											100%	8
Azerbaijan	73,345	10,370	4											100%	3
Bangladesh	134,619	24,720	8,897	93%	2					1%	4			6%	11
Bhutan	31,993	29,566	26,905	99%	1					1%	2				
Cambodia	177,080	102,823	49,760							<1%	1	96%	7	4%	25
China**	4,006,417	1,811,507	513,572	20%	6			3%	6	1%	52	59%	128	17%	785
Georgia	25,413	11,663	1,724									58%	1	42%	11
India	2,512,229	691,734	401,771	75%	35	1%	56	11%	38	4%	368	9%	54	<1%	55
Indonesia	555,207	252,147	88,899	58%	11	1%	**4**	29%	13	11%	64			1%	9
Iran	136,938	19,083	556											100%	10
Iraq	5,992	294	0												
Kazakhstan	148,031	12,275	5,419									86%	2	14%	11
Kyrgyzstan	107,447	5,969	15											100%	2
Laos	228,558	161,364	73,884					**2%**	1	<1%	2	92%	12	5%	47
Malaysia	128,983	74,103	41,713	83%	2			11%	3	6%	19			<1%	1
Myanmar	661,644	403,684	257,121	65%	7	<1%	2	10%	8	1%	23	22%	13	2%	62
Nepal	71,381	41,522	19,695	60%	1	1%	4	<1%	1	1%	6	31%	2	7%	17
North Korea	120,561	82,304	4,826									<1%	1	100%	27
Pakistan	272,378	14,360	1,481									43%	3	57%	25
Russia	376,857	306,012	234,972	83%	5			4%	3	1%	24	11%	1		
Singapore			0												
South Korea	92,522	56,454	446											100%	6
Syria	8,688	1	0												
Tajikistan	67,194	658	0												

(Continued)

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TABLE 2 Continued

				Species Landscapes		Species Fragments		Survey Landscapes		Survey Fragments		Restoration Landscapes		Restoration Fragments	
Thailand	507,060	161,012	46,884	30%	9	1%	2	34%	8	13%	55	14%	11	8%	60
Turkey	146,809	20,739	657											100%	10
Turkmenistan	49,735	131	0												
Uzbekistan	79,182	1,143	0												
Vietnam	322,149	153,669	37,187									72%	14	28%	91
Range-wide	11,123,576	4,462,834	1,816,666	50%	63	0.3%	67	8%	73	2%	608	32%	226	7%	1229

* Occupied habitat is inclusive of TCLs and species fragments; Available habitat is the sum of restoration landscapes/fragments and survey landscapes/fragments

** Includes area from Macao and Hong Kong

3 Results

3.1 The state of tiger conservation landscapes on 1 January 2020

As of 1 January 2020, planet Earth possessed only 63 localities where wild tigers were known to occur. These 63 Tiger Conservation Landscapes covered 911,920 km^2 across ten range states (Figures 1-3, 4A, Table 2). They represent only 8.2% of the tiger's likely resident indigenous range, suggesting a loss of approximately 91.8% of the world's tiger habitat.

These 63 areas are the key landscapes for tiger conservation. By definition, each TCL had a high probability of resident tiger populations during the previous five years (i.e., between 1 January 2015 and 31 December 2019) and enough habitat with sufficiently low levels of human influence to sustain a population of at least five adult females. Designating an area as a TCL does not mean tigers exist everywhere within the mapped habitat block(s), however. Within the TCLs, only approximately a third of the total TCL area (311,698 km^2) has been surveyed in the previous five years (Figure 4B).

Eight of the 63 TCLs identified in 2020 were transboundary. The largest TCL in the world was the Northern Triangle of India, Myanmar, China, Bhutan, and Bangladesh, which covered 294,847 km^2 in 2020, 32.3% of all TCL area worldwide. Unfortunately, tigers are unlikely to be continuously distributed throughout this vast area (Lwin et al., 2021; Sarkar et al., 2021; Sabu et al., 2022). Conflicts in Myanmar and India have constrained on-the-the ground surveys; the consequences of those conflicts for tigers and their prey remain poorly understood (Win, 2022).

All TCLs are important, but many were much smaller than the Northern Triangle. the Dawna Range, Ranthambore or Kaziranga TCLs, all cover less than 500 km^2. India had the largest number of TCLs in a single country at 35 landscapes due to fragmentation of what was once a much more continuous habitat but also concerted conservation efforts (Aylward et al., 2022). Nepal had the fewest TCLs (1), but a critical one, the inter-connected and extensive Terai Arc TCL of flooded grasslands and riparian forests, shared with India (Biswas et al., 2020; Thapa et al., 2021; Yadav et al., 2022). Other TCLs representing a diversity of habitats are found in the Russian Far East, parts of Southeast Asia, and on the island of Sumatra, as described below.

TCLs comprised only 50% of Asia's effective potential habitat extant on January 1, 2020 (Table 2). The remaining 50% was a combination of Restoration Landscapes, Survey Landscapes, or small fragments (tiger fragment, restoration fragment, or survey fragment; Table 1). Restoration Landscapes comprised 32% of the total effective potential habitat in 2020; Survey Landscapes, 8%, and all fragments, 9.3% (Table 2). Fragmentation has been increasing over time, generating shards of habitat that are of little use to tigers but may provide future building blocks for connectivity.

Our classification of landscapes is based on 102,418 observations collected from 362 unique sources over the last 20 years (Table S2). The majority of observations were of the "*ad hoc*" type, 55,684; sign survey observations, provided another 45,701 observations; and camera trap studies, 1,033 observations. By

TABLE 3 Analysis of Tiger Conservation Landscape areas by Tiger Range State, as of 2020-01-01.

