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RESEARCH ARTICLE OPEN ACCESS

The Indigenous Range of the Tiger (*Panthera tigris*)

Eric W. Sanderson^{1,2}  | Dale G. Miquelle³ | Abishek Harihar⁴  | Urs Breitenmoser⁵ | Christine Breitenmoser-Würsten⁵ | David M. Cooper⁶ | Kaveh Faziolahi⁷ | Kim Fisher¹ | John Goodrich⁴ | Thomas N. E. Gray⁸ | Aili Kang⁹ | Andrew C. Kitchener^{6,10} | Douglas C. MacMillan¹¹ | Stephane Ostrowski¹² | Lucinda Royte² | Kanchan Thapa¹³ | Nobuyuki Yamaguchi¹⁴

¹Global Conservation Programs, Wildlife Conservation Society, Bronx, New York, USA | ²New York Botanical Garden, Bronx, New York, USA | ³Russia Program, Wildlife Conservation Society, Bronx, New York, USA | ⁴Panthera, New York, USA | ⁵IUCN SSC Cat Specialist Group, c/o Foundation KOR, Ittigen, Switzerland | ⁶Department of Natural Sciences, National Museums Scotland, Edinburgh, UK | ⁷Freelance Researcher, Tehran, Iran | ⁸WWF Tigers Alive Initiative, WWF Cambodia, Phnom Penh, Cambodia | ⁹China Program, Wildlife Conservation Society, Beijing, China | ¹⁰School of Geosciences, University of Edinburgh, Edinburgh, UK | ¹¹Department of Conservation Economics, University of Kent, Canterbury, Kent, UK | ¹²Temperate Asia Program, Wildlife Conservation Society, Bronx, New York, USA | ¹³WWF-Nepal, Kathmandu, Nepal | ¹⁴Institute of Tropical Biodiversity and Sustainable Development, Universiti Malaysia Terengganu, Kuala Nerus, Terengganu, Malaysia

Correspondence: Abishek Harihar (aharihar@panthera.org)

Received: 14 January 2023 | **Revised:** 24 October 2024 | **Accepted:** 31 October 2024

Editor: Susan Jarvis

Funding: This study was supported by National Aeronautics and Space Administration (NASA Grant Number 80NSSC19K0201).

Keywords: carnivore | historical range | IUCN Green Status of Species | IUCN Red List of Species | mapping | wild felid

ABSTRACT

Aim: Indigenous range maps are fundamental documents in biogeography, phylogeny and conservation. We define the indigenous range of a species as ecoregions (or parts of ecoregions) where the species was likely found before humans became a major factor shaping the species' distribution, beginning at a time when the geographical alignment of the continents and the prevailing climate are (or at least were) roughly consistent with current conditions. We developed a structured, generally applicable method to map a species' indigenous range and applied this process to the tiger (*Panthera tigris*).

Location: Terrestrial Asia.

Methods: To guide our mapping, we synthesised a database of over 70,000 tiger observations with dates and locations. We developed a structured Delphi process to assign categories of indigenous range to ecoregions aided by a climate niche model. We analysed tiger habitat change at the ecoregional scale using the anthropogenically modified biomes ('Anthrome 12K') dataset to suggest dates of first significant human impact. Finally, we estimated extirpation dates for ecoregions where tigers have been extirpated.

Results: We found the tiger once occupied a likely indigenous resident range of approximately 11.5 million km², crossing 116 ecoregions. We also mapped an additional c. 11.7 million km² of exploratory range and 1.2 million km² of possible resident range. Collectively these areas overlap with 36 modern countries. Significant human disruption of the species' habitat seems to have begun over 6000 years ago in some areas, but in other regions has yet to materialise. In few arid ecoregions, human activities appear to have modestly increased habitat availability in the past, yet overall tigers have lost between 90% and 95% of their indigenous range over the last 8500 years.

Main Conclusions: We define the 'indigenous range' of a species, develop a replicable biogeographical procedure, apply the procedure to the tiger and discuss transferability to other species.

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1 | Introduction

A place belongs forever to whoever claims it hardest, remembers it most obsessively, wrenches it from itself, shapes it, renders it, loves it so radically that he remakes it in his own image.

Joan Didion (Didion 1979).

The idea of indigeneity is indigenous to biogeography. The concept is literally embedded in the discipline's name: 'bio', meaning life, 'geo' meaning Earth, or more generally place, and 'graph' in the sense of a description, or mapping, of the relationship of an organism to a place. To be 'indigenous' means to originate in a locality, such that species occurs there naturally (i.e., without human intervention). Hence, an indigenous range is the map of where a species occurred before major human impacts from a period with a roughly contemporaneous arrangement of the continents and broadly similar climate as today (Sanderson 2019; Stephenson et al. 2019; Grace et al. 2019).

Mapping the indigenous range of a species is fundamental to its biogeography, phylogeny and conservation (Wiens and Donoghue 2004). The indigenous range enables a biogeographer to operationally define other concepts important to the diversity and distribution of organisms, including: loss (Beyer and Manica 2020; Wolf and Ripple 2017; Yackulic, Sanderson, and Uriarte 2011) or expansion of range (Corlett 2016; Fener et al. 2005); extirpation, extinction and recovery (Sanmartín 2012; Tingley and Beissinger 2009); and species status as native (i.e., autochthonous) or introduced (i.e., allochthonous) (Richardson et al. 2000; Webber and Scott 2012).

Implicit in the definition of indigenous range are three interlocking claims. First, such maps suggest that the organism evolved in close association with certain climatic and landscape conditions, and therefore has been shaped by them through natural selection (Thomas 2010; Kirkpatrick and Barton 1997). Second, because of this evolutionary history, the organism depends on the ecological factors of the place in specific and important ways (Graham and Hijmans 2006; Kearney and Porter 2009). Third, because of the organism's evolutionary legacy and ecological requirements, conservation of a species should be based, at least in part, on its indigenous geography (Grace et al. 2019).

This third claim links a biogeographic exercise to the practicalities of everyday conservation (Alagona, Sandlos, and Wiersma 2012). Given the widespread defaunation of modern times (Dirzo et al. 2014), we think one goal of conservation is to maintain the indigenous range of a species by alleviating anthropogenic threats (Sanderson et al. 2002; Redford et al. 2011; Akçakaya et al. 2018). Analogously, if a species has been extirpated from an area because of human activities, we believe it is the role of conservationists to restore or facilitate the return of the organism to its indigenous range where safe and feasible (Sanderson et al. 2021; Hendricks et al. 2016; Donlan et al. 2006; Hayward and Somers 2009).

Biogeographers map the species' historical range by compiling observations through time and relating them either qualitatively

or quantitatively to landscape features (Sanmartín 2012; Wiens and Donoghue 2004; Katinas, Posadas, and Crisci 2003). The details of mapping vary by species and researcher, yet all include some set of trusted observations with localities that are extrapolated using a repeatable method to range maps. Extrapolations can be parsed by historical period to obtain different maps over time, and thus obtain metrics of change (Clavero et al. 2022; Loveridge et al. 2022). In more recent times, extrapolations are often supported by use of statistical algorithms to compute species distribution models that employ spatial covariates such as climate, land cover type, other species, and human impacts (Graham and Hijmans 2006; Kearney and Porter 2009). IUCN mapping guidelines for Red List assessments currently suggest a combined approach, asking the geographer to collect species locality information—points or polygons—and then mapping a species' 'extent of occurrence' (EOO) using minimum convex hull techniques (IUCN 2018; Joppa 2015). While having the virtue of ease of use for a wide variety of species, convex hulls are sensitive to outlying points and provide little insight into aspects of a species' relationship to its habitat, so are less useful for biogeographic studies.

Depending on the life history of the species in question, different categories of 'indigenous range' can be recognised: areas of year-round residence, areas of exploration or dispersal ('areas of vagrancy'), breeding range, migratory range, wintering range and so forth. These classifications help mitigate a longstanding issue of a species not respecting its mapped boundaries. In fact, species are constantly testing their distributions, seeking to expand their range (Lubina and Levin 1988; Robertson et al. 2009). Especially in a time of global change, we need mapping techniques that explicitly allow for uncertainty and flexibility with respect to past, present, and future distribution. There is no one 'historical' map of a species, but many such maps (Jackson, Alexander, and Sala 2011). Such time series have relevance to many domains, most especially conservation (Akçakaya et al. 2018) and restoration (Nogué et al. 2022), where the uses of historical baselines remains a hotly debated topic (Sanderson 2019; Rodrigues et al. 2019; Alagona, Sandlos, and Wiersma 2012; Bjorkman and Vellend 2010).

Here we propose a pragmatic, ecoregion-based method (Figure 1) for defining the indigenous range of a particular wide-ranging species, the tiger (*Panthera tigris*). The tiger challenges and illuminates the process of indigenous range mapping. Historically the tiger had a vast distribution in Asia, from the Black Sea to the Pacific Ocean, and from the boreal forest in Siberia to the tropical moist forests of Bali (Mazák 1996), yet as of the early 21st century, the tiger had been extirpated from an estimated 93% of its historical range (Dinerstein et al. 2007). Previous historical range maps for the tiger, notably the landmark efforts of Vratislav Mazák (Mazák 1968, 1981, 1996), advanced the state of knowledge in the late 20th century, using time-tested, scholastic techniques. Mazák's maps, drawn at coarse scales and without the benefits of modern computational geography, have nevertheless been the 'gold standard' biogeographic reference for the tiger for a generation, repeated with minor modifications in later publications (Nowell and Jackson 1998; Sanderson et al. 2006; Dinerstein et al. 2007). Because several important new syntheses of distribution information have been published over the last 25 years (Kang et al. 2010; Cooper et al. 2016; Faizolah 2016;

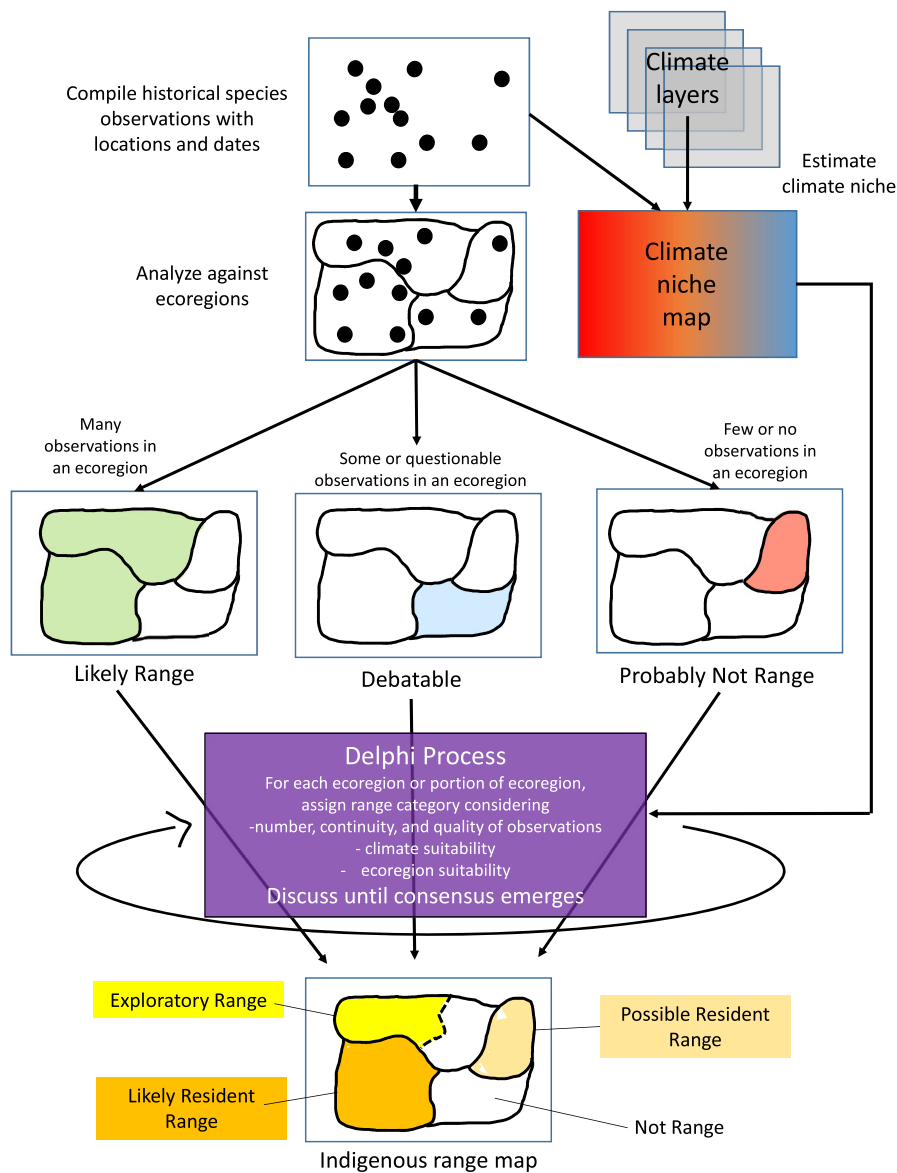


FIGURE 1 | Schematic diagram of the indigenous range mapping process for the tiger (*Panthera tigris*).