		Areas[1] within Tiger Conservation Landscapes and Country as of 2020-01-01										
Lsid	TCL Name	India	Russia	Myanmar	China	Indonesia	Bhutan	Malaysia	Thailand	Nepal	Bangladesh	Total
1	Kaziranga	94										94
2	Northern Triangle*	101,211		144,542	17,562		26,765				4,768	294,847
3	Leuser Landscape					27,703						27,703
4	Northern Kawthoolei			5,323					34			5,357
5	Trumon - Singkil					684						684
6	Dawna Range			466								466
7	Southern Tanintharyi*			16,929					4,092			21,022
8	Southern Western Forest Complex*			345					1,362			1,707
9	Mulayit Tuang*			716					6			723
10	Western Forest Complex*			93					5,335			5,429
11	Batang Gadis - Malampah Alahan Panjang					1,004						1,004
12	Khao Luang								889			889
13	Kerinci Seblat					7,989						7,989
14	Bukit Rimbang Baling					2,078						2,078
15	Batang Hari					1,447						1,447
16	Taman Negara - Hala-Bala*							31,296	73			31,368
17	Thap Lan - Pang Sida								2,239			2,239
18	North Bukit Balai Rejang Selatan					816						816
19	Kerumutan					3,718						3,718
20	Endau Rompin							3,352				3,352
21	South Bukit Balai Rejang Selatan					1,335						1,335
22	Bukit Barisan Selatan					671						671
23	Berbak - Sembilang					3,842						3,842
24	Southern Zhangguangcailing				8,077							8,077
25	Lesser Khingan				53,493							53,493
26	Pri - amur		72,138									72,138
27	Laoyeling*		2,691		14,187							16,879

(Continued)

TABLE 3 Continued

		Areas[1] within Tiger Conservation Landscapes and Country as of 2020-01-01										
Lsid	TCL Name	India	Russia	Myanmar	China	Indonesia	Bhutan	Malaysia	Thailand	Nepal	Bangladesh	Total
28	West Wandashan				3,088							3,088
29	East Wandashan				3,962							3,962
30	Sikhote-Alin		120,993									120,993
31	Sahyadri	1,669										1,669
32	Radhanagari	1,328										1,328
33	Western Ghats	22,739										22,739
34	Yawal	2,103										2,103
35	Jawahar Sagar	459										459
36	Sariska	846										846
37	Ranthambore	253										253
38	Anamalai-Parambikulam	3,620										3,620
39	Akola District	247										247
40	Ratapani-Singhori	1,808										1,808
41	Periyar - Megamala - Shendurney	4,467										4,467
42	Rajaji Minor	390										390
43	Terai Arc*	9,775								11,762		21,538
44	Ghatigaon	2,443										2,443
45	Painganga	4,542										4,542
46	Eastern Dehgaon-Bamori Range	273										273
47	Bor	193										193
48	Nagarjunasagar	6,615										6,615
49	Sri Lankamalleswara	413										413
50	Melghat	8,511										8,511
51	Andhari - Tadoba	2,288										2,288
52	Sri Penusila Narasimha	5,219										5,219
53	Pilibhit	399										399
54	Bandhavgarh	423										423

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TABLE 3 Continued

Lsid	TCL Name	Areas[1] within Tiger Conservation Landscapes and Country as of 2020-01-01										
		India	Russia	Myanmar	China	Indonesia	Bhutan	Malaysia	Thailand	Nepal	Bangladesh	Total
55	Umaria District	253										253
56	Panpatha	1,892										1,892
57	Panna West	3,950										3,950
58	Central Indian Landscape	51,656										51,656
59	Papikonda	7,910										7,910
60	Satkosia Gorge	19,250										19,250
61	Palamau District	28,545										28,545
62	Simlipal	3,411										3,411
63	Sundarbans*	1,324									3,540	4,864
	Total	**300,519**	**195,822**	**168,415**	**100,368**	**51,286**	**26,765**	**34,647**	**14,030**	**11,762**	**8,308**	**911,920**

*Transboundary TCLs.
[1]All areas measured in km2 of "potential effective habitat" as defined in the text.

combining these observations with billions of satellite-based observations and human footprint calculations, we were able to follow range-wide trends in TCLs and related landscape types.

3.2 Trends in tiger conservation landscapes, 2001 - 2020

There are many ways to measure tiger habitat loss. The baseline deployed here is the "likely resident indigenous range", an area of approximately 11.1 million km^2 where tigers are thought to have once lived (Sanderson et al., in press). This enormous range in Asia encompasses areas included in 30 modern countries, from Turkey to Russia, and China to Indonesia (Table 2).

Since the time tigers were first significantly impacted by human beings, hundreds to thousands of years ago, up until 1 January 2020, tigers have lost an estimated 60% of the structural habitat, meaning that approximately 6.7 million km^2 of vegetative cover suitable for tigers has been lost through conversion to other uses such as agriculture or urban development. High levels of human influence have reduced the utility of another 2.5 million km^2 of structural habitat (23% of the indigenous range) through fragmentation, human-wildlife conflict, and likely concomitant reduction of the prey base. Direct persecution of tigers and/or tiger prey has further extirpated tigers from another 711,634 km^2 of suitable habitat (6% of indigenous range) that otherwise appears to be structurally sound and with low levels of human influence, as measured by the mapping of Restoration Landscapes. Regarding tigers, these areas can be considered "empty forests" (sensu Redford, 1992). Finally, lack of knowledge constrains our ability to understand tiger habitat, as measured by the Survey Landscapes. The status of tigers remains uncertain in 188,364 km^2 of habitat (2% of indigenous range), a decline of -75% since 2001. The decreasing amount of area needing survey reflects the increased effort to assess tiger status across Asia, but also underscores that there are fewer and fewer places to look.