Chestin et al. 2017), and because the conservation landscape for tigers appears to be changing again (Goodrich et al. 2022; Sanderson et al. 2023), we embarked on this latest effort to understand the indigenous range of this important and emblematic species. We hope that the methods developed here might be applied to other species in the future and consider some critical issues with respect to wider application.

2 | Methods

2.1 | Definition of Indigenous Range

Following Sanderson (2019), we define the indigenous range of a species as ecoregions (or parts of ecoregions) ‘where the species was likely found before human beings became a major factor shaping the species’ distribution ... at a time when the geographic alignment of the continents and the prevailing climate are (or at least were) roughly consistent with current conditions’. We allow the time of ‘first significant impact by humans’ to vary

by ecoregion. In this study, we focused on the last 8500 years, after the Holocene climate of Asia had settled into current patterns (minus recent anthropogenic changes; see Duncan, Boyer, and Blackburn 2013; Earl of Cranbrook 2010) and sea levels rose to approximately to their modern positions (Meltzner et al. 2017; Meijaard 2003; Woodruff 2010).

Ecoregions are defined as ‘relatively large units of land containing a distinct assemblage of natural communities and species, with boundaries that approximate the original extent of natural communities prior to major land-use change’ (Olson et al. 2001). For purposes of this study, we deployed terrestrial ecoregions mapped by Dinerstein et al. (2017), which are slightly edited from Olson et al. (2001).

We recognised three categories of range in our assessment:

Likely resident range = ecoregions with breeding population(s), as evidenced by females, cubs, or continued tiger presence over multiple generations (30 years or more); where the range

category assignment is well supported by the available evidence and experts concur.

Possible resident range = ecoregions where the residence is possible but important questions remain and experts may not concur.

Exploratory range = ecoregions occasionally used by dispersing male tigers or where tiger populations persisted for only short periods of time.

A schematic diagram of our mapping process is shown in Figure 1.

2.2 | Compiling Species Observations

The fundamental data for mapping species range are observations, that is, dates and locations where free-living individuals have been observed reliably by people (Figure 2a,b). We collected existing compilations of tiger observations, some of which were themselves collections of other observations. For example, Cooper et al. (2016) combined observations from Kitchener and Dugmore (2000), Yamaguchi et al. (2013) and Walston et al. (2010). Kitchener and Dugmore (2000) in turn digitised locations compiled by Mazák (1996). In a series of publications (Mazák 1968, 1983, 1996), Vratislav Mazák worked extensively through the European language literature, but unfortunately for our purposes, did not document essential connections between source, date and place name. To provide dates and place names to the Mazák (1996) data, we worked back through his most important sources, notably Heptner and Sludskii (1992), Mazák (1968), Sody (1949), Brongersma (1935), Hunter et al. (1908), Aitchison (1889), Hunter (1881), and Brandt (1856). We added additional summaries of historical data subsequent to Mazák (1996) by Duckworth and Hedges (1998), Meijaard (1999), Lynam (2003), Habibi (2004), Khan (2004), Kang et al. (2010), Barnard and Emmanuel (2014), Faizolahi (2016) and Chestin et al. (2017). To minimise duplication, where possible we matched observations by location and date and recorded cross-references.

We also included a small number of fossil localities on islands near the tiger's continental range (Taiwan, Japan, Borneo, Sri Lanka, Palawan), where tigers may have lived in the mid- to late Pleistocene or early Holocene times (Hasegawa 1979; Hasegawa et al. 1988; Meijaard 2003; Manamendra-Arachchi et al. 2005; Piper et al. 2008; Chi et al. 2021; Sherani 2021).

The list of sources with observations prior to 1995 C.E. is provided in Appendix S1. Sources from 1996 to 2020 are listed in Appendix S2. Ecoregion maps and species observations were analysed in ArcGIS, version 10.7 (ESRI 2021).

2.3 | Climate Niche Map

We followed Cooper et al. (2016) in defining a climate niche map for the tiger using the observations described above and a series of climate layers (Figure 2c). WorldClim provides 19 current bioclimatic layers (1970–2000) at 2.5 arc minutes spatial resolution

(Fick and Hijmans 2017). To map the current climatic niche of the species, we used observation spanning from 1970 to 2000, to match with the available climatic data. We minimised sampling bias by implementing the spThin R package (Aiello-Lammens et al. 2015) with a thinning radius of 10 km (Boria et al. 2014). To eliminate highly correlated variables, we used a stepwise procedure to calculate variance inflation factors in the USDM R package (Naimi et al. 2014). Multicollinearity was considered when $VIF > 10$. We used the Wallace R package (Kass et al. 2018) to implement Maxent models (Phillips 2021), and the ENMeval R package (Muscarella et al. 2014) for evaluating models. By employing a spatial partitioning scheme (random k-fold), we could 'fine-tune' two parameters (regularisation multipliers (RM) and feature classes (FC)) that could influence the complexity and predictability of the model (Muscarella et al. 2014). We ran all the models with 20 replicates with cross-validation, 10,000 background points, no clamping, and extrapolation. The background points were sampled from a spatial extent defined by a minimum bounding box around all occurrence records buffered by 5°. Using all FCs (Linear (L), Quadratic (Q), Hinge (H) and Product (P)), we adjusted the RM by steps of 0.5 between 1 and 5 to allow for model complexity and tuning (Morales, Fernández, and Baca-González 2017). The predictor variable coefficients were progressively reduced until they reached 0, eliminating them from the model. Only variables that contributed most to the prediction were retained. Following Warren and Seifert (2011), the best model was selected based on the lowest corrected Akaike information criterion (AICc) and their average area under the curve (avg.test.AUC). In total, 45 different models were constructed, run and tested.

2.4 | Delphi Process

We developed a structured Delphi process to bring together qualitative and quantitative information using expert judgement (MacMillan and Marshall 2006; Figure 1). We overlaid the synthesised historical point observations with the terrestrial ecoregion maps using ArcGIS 10.7 (ESRI 2021). Examining the summaries of observation by ecoregion enabled the authors to identify three broad divisions among the 394 terrestrial ecoregions of the Australasian, Indo-Malayan, and Palearctic realms: (1) those that were clearly tiger range, because of an abundance of historical observations (defined arbitrarily as more than 10, but running into the hundreds for some ecoregions); (2) those that were clearly not tiger range, because we had no observations or few, potentially spurious, ones; and (3) those ecoregions with a few observations, typically less than 10, where the significance of the observations was unclear or debatable. Twenty experts focused their efforts on this third group of 97 ecoregions with uncertain meaning. Independently, each expert classified these ecoregions using the three categories of indigenous range (likely resident, possible resident, exploratory), considering the observational data, ecoregion description, climate suitability, and their professional experience and judgement. Where the experts largely agreed, we assigned categories accordingly, and where they disagreed, we discussed the issues until we reached consensus. In some cases, we divided ecoregions along mountain ranges, rivers or other putative barriers, assigning different categories in different portions of the ecoregion and recording

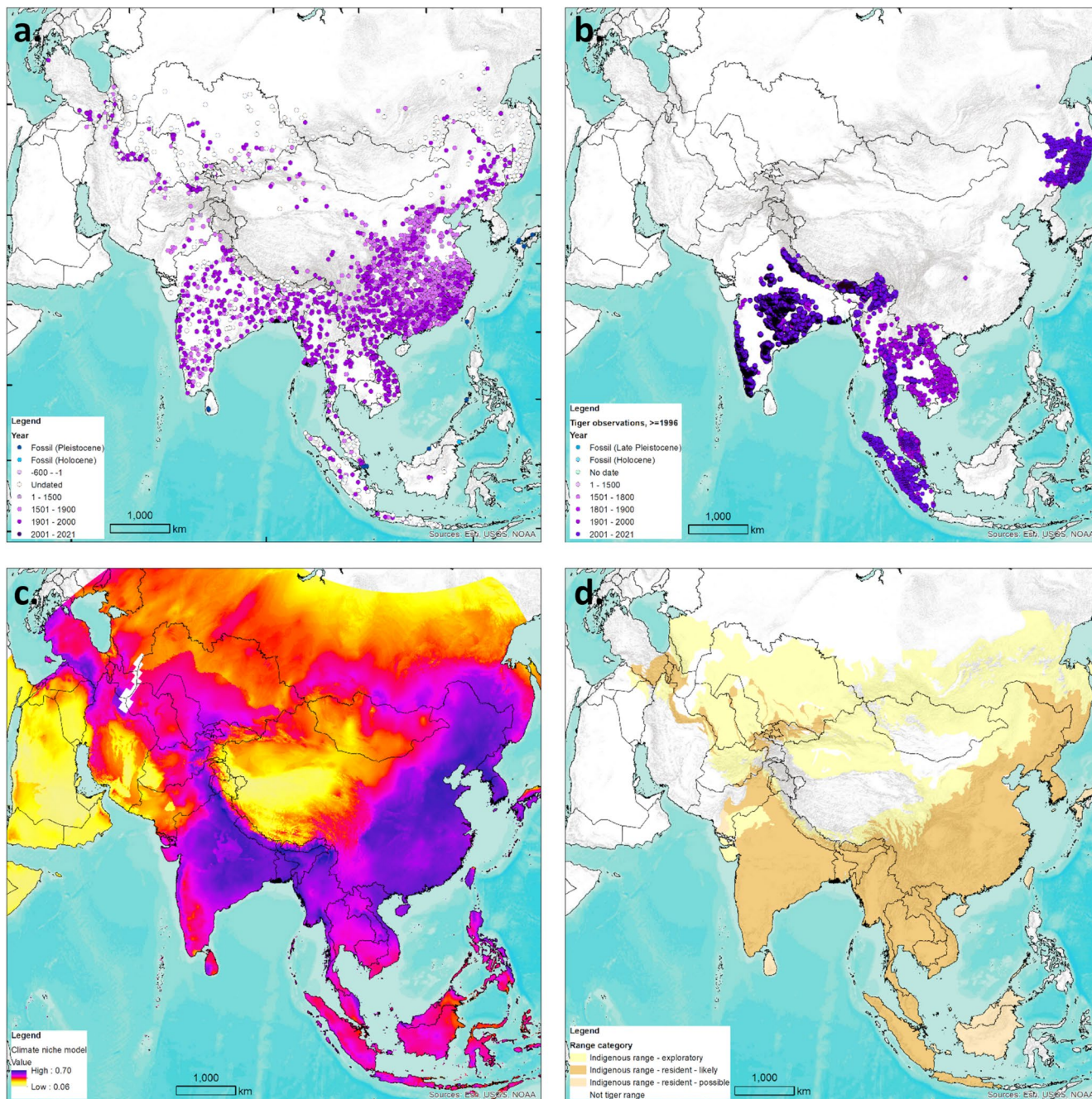


FIGURE 2 | Data inputs and output of indigenous range mapping for the tiger (*Panthera tigris*). (a) Synthesis of tiger observation localities made from 600 BCE to 1995 CE. (b) Tiger observation localities from 1995 to 2000. (c) A climate niche model based on the observational data. (d) The indigenous range of the tiger. The dark orange represents likely resident range; light orange, possible resident range; and yellow, exploratory range.

brief notes on the rationale for divisions (Table S2). We did not edit the ecoregion boundaries beyond subdividing them as noted. In some cases, especially in Central Asia, we sought additional observations and experts to resolve difficult biogeographical and historical issues (Figure 2d).

2.5 | Analysis of Human Impacts

Human impacts on tigers usually come in one of two forms: direct persecution of tigers and/or their prey, and destruction of tiger

habitat (Chapron et al. 2008). To assess how human modification might have impacted tiger habitats over time, we turned to the Anthrome 12K data (Ellis and Goldewijk 2020; Ellis, Beusen, and Goldewijk 2020). Anthromes are ‘anthropogenically modified biomes’, which are a combination of natural vegetation types, estimated human densities and types of use (e.g., ‘residential woodlands’ and ‘remote rangelands’). Although coarse (5 arc-minute cell resolution), anthromes provide the longest, systematically mapped series of land cover changes over the last 12,000 years. Anthromes are mapped at 1000-year intervals before the Common Era (CE), 100-year intervals to 1700 CE, 10-year intervals to 2000 CE, and

annually thereafter to 2015CE. We selected anthrome classes compatible with tiger habitat (Table S1) and calculated the habitat area in each ecoregion of the indigenous range. We used these analyses to identify ecoregions that seem to have very limited or no tiger habitat in the last 8500years; in these cases, we changed the range category, typically from resident to exploratory, unless there was strong historical evidence to the contrary.

2.6 | Analysis of Time of First Significant Human Impact

We used the anthrome analyses to estimate the time at which humans first significantly impacted tigers, defined arbitrarily as a loss of 10% more of habitat area within the ecoregion. We recognise that habitat loss is not the only reason tigers to disappear: for example, prey depletion and direct persecution may be more important extirpation factors in some cases. Habitat loss does help represent the opportunity for interaction between people

and tigers, as habitat fragmentation increases edges where conflicts can occur (Rybicki, Abrego, and Ovaskainen 2020; Parsons et al. 2019).