Over the last 20 years, the total area of Tiger Conservation Landscapes (TCLs) declined from 1,025,488 km^2 in 2001 to 911,901 km^2 in 2020, a range-wide loss of 11% of TCL area (Figure 4B). TCLs also became more fragmented. The area of tiger fragments has increased 37%, from 3,477 km^2 in 2001 to 4,787 km^2 in 2020, though such fragments with tigers represent only a tiny percentage – less than 1% – of overall occupied habitat. Because of fragmentation, the number of TCLs has also increased, from 53 in 2001 to 63 in 2020.

These range-wide trends can be further decomposed at the national scale. In the following sections, we describe important differences in trends among tiger range countries over the first two decades of the 21st century.

3.2.1 South Asia (India, Nepal, Bhutan, Bangladesh)

In 2020, India had the greatest area of Tiger Conservation Landscapes (300,508 km^2) of any range country, 33% of the global total (Table 2; Figure 5D). Our analysis suggests that India's TCL has expanded by approximately 10% in area over the last 20 years, through a combination of conservation efforts and improved

TABLE 4 Ecological representation of Tiger Conservation Landscapes as of 2020-01-01.

Lsid	TCL Name	Tropical & Sub-tropical Moist Broadleaf Forests	Tropical & Subtropical Dry Broadleaf Forests	Tropical & Subtropical Grasslands, Savannas & Shrublands	Tropical & Subtropical Coniferous Forests	Mangroves	Temperate Broadleaf & Mixed Forests	Temperate Conifer Forests	Flooded Grasslands & Savannas	Montane Grasslands & Shrublands	Boreal Forests/ Taiga	Deserts & Xeric Shrublands
1	Kaziranga	100%	-	-	-	-	-	-	-	-	-	-
2	Northern Triangle*	57%	<1%	<1%	2%	-	23%	14%	-	3%	-	-
3	Leuser Landscape	96%	-	-	4%	-	-	-	-	-	-	-
4	Northern Kawthoolei	99%	1%	-	-	-	-	-	-	-	-	-
5	Trumon - Singkil	100%	-	-	-	-	-	-	-	-	-	-
6	Dawna Range	100%	-	-	-	-	-	-	-	-	-	-
7	Southern Tanintharyi*	100%	-	-	-	<1%	-	-	-	-	-	-
8	Southern Western Forest Complex*	100%	-	-	-	-	-	-	-	-	-	-
9	Mulayit Tuang*	100%	-	-	-	-	-	-	-	-	-	-
10	Western Forest Complex*	100%	-	-	-	-	-	-	-	-	-	-
11	Batang Gadis - Malampah Alahan Panjang	100%	-	-	-	-	-	-	-	-	-	-
12	Khao Luang	100%	-	-	-	-	-	-	-	-	-	-
13	Kerinci Seblat	96%	-	-	4%	-	-	-	-	-	-	-
14	Bukit Rimbang Baling	100%	-	-	-	-	-	-	-	-	-	-
15	Batang Hari	100%	-	-	-	-	-	-	-	-	-	-
16	Taman Negara - Hala-Bala*	100%	-	-	-	-	-	-	-	-	-	-
17	Thap Lan - Pang Sida	-	100%	-	-	-	-	-	-	-	-	-
18	North Bukit Balai Rejang Selatan	100%	-	-	-	-	-	-	-	-	-	-
19	Kerumutan	100%	-	-	-	<1%	-	-	-	-	-	-
20	Endau Rompin	100%	-	-	-	-	-	-	-	-	-	-

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TABLE 4 Continued

Lsid	TCL Name	Tropical & Sub-tropical Moist Broadleaf Forests	Tropical & Subtropical Dry Broadleaf Forests	Tropical & Subtropical Grasslands, Savannas & Shrublands	Tropical & Subtropical Coniferous Forests	Mangroves	Temperate Broadleaf & Mixed Forests	Temperate Conifer Forests	Flooded Grasslands & Savannas	Montane Grasslands & Shrublands	Boreal Forests/ Taiga	Deserts & Xeric Shrublands
21	South Bukit Balai Rejang Selatan	100%	-	-	-	-	-	-	-	-	-	-
22	Bukit Barisan Selatan	100%	-	-	-	-	-	-	-	-	-	-
23	Berbak - Sembilang	88%	-	-	-	11%	-	-	-	-	-	-
24	Southern Zhangguangcailing	-	-	-	-	-	100%	-	-	-	-	-
25	Lesser Khingan	-	-	-	-	-	97%	-	3%	-	-	-
26	Pri - amur	-	-	-	-	-	94%	<1%	6%	-	<1%	-
27	Laoyeling*	-	-	-	-	-	100%	-	<1%	-	-	-
28	West Wandashan	-	-	-	-	-	78%	-	22%	-	-	-
29	East Wandashan	-	-	-	-	-	45%	-	55%	-	-	-
30	Sikhote-Alin	-	-	-	-	-	97%	-	2%	-	1%	-
31	Sahyadri	100%	-	-	-	-	-	-	-	-	-	-
32	Radhanagari	100%	-	-	-	-	-	-	-	-	-	-
33	Western Ghats	84%	16%	-	-	-	-	-	-	-	-	-
34	Yawal	-	100%	-	-	-	-	-	-	-	-	-
35	Jawahar Sagar	-	100%	-	-	-	-	-	-	-	-	-
36	Sariska	-	100%	-	-	-	-	-	-	-	-	-
37	Ranthambore	-	100%	-	-	-	-	-	-	-	-	-
38	Anamalai-Parambikulam	88%	12%	-	-	-	-	-	-	-	-	-
39	Akola District	-	100%	-	-	-	-	-	-	-	-	-
40	Ratapani-Singhori	-	100%	-	-	-	-	-	-	-	-	-
41	Periyar - Megamala - Shendurney	96%	4%	-	-	-	-	-	-	-	-	-
42	Rajaji Minor	100%	-	-	-	-	-	-	-	-	-	-