We also examined visually the trajectory of habitat change for each ecoregion, or portion of an ecoregion (see examples in Figure 3 and all instances in Figure S1). We cross-referenced our analytical findings against the observational data, especially sources that noted periods of important historical disruption for tigers, made notes of these changes, and in some cases adjusted the date of first significant human impact (Figure 4a).

2.7 | Analysis of Extirpation and Recovery Times

Finally, we reviewed the literature and observational record to estimate dates of extirpation and in one case (the Russian Far East) restoration, by ecoregion (Figure 4b; Table S3).

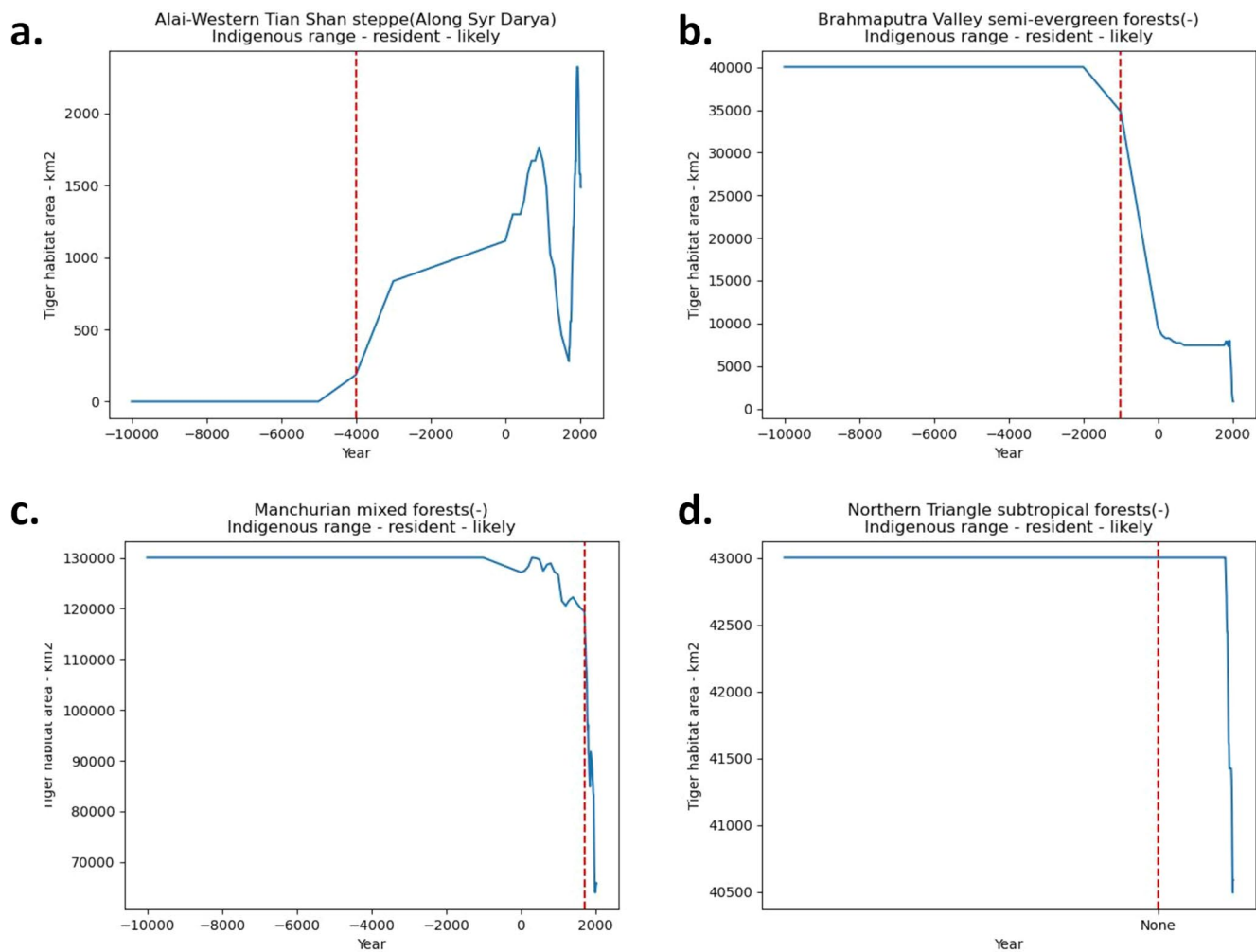


FIGURE 3 | Analysis of trends in tiger habitat as modelled with Anthrome 12K dataset (Ellis, Beusen, and Goldewijk 2020) for the last 10,000 years for four example ecoregions (Dinerstein et al. 2017). (a) Altai-Western Tian Shan Steppe (along the Syr Darya); (b) Brahmaputra Valley semi-evergreen forest, (c) Manchurian mixed forests, and (d) Northern Triangle subtropical forests. On each plot, the red line indicates the first time the amount of habitat changes by more than 10% compared to the baseline of habitat 10,000–6000 years before present. The figures for 242 other ecoregions (or portions of ecoregions) of the tiger’s indigenous range are provided in Figure S1.