(Continued)

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TABLE 4 Continued

Lsid	TCL Name	Tropical & Sub-tropical Moist Broadleaf Forests	Tropical & Subtropical Dry Broadleaf Forests	Tropical & Subtropical Grasslands, Savannas & Shrublands	Tropical & Subtropical Coniferous Forests	Mangroves	Temperate Broadleaf & Mixed Forests	Temperate Conifer Forests	Flooded Grasslands & Savannas	Montane Grasslands & Shrublands	Boreal Forests/ Taiga	Deserts & Xeric Shrublands
43	Terai Arc*	52%	-	16%	31%	-	0%	-	-	-	-	-
44	Ghatigaon	<1%	100%	-	-	-	-	-	-	-	-	-
45	Painganga	81%	19%	-	-	-	-	-	-	-	-	-
46	Eastern Dehgaon-Bamori Range	-	100%	-	-	-	-	-	-	-	-	-
47	Bor	-	100%	-	-	-	-	-	-	-	-	-
48	Nagarjunasagar	-	97%	-	-	-	-	-	-	-	-	3%
49	Sri Lankamalleswara	-	100%	-	-	-	-	-	-	-	-	-
50	Melghat	38%	62%	-	-	-	-	-	-	-	-	-
51	Andhari - Tadoba	<1%	100%	-	-	-	-	-	-	-	-	-
52	Sri Penusila Narasimha	-	22%	-	-	-	-	-	-	-	-	78%
53	Pilibhit	85%	-	15%	-	-	-	-	-	-	-	-
54	Bandhavgarh	4%	96%	-	-	-	-	-	-	-	-	-
55	Umaria District	-	100%	-	-	-	-	-	-	-	-	-
56	Panpatha	44%	56%	-	-	-	-	-	-	-	-	-
57	Panna West	7%	93%	-	-	-	-	-	-	-	-	-
58	Central Indian Landscape	79%	21%	-	-	-	-	-	-	-	-	-
59	Papikonda	100%	<1%	-	-	-	-	-	-	-	-	-
60	Satkosia Gorge	79%	21%	-	-	-	-	-	-	-	-	-
61	Palamau District	31%	69%	-	-	-	-	-	-	-	-	-
62	Simlipal	94%	6%	-	-	-	-	-	-	-	-	-
63	Sundarbans*	-	-	-	-	100%	-	-	-	-	-	-

* These TCLs are trans-national.

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surveys, including several, massive, country-wide surveys (Jhala et al., 2008; Jhala et al., 2011; Jhala et al., 2015; Jhala et al., 2018). The quality and precision of these surveys have improved over time as new methods have been implemented (Jhala et al., 2021), making it possible for the Indian government and people to understand where its tigers are and how their long-term survival can be encouraged. These results are also critical for range-wide assessments such as TCL 3.0.

Nepal's TCL area grew 21% from 2001 to 2020, especially after tigers were reported in the eastern part of the Terai Arc (Figure 5H; Lamichhane et al., 2018; Bista et al., 2021). Nepal's TCL area lies in one, long, inter-connected landscape, the Terai Arc, shared with India. The connection to Bhutan and the North Triangle TCL through Sikkim has been lost, though a few recent sightings (Ganguli-Lachungpa, 1998; Umariya et al., 2022) suggest there may be hope for future reestablishment in that high-altitude area.

Bhutan's tigers and tiger habitat are relatively well-protected compared to many parts of the range, with little overall change in landscape area over the last 20 years (Figure 5A). The apparent increase in TCL area from 2001 to 2020 is large at 274%, but that change reflects a relatively weak-observational base prior to the full country-wide survey in 2015 (Thinley and Curtis, 2015). Bhutan's TCL area subsequently slightly declined (-1.8%) and, as of 2020 stands at 26,762 km^2. Though not obvious because of the general connectivity of the habitat, the level of protection and the continuous cover has enabled tigers to reestablish in some previously vacated areas (Thinley et al., 2020).

Bangladesh's tigers primarily live in the Sundarbans mangrove forest shared with India (Jhala et al., 2016; Hossain et al., 2018). Improved survey results since 2006 showed a TCL area that year of 8,783 km^2 compared to 8308 km^2 in 2020 (a marginal decline of 5% since 2006 but an apparent increase of 130% since 2001 because of additional survey efforts; Figure 5B). Sea level rise affecting the mangrove forest habitat is a major concern for the long-term future of Bangladesh's tiger populations (Mukul et al., 2019), since they are extirpated from the northern part of the country. However, there may be some possibility of reestablishing tigers in the Chittagong Hills (Chakma, 2016; Creative Conservation Alliance, 2016), an area of habitat contiguous with the forests of western Myanmar.

3.2.2 Southeast Asia (Myanmar, Thailand, Malaysia, Indonesia, Vietnam, Cambodia, Laos)

The status of tigers in Southeast Asia has shifted from worrying to extremely concerning to dangerous. Three countries have lost tigers entirely over the last 20 years, and others have seen notable reductions in TCL area.