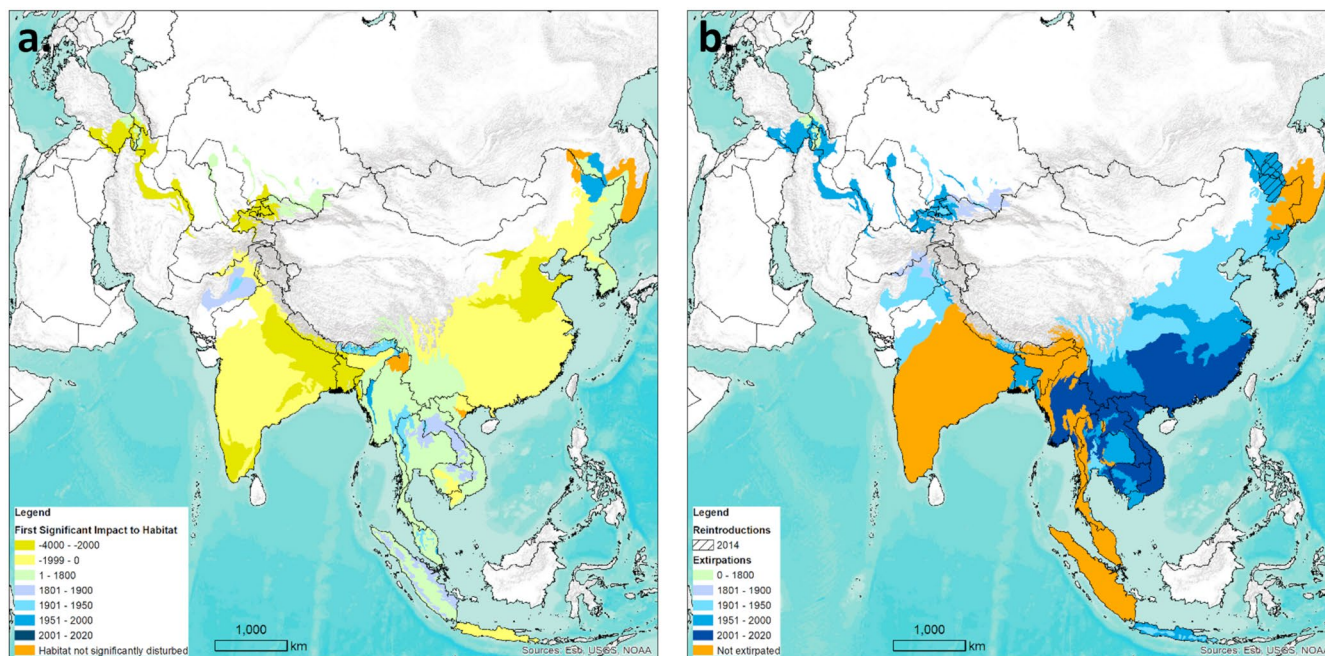


FIGURE 4 | Views into the biogeographic history of the tiger within the likely resident indigenous range. (a) Map of the putative dates when human beings significantly influenced the distribution of the tiger through ecosystem conversion; (b) Map of the putative dates of extirpation and reintroduction.

3 | Results

We collected 4332 tiger observation locations from the late Pleistocene (approximately 12,000 BCE) to 1995 (Figure 2a) from 120 references (Appendix S1), and an additional 66,189 observations from 1996 to 2020 (Figure 2b) from 346 references (Appendix S2). A detailed analysis of the number of observations, ecoregional divisors, and list of supporting references by ecoregion (or portion of ecoregion) is provided in Table S2.

Spatial thinning reduced the number of observations used in our climate analysis from 41,576 to 3224. Based on the variance inflation factor analysis, 10 predictors were retained reflecting the importance of aridity (Temperature of the Wettest Quarter (BIO8), Mean Temperature of the Driest Quarter (BIO9), Precipitation of the Wettest Month (BIO13), Precipitation of the Driest Month (BIO14), Precipitation Seasonality (BIO15), Precipitation of the Warmest Quarter (BIO18) and Precipitation of the Coldest Quarter (BIO19)) and constancy of temperature (Mean Diurnal Range (BIO2), Isothermality (BIO3), Temperature Annual Range (BIO7)) for tigers. The Mean Calibration/validation of the model was conducted using four and two random folds. A model with a beta value of 1 for the L, Q, and H features was selected after running 45 models consecutively with the lowest delta corrected Akaike information criterion (delta.AICc). In training, the AUC was 0.9, and in testing, it was 0.92. Out of all the variables in the model, Mean Temperature of the Driest Quarter (BIO9) responded positively, Isothermality (BIO3) negatively, Mean Temperature of the Wettest Quarter (BIO8) positively, and Precipitation of the Driest Month (BIO14) negatively and combined they contributed 95% to model variance.

TABLE 1 | Summary of indigenous range of the tiger (*Panthera tigris*) by category.

Range category	No. of ecoregions	Area (km ²) ^b
Resident—likely	116	11,496,408
Resident—possible	36	1,255,642
Exploratory	58	11,737,062
All categories	115 ^a	24,489,112

^aThe number of ecoregions within the indigenous range is not the sum by category because some ecoregions are shared across range categories.

^bMeasured in Lambert Equal Area map projection.

Based on the best model, we mapped the raw climate niche (Figure 2c).

Through our structured Delphi process, we identified 155 ecoregions associated with tiger range (Figure 2d; summary in Table 1; details in Table S2). We assigned portions of 116 ecoregions as likely resident range and another 36 ecoregions as possible resident range. We also identified portions of 58 ecoregions as exploratory range.

Humans and tigers have a long, shared, and tumultuous history. In China and India our analysis indicates human impacts on tiger habitat in the Huang He (Yellow River) Basin and Ganges and Brahmaputra Valleys, respectively, began as far back as 6000 years ago (4000 BCE). In Central Asia the first significant human impacts range from 4000 to 2000 BCE. In some arid Central Asian ecoregions, human influence appears to have driven apparent increases in tiger habitat, not decreases. The apparent increase may have come through water management

practices and the introduction of livestock in outlying areas (Jeong et al. 2018). In Southeast Asia, our analysis suggests major changes in tiger habitat only started occurring in the last 200 years, most especially during the 20th century. In some ecoregions of the Russian Far East, the arbitrary 10% habitat change threshold has yet to be met (Figure 4a).

Finally, we estimated dates of extirpation for the tiger in areas mapped as likely resident range (Figure 4b; Table S3), showing a progressive reduction in tiger range to what we hope is the nadir of the early 21st century. The 20th century, unlike previous centuries, saw major region-wide extirpations. In what is now Afghanistan, Pakistan, most of northern China and the Korean Peninsula, these extirpations occurred between 1900 and 1950. In the rest of Central Asia and central China, extirpations have largely occurred since the end of World War II. Tigers were declared extinct in the early 21st century in south-east China (Zhang et al. 2019; Qin et al. 2015). In south-east Asia, the countries of Cambodia, Laos and Viet Nam have lost their tigers just within the last two decades (Rasphone et al. 2019; Goodrich et al. 2015; Sanderson et al. 2023). Extirpations can be reversed, however. Tigers have been restored to occupied tiger habitat in the Pri-Amur region of Russia (Rozhnov et al. 2021) and are continuing to expand (Zhou et al. 2022). Most extirpations were not caused by habitat loss alone. Rather habitat loss coupled with direct persecution and depletion of tiger prey (Karanth et al. 2004; Chapron et al. 2008) appeared to drive regional extinctions.

4 | Discussion

The ultimate aim of indigenous range mapping is to improve our understanding of the distribution of species before people were the major factor limiting their distribution. We believe such work has broad applicability in biogeographic research, helping open up issues about why species are where they are, how they got there, and what people can do now to conserve or restore species ranges. Here we highlight what this analysis tells us about the distribution of the tiger, and then suggest how our ecoregion-based methods could be transferred to other species with some caveats and considerations.