On the map, Myanmar is apparently in the best shape because large blocks of available habitat are revealed in structural habitat analysis, but the status of tigers in those landscapes is very poorly understood (Figure 5G; Rao et al., 2010; Ministry of Natural Resources and the Environment, 2020; Lwin et al., 2021). Civil disorder and strife have limited research access to many promising-looking areas over the last two decades. According to our analysis, Myanmar's TCLs have lost a minimum of one-fifth (22%) of their area since 2001. Some areas mapped as TCL might be better classified as Survey or Restoration Landscapes, though they technically meet the minimum definition of a TCL given how interconnected forested areas appear in satellite-based analysis. The large "Northern Triangle" TCL in the northern part of the country remains connected with tiger habitat in northeast India, eastern Bangladesh, southern China, and Bhutan. Together these areas comprise the largest TCL in the world, however, the majority of this TCL may be missing its tigers. The total population of tigers within Myanmar was estimated to be less than 50 individuals (Ministry of Natural Resources and the Environment, 2020).

Thailand's TCLs have lost 43% of their area since 2001 (Figure 5J). Relatively large blocks of habitat are present in the northern part of the country, where the status of tigers is unknown, but it seems unlikely that many, if any, tigers remain there. The status of such areas depends in part on what's happening across the border in Myanmar, which is poorly understood. Total effective potential habitat has declined 25% over the last 20 years, and connectivity has dropped (Suttidate et al., 2021). On the positive side, the few landscapes where tigers are found today, in the eastern part of the country (Ash et al., 2020; Sukmasuang et al., 2020) and especially in the Western Forest complex, are frequently and thoroughly surveyed, well-protected, and maybe providing a source of dispersing tigers (WCS Thailand, 2020; Phumanee et al., 2021).

Malaysia's TCLs have lost 29% of their area since 2001, and overall effective potential habitat is down 20% since 2001 (Figure 5F). Tiger numbers also appear to have dropped below 200 individuals (Ten et al., 2021). A gap in survey coverage between 2009 – 2015 caused an apparent precipitous 79% drop in TCL area between 2001 – 2011, but tigers probably persisted throughout this period, just in increasingly fragmented habitats. The largest TCL in 2020 is the Taman Negara – Hala Bala TCL, at 31,296 km^2, which shares a small amount of habitat in extreme southern Thailand and is comprised of several large forest blocks at risk of further fragmentation by development in the north-central part of the mainland (Adyla et al., 2016; Rayan and Linkie, 2016; Ghazali et al., 2019; Kawanishi, 2020). The Endau Rompin TCL is an island of habitat in the south, divided by major highways from areas to the north (Gumal et al., 2014). Malaysia has no Restoration Landscapes.

Indonesia's TCLs on Sumatra have declined -43% in area from 2001 – 2020, and overall effective potential habitat is down 40% over that same period (Figure 5E). Like Malaysia, there are no Restoration Landscapes as of 2020-01-01 in Indonesia. Tigers lived on Bali into the 1940s and Java into the 1980s (Xue et al., 2015), but no low human footprint forest blocks appear large enough to support even five tigers on those islands. On Sumatra, the Leuser Ecosystem in the north remains the largest remaining TCL, at 27,703 km^2, though human-wildlife conflict remains a problem (Lubis et al., 2020). Several smaller TCLs persist in the western mountains, especially in and around Kerinci Seblat National Park, and a combination of TCLs and Survey Landscapes in the southwest around Bukit Barisan Selatan National Park (Pusparini et al., 2018). The relative number and status of TCL and Survey Landscapes across years vary because of gaps in the data, making it difficult to draw strong conclusions about trends from our analysis. Other work suggests that tiger population trends are mainly downward for tigers through a combination of poaching, human reprisals after conflict, loss of habitat connectivity, and deforestation (Sunarto et al., 2012; Risdianto et al., 2016; Luskin et al., 2017; Poor et al., 2019). Limitations on data availability meant we had to lean heavily into newspaper accounts of human-wildlife conflict (Marthy, 2021).

As noted above, Vietnam, Cambodia, and Laos all lost their tigers during the last 20 years (Gray et al., 2017; Rasphone et al., 2019; Vietnam News Agency, 2022). In these countries, total effective potential habitat has declined 33%, 35%, and 21%, respectively (see Figures 5M, R, W) Although the pattern may be correlative, not casual, loss of tigers seems to be accompanied by increased rates of loss of effective potential habitat. In Cambodia, tigers were extirpated around 2008. From 2002 – 2007, the annual rate of loss of effective potential habitat in Cambodia was, on average, 927 km^2 per year. From 2008 – 2020, the rate of loss was 1,638 km^2 per year, or an increase of 77% since extirpation. In Laos, tigers seem to have been extirpated around 2014. From 2002 – 2013, the annual rate of loss of effective potential habitat in Laos was on average 422 km^2 per year. From 2014 – 2020 the average annual rate of loss was 2,114 km^2, or a quadrupling of the rate of loss of tiger habitat (401% increase in the annual rate of loss post-extirpation). In Vietnam, tigers seem to have been extirpated around 2004. From 2002 – 2004, the annual rate of loss of effective potential habitat in Vietnam was, on average, 218 km^2 per year. From 2005 – 2020, the annual rate of loss was 1,112 km^2, or a quadrupling of the rate of loss of tiger habitat (410% increase in annual rate of loss post-extirpation). Although only a few data points, these results suggest that losing tigers is a leading indicator of deforestation.

3.3.3 Northeast Asia (China, Russia, North Korea, South Korea)

Eastern Russia remains a critical area for tiger conservation, both because of the size of the area and their ecological distinctiveness as a mixed temperate forest on the margins of the boreal (Seryodkin et al., 2017; Dou et al., 2019; Qi et al., 2021). Following India, Russia is the country with the most TCL area in the world (195,819 km^2), 19% of the world's total (Figure 5I). Russia's TCL area has grown by 53,918 km^2 (40%) since 2001, especially after the reintroduction of tigers in the Pri-Amur region in 2014 (Ning et al., 2019; Rozhnov et al., 2021). This area represents the only major expansion of tigers into a new TCL, as opposed to the fragmentation of existing TCLs, over the last 20 years.

China has more effective potential habitat than any country on Earth, but most of that habitat lacks tigers (76% of its effective potential habitat is in Restoration Landscapes or Restoration Fragments; see Figure 5C). Over the last twenty years, the so-called South China tiger has been extirpated (Zhang et al., 2019) and its former habitat severely fragmented (Qin et al., 2015), though cumulatively much habitat still exists. Over the last two decades, China has seen some expansion of TCL area in Northeast China, which is part of larger transboundary areas with Russia (McLaughlin, 2016; Wang et al., 2016; Qi et al., 2021). A smaller area of occupied tiger habitat also exists in southern China, part of the larger Northern Triangle TCL, in southern Tibet (Wang et al., 2019). Together Chinese TCLs in 2020 stood at 100,368 km^2, a remarkable increase of +77% over 2001 levels, representing significant conservation investment (Zhou et al., 2022). In 2020, these areas represent 10% of the world's total.

Tigers persisted on the Korean peninsula until the 1950s (Seeley and Skabelund, 2015). The best remaining prospects are fragmented habitats in North Korea on the border with China and Russia, part of a transboundary TCL (Figure 5S; Noone, 2018). Very little habitat with low human footprint persists in South Korea now (Figure 5U).

3.2.4 Central Asia

Central Asia has no tigers currently, but three range states still have effective potential tiger habitat of landscape-scale dimensions: Georgia (Figure 5N), Kazakhstan (Figure 5P), and Pakistan (Figure 5T). The best possibilities seem to exist in Kazakhstan in the river deltas adjacent to Lake Balkhash, an area currently being investigated for the possibility of reintroduction (Driscoll et al., 2012; WWF Russia, 2022). Restoration fragments remain in Iran (Figure 5O), Kyrgyzstan (Figure 5Q), and Turkey (Figure 5V), but are dwindling in number and area rapidly. Similar situations attain in Armenia (Figure 5K) and Azerbaijan (Figure 5L), though in the latter case, tigers were still extant into the 1970s (Faizolahi, 2016). All tiger habitat, as well as tigers themselves, have been lost in Afghanistan, Turkmenistan, Tajikistan, Uzbekistan, and arid portions of western China. Historically there were small amounts of habitat within the modern boundaries of Syria and Iraq, the only memory of which lurks in the species' English name, associated with former habitat along the Tigris River (Liddell and Scott, 2007).

3.2.5 Tiger tolerance for human activity

Finally, we detected important variations in the tolerance tigers have to human activity in different parts of the range (Figure S1). In South Asia, the social tolerance threshold was 18 on the human footprint's 0 – 64 scale; in Southeast Asia, 8; and in Northeast Asia, 5. Differences in conservation efforts, infrastructure development, human-wildlife conflict, and culture seem to underlie these results (Carter et al., 2020; Jhala et al., 2021; Macdonald et al., 2022; Mukhacheva et al., 2022), but these results point to issues where more trans-national research is warranted.

4 Discussion

4.1 The global state of wild tiger habitat

For tigers living in the wild, the news is not all bad. Encouragingly, this iconic species no longer teeters on the brink of extinction; an estimated 4,485 (3,726–5,578) tigers (Goodrich et al., 2022) live in the wild across ten countries in approximately a million square kilometers of habitat in the 63 Tiger Conservation Landscapes mapped here (Table 2). Globally the loss of structural habitat has been largely arrested, albeit at historically low overall amounts (~40% of the likely resident indigenous range) (Figure 4A). Similarly, effective potential habitat now stands at only 16% of the indigenous range. Most encouragingly, metrics of occupied tiger habitat (as measured by TCL area) have declined only 11% in a two-decade period when Asia's population grew 14% to 2.36 billion people, and the East Asian & Pacific economy grew 248% to 27.13 trillion US dollars (World Bank, 2023). Observed TCL areas fluctuated year-by-year (Figure 4B), largely as a function of the available knowledge base. Improved information may show less loss in the future. Taken together, our results suggest that tigers may have reached the bottom of the species recovery curve (Moorcroft, 2017). Tiger habitat is less tiger-filled and more fragmented than at any time in the last 200 years, but perhaps now the world is poised for a recovery in tiger populations not seen in generations.

This relatively optimistic reading of the trends at the global scale (Figure 4) should not disguise the fact that tigers continue to lose habitat in many places, with different trajectories of loss in different nation-states (Figure 5). The mechanisms of habitat loss at the grossest level are loss of vegetation (i.e. structural habitat) and expansion of human encroachment (i.e. reducing effective potential habitat). The expansion of linear infrastructure remains a concern for tiger conservation (Carter et al., 2020; Nayak et al., 2020). Concomitant declines in the prey base are probably also important but were not estimated here. (Modelling prey remains an important research topic.) During the last 20 years, tigers have become extinct in three Southeast Asian countries (Cambodia, Laos, and Vietnam) and across a large part of southeastern China. Tigers remain under pressure everywhere, which is especially acute in Southeast Asia. The tiger's situation in vast parts of Myanmar remains unclear and is probably poor; ongoing conflict limits our ability to understand what is happening below the canopy. Human-wildlife conflict is frequent in Sumatra, leading often to harsh reprisals (Figel et al., 2021; Widodo et al., 2022; Patana et al., 2023). Malaysia's tiger populations may have stabilized but at low levels, but how low remains unclear until the results of the recently finished country-level survey are released (Ding, 2022). Human influence appears much more harmful for tigers in Southeast Asia than in South Asia (Figure S1). Though important questions about the situation remain, the evidence presented here suggests that without stepped-up conservation efforts, further losses are likely. Meanwhile, TCLs appear to be expanding in India, Nepal, Bhutan, northern China, and southeastern Russia.