4.1 | What the Indigenous Range Means for the Tiger

Tigers are survivors, having outlasted the Roman Empire, the Parthian Empire, the Mongol Empire, the Mughal Empire, some 83 Chinese dynasties, hundreds of sultanates, principalities, and kingdoms, and European colonisation. Nine millennia ago, tigers lived on a truly continental scale, for which the modern distribution is only splintered remnant (Sanderson et al. 2010, 2023; Dinerstein et al. 2007). Our results suggest significant expansion in our collective understanding of the area and ecological diversity, compared to ‘historical’ or ‘past distribution’ maps often cited in the rich literature on the tiger (Mazák, 1983, 1996; Driscoll et al. 2009). Our analysis is supported by a compilation of over 70,000 localities where the tiger has been observed: from near the Arctic Circle 63° N (Heptner and Sludskii 1992) to 8° S of the Equator on Bali (Mazák, 1979), and as far west

as modern Ukraine (Heptner and Sludskii 1992) and western Turkey (Can 2004) and as far east as Japan.

The scale and diversity of the tiger's indigenous range is supported not only by a vast number of widely distributed observations, but also our analysis of the tiger's climatic niche, which seems to be well defined by four explanatory factors, three of which represent aridity (Mean Temperature of the Driest Quarter (BIO9), Precipitation of the Driest Month (BIO14), and Mean Temperature of the Wettest Quarter (BIO8)) and one of which represents the constancy of temperature, Isothermality (BIO3). If tigers and their prey are free from human persecution, then these large cats can persist in tropical and temperate climates given they are not too hot and dry.

Tigers are often described as habitat generalists (Miquelle et al. 1999; Schaller 1974). Here we detail the diversity of ecoregions where tigers were considered likely residents over the last 9000 years: from tropical to temperate forests, and from tropical and temperate grasslands to deserts. What connects these ecoregions is cover and prey. Tigers consume relatively large prey animals, a size-dependent predator–prey interaction that has evolved in relation to productive habitats, where sufficient cover for stalking and striking within close proximity is available. Such habitats—usually forests, but also tall grasslands and shrublands and riparian zones—depend upon moisture. With relatively abundant water resources, these same vegetation types swell with forage resources for the tiger's primary prey—large deer (Cervidae), wild pigs (Suidae), and wild cattle (Bovidae) species (Sunquist, Karanth, and Sunquist 1999). Natural carrying capacities of likely resident ecoregions vary by a factor of 40 or more in modern studies, from less than 0.5 tigers/100 km² in the Russian Far East (Soutyrina et al. 2013; Miquelle et al. 2015; Xiao et al. 2015), to over 20 tigers/100 km² in the most productive, mild climates of the Indian subcontinent (Karanth and Nichols 1998; Harihar et al. 2020; Kumar 2021). This range of densities is consequential for the interactions of tigers with other species, including people (Miquelle et al. 2005; Harihar, Pandav, and Goyal 2011). As prey densities drop below some critical threshold, whether that be from climate- or human-induced causes, tigers cannot persist (Karanth et al. 2004).

The meaning of the numerous observations dotted across the steppes of Central Asia were the subject of great debate during our Delphi process, which led us to eventually categorise such regions as ‘exploratory range’. We tentatively interpret these ecoregions as part of the tiger's distribution but without lasting resident populations, where observations represent dispersal from adjacent, more tiger-rich ecoregions. In ‘exploratory range’, either females were unable to successfully disperse or reproduce in sufficient numbers, or other conditions limited the duration of tiger populations, such as lack of prey, competition with other species or conflicts with people.

We note, however, that some parts of exploratory range are hundreds, even thousands, of kilometres from likely resident range, which suggests there must have been some localised breeding and multi-generational occupation in some high-quality habitat patches, perhaps forming extended meta-populations (cf. Sharma et al. 2013). On the steppes, small stands of shrub and forest near water, which are also habitats for wild pigs (*Sus*

scrofa) and Central Asian red deer (*Cervus hanglu*), may have helped sustain tigers locally. In arid environments, riparian corridors were key.

More importantly, mapping exploratory range reminds us as biogeographers that tigers—and other species—are not constrained at all by the lines we draw on maps. Individual tigers, especially young adult male tigers, are known through repeat field observations and tracking studies to occasionally make extraordinary dispersal moves (Lukarevskiy 2021; Wang et al. 2015; Sarkar et al. 2016; Heptner and Sludskii 1992). Our mapping needs to accommodate such geographic potential.

Such extraordinary dispersal also informs how we see tiger range evolution over the long run. Biogeographers have suggested three potential pathways to explain how tigers dispersed into Central Asia: (1) a southern route out of India northwest across Pakistan and Afghanistan (Heptner and Sludskii 1992); (2) a northern route out of the Russian Far East across southern Siberia westward, north of the Mongolian steppe (Mazák 1981, 1983; Hemmer 1987); or (3) a middle route via the historical ‘Silk Road’ through the Gansu corridor, between the Himalayan Plateau and the Mongolian Gobi desert (Mazák 1983; Driscoll et al. 2009). Our documentation of the indigenous range supports all three hypotheses, a conclusion consonant with recent genetic evidence (Wilting et al. 2015; Sun et al. 2022). Most studies now point to multiple paths of genetic exchange among continental tigers, influenced by factors such as snow, aridity, vegetation and prey density through time (Kitchener and Dugmore 2000). Competition may also have played a role (Schnitzler and Hermann 2019; Seryodkin et al. 2017; Miquelle et al. 2005).

For insular tiger populations, changing sea levels are a critical part of the story (Cooper et al. 2016). Sea level change alters connectivity to mainland areas, creating the possibility of trapping tiger populations in Japan, Taiwan, Palawan, Borneo and Sri Lanka. We mapped these areas as ‘possible resident’ range areas, because these areas have fossil evidence of tigers in the late Pleistocene or early Holocene but lack more recent historical evidence (with the debatable exception of Borneo—see Meijaard 1999). The presence of these possible range areas complements known historical populations on Bali and Java and the extant populations of Sumatra. Sea level rise and coastal storms seem likely to continue to impact the tiger’s distribution, most notably in the mangrove forests of the Sundarbans (Loucks et al. 2010; Mukul et al. 2019).