Survey Landscapes have declined dramatically in the last 20 years (Figure 4B). Greatly expanded survey efforts, largely associated with increased use of remotely triggered camera traps (Karanth et al., 2004), have greatly increased scientific knowledge, allowing us to determine which areas with suitable habitat no longer have tigers (hence becoming Restoration Landscapes) or do still retain tigers, in which case they were incorporated as TCLs. The decline in area of Survey Landscapes represents our collectively improved knowledge of tiger distributions: we now know much more, even though there are fewer places where tigers persist. But because scientists often focus on repeated camera trap monitoring to detect trends in the best-known protected areas, large swaths of connected landscapes remain unsurveyed: typically, less than 50% of TCL area has confirmed sightings from the last five years. Therefore, even though we can confirm that a TCL retains tigers, in few cases, can we clearly understand what proportion of a TCL holds tigers and which areas are still in need of conservation efforts to allow populations to recover. These issues could use more attention in future iterations of the model.

TCL 3.0 demonstrates that there is still abundant effective potential habitat in Restoration Landscapes; these areas just lack tigers (Gray et al., 2023). If these extant habitats could be made suitable again in terms of prey base and were tigers to re-establish *via* natural dispersal or through active reintroduction efforts, we could increase the land base for tigers by 50%. Two conservation objectives – ensuring tigers are distributed at carrying capacity across the entirety of TCLs, and that they are recovered across Restoration Landscapes, could more than double, perhaps even triple, the number of free-living tigers on Earth (Lynam, 2010; Wikramanayake et al., 2011; Harihar et al., 2018). Given the tiger's resilience and changes in Asia's social and political landscape (Sanderson et al., 2019), this long-sought goal could be met within a human generation, if not sooner.

Models are only as useful as the data put into them. This model depends on *in situ* biological observations: surveys, with dates and locations, measures of effort, and verifiable evidence of tiger occurrence. The system doesn't function without this information. Discovering a previously unknown or recently established tiger population is the easiest way to turn a landscape from green (Survey) to orange (TCL). On-going, extensive surveys in existing TCLs and Survey Landscapes are needed continuously to maintain the system and make its results useful.

Restoration Landscapes provide a remarkable, and until now, mostly unrealized opportunity to increase the area of occupied tiger range. Our analyses suggest that suitable habitat without tigers may be more susceptible to degradation and fragmentation than tiger-inhabited landscapes, as demonstrated by our analysis of what happened to former TCLs in Vietnam, Cambodia and Laos after extirpation. These findings highlight the urgency to halt deforestation, increase the prey base, and provide connection to TCLs to encourage dispersal. In some cases, where connectivity to an existent tiger population is not possible (e.g. the Balkash delta of Kazakhstan. some forest blocks in Thailand), active reintroduction efforts will be required. The Kazakhstan efforts seem particularly important because, were efforts to succeed, those tigers would be the first to live in Central Asia in more than a half-century.

Finally, there is – over some very long time scale – the issue of recovering some of the 60% of tiger indigenous range that has been lost, by redressing the conversion of former tiger structural habitat to other land use classes. Socioeconomic change in Asia, which has nothing per se to do with tigers, may provide enormous benefits to recovering tiger habitat (Sanderson et al., 2018; Sanderson et al., 2019). Rural-to-urban migration, urbanization, poverty reduction, and improved education may eventually make much more tiger habitat available, if (and only if) tigers remain in the wild and are capable of re-establishing in these areas. This is largely a civilizational project, to be enacted not only passively but proactively as national governments, civil society, and the global community pivot toward the realization that we are not separate from the Earth's nature, but part of it, dependent as the tiger is, on the value of natural ecosystems for providing water, food and fiber, and a moderate climate. The United Nations Sustainable Development Goals and the recent "30 by 30" agreement adopted at the Convention on Biological Diversity CoP15 in Montreal (Einhorn, 2022), represent positive steps, which, if implemented well, can serve tigers, people, and the rest of nature.

4.2 The state of tiger habitat mapping

Habitat maps and metrics are essential documents to plan species conservation efforts, reverse defaunation, and expand environmental protection amid the paired biodiversity and climate crises. National leaders must understand trends to make informed policy decisions and fulfil their international obligations (Table 3). State and provincial officials need tabulations tailored to their local jurisdictions, with attention to protected areas, human-wildlife conflict, sustainable use, and connectivity to adjacent jurisdictions (see act-green.org). Non-governmental organizations and donors may be interested in trends of habitat availability range-wide (Table 2) and in different ecologically defined areas (e.g. ecoregions, biomes), to inform ecological representation (Table 4), or within collections of countries where they work (Table 3). "On-the-ground", landscape managers are most interested in the fine but pertinent details: Where is my landscape changing? How much habitat is available right now? Does the model match expectations or not? How does it relate to comparable areas?

Remarkably, existing technology can go a long way to serving all of these needs simultaneously. As described here, we have constructed not a map of tiger-relevant landscapes, but a system for mapping them. That system depends on clearly-defined inputs (an indigenous range map, species observations, a notion of what land cover are suitable for the species, and the human footprint) and delivers clear-defined outputs suitable for planning tiger conservation efforts at landscape, national, and range-wide scales. Because it is a mapping of the system, updates are possible by "simply" changing the inputs and re-running the process. Because it is a system when new inputs become available, for example, for 2021 or 2036, we can produce new, comparable maps and statistical outputs to measure progress.

One implication of a "mapping system" versus "a map" is that there is no one final map. Each new version is an improvement on the previous attempt, dependent on improvements in the accuracy and timeliness of the inputs, where within a few hours, a new observation can literally change the map for tigers. Versioning of results and linking back clearly to the inputs become even more important, even as we try to draw declarative statements about the status of tigers and trends in their habitat. This dynamic assessment system lies at the core of any adaptive management strategy.