Other climate-driven factors are also in play. Fire and aridity, as they impact vegetation productivity and, therefore, prey density, are climate-related factors acting on the tiger’s range in the 21st century (Bagchi, Goyal, and Sankar 2004; Verma et al. 2017), as they probably have done for millennia (Cooper et al. 2016). In the future, climate change might open ‘possible resident range’, probably in areas mapped here as ‘exploratory’, rendering some areas more suitable, notably in North Asia, while possibly reducing suitability of some southern landscapes near the Equator (Tian et al. 2014; Dobrowski et al. 2021; Zhang et al. 2022) and impacting riparian zones along glacially fed rivers in Central Asia (Chen et al. 2016; Didovets et al. 2021). These effects, rather than invalidating

the indigenous range we have drawn here, in fact enhance its value as a research and conservation tool.

The analysis of possible ecoregional extirpation dates, while rudimentary, suggests the futility of trying to choose any one date as the most relevant historical range for conservation planning. Rather we suggest that researchers adopt a flexible approach that weaves human history with biology to better understand why a species might have been extirpated and what conservationists might do about it. As an example, the IUCN Green List assessment requires an understanding of the indigenous range of a species as a baseline to define what recovery might look like. Basing assessments of species by each ecoregion within the indigenous range provides a spatially explicit means of assessing status and potential for recovery regionally, without having to rely on subspecific delineations, which in some cases, as with the tiger, may be controversial (Kitchener et al. 2017; Liu et al. 2018).

Finally, our results, while focused on the long past of tigers, have important implications for conservation today. As drawn here, the indigenous range touches on 36 countries, which by virtue of the sovereignty claims have a direct stake in tiger conservation. Ten countries retain viable tiger populations, where efforts to maintain and grow existing tiger populations in extant conservation landscapes (*sensu* Sanderson et al. 2006, 2010, 2023) is an obvious high priority. But it should not be our only one. Restoration must complement conservation. Reintroduction programmes are contemplated for Kazakhstan (Chestin et al. 2017), Thailand (Suttidate et al. 2021) and Cambodia (Gray et al. 2017). Scientific reintroductions of tigers have worked, notably in Russia (Rozhnov et al. 2021), India (Jhala et al. 2021) and China (Qi et al. 2021) and for other large cat species elsewhere (Zamboni, Di Martino, and Jiménez-Pérez 2017). Now is the time to engage in a project of the long future to return tigers to safe and suitable localities across the indigenous range (Gray et al. 2023).

4.2 | What the Example of the Tiger Means for Indigenous Range Mapping

While we care a great deal about the past and future trajectory of tigers, our general approach was constructed with an eye toward indigenous range mapping for species as well, whether they be as wide-ranging as the tiger or not. Here we highlight qualities of this analysis germane to indigenous range mapping of other species.

Ecoregions are a suitable spatial template for all species except narrow endemics. They are broad enough to help mitigate some of the uncertainties around locating historical observations, but narrow enough to reflect ecologically relevant factors in a species’ distribution. As we demonstrate for the tiger, in some instances, ecoregions may need to be subdivided, which of course, only opens the interesting biogeographic question about what factors make one part of an ecoregion suitable and while other parts are less suitable. Ecoregions are an established geography on which other kinds of analyses can be built, such as our Anthrome analysis to suggest times of expiration or conservation-oriented analyses examining

the overlap with political boundaries (such as countries) or cultural boundaries (such as Indigenous groups). One prominent way to think of conservation for wide-ranging species, such as the tiger but applying to other species as well, is conserving ecologically representative populations (Dinerstein et al. 2007; Sanderson et al. 2002). Ecoregions provide a convenient natural surrogate for representation across ecologies (though see Hanson et al. 2020).

Another potential advance here is using the Delphi process to structure the discussion. By collecting opinions separately and then combining them, we could rapidly find areas of agreement (indigenous range, not indigenous range) and more importantly, areas where more discussion, and in some cases, more research, was required. Having multiple categories of range (likely range, exploratory range, possible range) helped us bring more precision to the mapping and also increased our ability to find consensus among the expert panel. For some species, it is essential to have a team with different areas of geographic or historical expertise. The Delphi process helps bring all the insights together in a collegial, equitable and transparent way.

The primary data requirement beyond ecoregions are species localities with dates. For a charismatic and dangerous species such as the tiger, the issue was not a paucity of data but a superabundance of information, scattered across a vast literature, in multiple languages. Potential sources of spatio-temporal information include local histories, travelogues, hunting records, museum specimens and, in more recent times, scientific surveys. For other species, there may be less to go on. If one cannot find more than one or two observation per ecoregion, then our method would start to lose meaning. That does not seem to be a flaw in the method in itself, as the lack of observations will likely hinder any range mapping effort.

Finally, a major question is how deeply to look back in time to find relevant species observations. Our advice is not to pick an arbitrary time point (e.g., 1500AD, 1900AD) but rather grapple with the definition offered here: a time before human beings started shaping the species distribution, when the climate and continents were largely consistent with modern situation (climate change notwithstanding). For most species, such a definition will probably lead one toward the beginning of the Holocene, but the historical and biological details matter. We would advise fellow biogeographers to lean on the insights of biologists, anthropologists, historians, and climatologists to inform such decisions.

5 | Conclusions

Our process of mapping the indigenous range of tigers provides a framework for future efforts focused on other species. We believe the general framework will be appropriate for most species except those with small, endemic populations or extreme specialisations. In addition to the rigour provided by this process, it also integrates well with conservation processes such as the IUCN Red and Green Lists, and provides a baseline for setting conservation priorities (Coalition for Securing a Viable Future for the Tiger 2022). As such, we hope the approach described here will be useful to biogeographers, historical ecologists,

and conservationists, as well as a reminder to all that ‘A place belongs forever to whoever ... remembers it most obsessively’ (Didion 1979).

Author Contributions

E.W.S., D.G.M. and A.H. conceived the paper; D.C.M. suggested the Delphi methods; K.Fi. built an online survey tool; A.H., A.K., C.B.-W., D.G.M., K. Fa., K.T., J.G., L.R., N.Y., S.O., T.N.E.G. and U.B. contributed observations or sources of observations; A.H., A.C.K., A.K., D.C.M., D.G.M., D.M.C., E.W.S., K. Fa., K.T., N.Y., S.O. and T.N.E.G. assigned range categories; E.W.S., L.R. and A.H. conducted the analysis; E.W.S., D.G.M. and A.H. drafted the manuscript; all authors reviewed the results and contributed to the final manuscript.

Acknowledgements

We gratefully acknowledge funding from the National Aeronautics and Space Administration (NASA Grant Number 80NSSC19K0201) and institutional support from the Wildlife Conservation Society and Panthera. We appreciate helpful comments from Grigory Mazmanians and Olga Peredetlova on earlier versions of our maps.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The spatial data on the indigenous range of the tiger can be accessed at <https://doi.org/10.5061/dryad.tqjq2bw81>.

Peer Review

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ddi.13947>.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.