A real constraint on improving understanding rests on the sharing of species observations. Conservationists and biologists have made huge gains in survey methods, repetition of tiger surveys, and documenting distribution in scientific papers and reports. But will people share the raw data they so laboriously collect? In this instance, despite a promising start with some commitments, enormous efforts and huge amounts of time were required to obtain the *in situ* biological observations required. After relentless emailing and Zoom calls failed to produce enough information, we resorted to a systematic literature search to re-capture and re-digitize information that sits on laptops across Asia and elsewhere. To develop a twenty-year analytical synthesis, we had to read every paper and report we could find published over the last 25 years and schedule dozens of follow-up conversations with individual researchers and research teams to cajole them into what should be the regular scholarly practice of sharing data for conservation, for example, using public Internet fora such as the Global Biodiversity Information Facility (Edwards, 2004; Ivanova and Shashkov, 2021) or Wildlife Insights (Ahumada et al., 2020). Many eventually complied and shared, including most of the co-authors of this paper (See also Table S1). One would expect scientific publishing to be one mechanism for better data sharing (Christensen et al., 2019). However, we found that the wide variety of ways that data are published in scientific papers and uneven review standards across journals ensure plenty of scope for researchers to dull the precision of the original data, hide or not report important details, and obfuscate the observations, even as authors claim to illuminate conservation issues. Not only are such abuses of the scientific literature process annoying, they ultimately delay decision-making, which is the ostensible reason for most studies in the first place.

Were such difficulties to be overcome, whether through ongoing, brute force literature searches or by better data sharing, then systems such as TCL 3.0 could help countries report on their commitments to the Sustainable Development Goal (SDG) agenda (United Nations Department of Economic and Social Affairs, 2022) and the Global Biodiversity Framework under the Convention for Biological Diversity (CBD Secretariat, 2022). Among other goals, SDG signatory countries have committed to Goal 15, Life on Land, which enjoins nations to protect, restore, and promote the sustainable use of terrestrial ecosystems, sustainably manage forests, combat desertification, and halt and reverse land degradation and halt biodiversity loss. TCL 3.0 enables countries to integrate ecosystem and biodiversity values into national and local planning processes, to understand how tiger conservation landscapes are protected and overlap with key biodiversity areas, and to halt forests loss since tigers are a species of forests in most parts of the range. Similarly, TCL 3.0 enables countries to measure the ecological integrity implied by and reinforced through long-lasting tiger populations.

Finally, we note the cultural aspects of technological innovations such as TCL 3.0 among conservationists. This project has depended on collaboration from across the tiger range, between governments and non-governmental organizations, and among the NGO sectors. Although tiger habitat has been much reduced, tigers live in too many places for any one actor or organization to successfully conserve them on its own. Rather technological tools such as this one, which depend on collaboration, also provide a framework to make the necessary collaborations desirable and rewarding. To this end, we have worked hard to link these results to other assessments, including the recently completed IUCN Red List assessment (Goodrich et al., 2022) and the ongoing IUCN Green Status assessment (Hunter et al., in prep.) for tigers. One important collateral product of TCL 3.0, which was not achieved through either of the previous versions, was a new range-wide vision for tigers written by and jointly endorsed by a coalition of conservation organizations (Coalition for Securing a Viable Future for the Tiger, 2022). The success metrics specifically prescribed under this shared vision ensure the continued application of the TCL 3.0 system into the future, which will reinforce the kinds of collaborations and mutual calls to action that tigers, and other wildlife, so richly deserve.

5 Conclusions

What have we learned about tiger conservation over the last two decades? Conservation works when we choose to make it so. Species, even dangerous ones such as the tiger, can thrive on the 21st century Earth, if well-conserved. Conservation is straightforward. Don't cut down their habitat. Don't stalk them, harass them, or kill them or their prey. Control poaching and extinguish the illegal trade in tiger bones and parts. Prevent conflicts with people and livestock wherever possible, and where and when not, then mitigate losses to forestall retaliation. Tigers need and have a right to move, pass over or under highways, find prey and mates, and raise their families undisturbed; therefore, connections need to be established between landscapes where tigers can hunt in suitable vegetation and roam free from persecution. Where possible, restore native vegetation that supports native prey and, therefore, set the stage for the recovery of tigers. Deploying these strategies has enabled some countries to stabilize, even grow, tiger habitats, as we show here, notably in China, Russia, India, Bhutan, and Nepal. Monitoring progress at a pace relevant to decision-making is key. If these countries can do it, so can others, especially if the world community bands together to support tiger range states with funds, encouragement, science, and a bit of technological magic.

Data availability statement

The open-source code for this project is available at https://github.com/SpeciesConservationLandscapes. Summaries of the results, Earth Engine assets, and shapefiles of the landscape data for each year are available at act-green.org. All other data in the study are available on request from the corresponding author.

Author contributions

ES, KF, and DM conceived the project and this paper. PP analyzed the vegetation height data. ES, DM, KF, JS, and CY developed the methods. KF engineered the task architecture. KF, NR, JS, CY, and DuS wrote the computer code. SR, ES, DM, and SC reached out to governments. PC, AD, DM, AH, TG, JG, ML, WM, AP, AR, EF, UB, CB-W and HR contributed observations, among others (see Table S1). CC, LR, JM, and ES conducted the literature survey and formatted the data. ES, LR, and DeS analyzed the landscape results. ES, DM, AH, and LR drafted the manuscript. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The author DuS is employed by company SparkGeo.

The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fcosc.2023.1191280/full#supplementary-material

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