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Science-based conservation of tigers: Assessing the past to prepare for the future

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Science-based conservation of tigers: Assessing the past to prepare for the future

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Disease threats to tigers and their prey

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The contraction of the global tiger population over the last 100years into small, often isolated subpopulations has made them increasingly vulnerable to the impact of disease. Despite this, the health of wild tigers continues to be insufficiently funded and explored. For example, canine distemper virus (CDV), has been associated with localized declines and increased risk of extinction, and yet has received little research attention in most tiger range countries. The emergence of new pathogenic threats has posed fresh challenges, including African swine fever virus (ASFV), which has the potential to devastate wild boar populations, and severe acute respiratory syndrome coronavirus (SARS-CoV2) with implications for tiger conservation that remain unknown. The objective of this review is to synthesize current research on the health of tigers and their prey that impacts the conservation of tigers in the wild. Published sources are interpreted based on three mechanisms through which disease can affect the viability of tiger populations: (1) by reducing the survival of adult tigers, (2) by reducing breeding productivity, and (3) by reducing the carrying capacity of tiger habitat through decreased prey abundance. Examples of CDV, SARS-CoV2, carnivore protoparvovirus 1 and ASFV are used to illustrate these processes and inform discussion of research and mitigation priorities.

KEYWORDS

Tiger (*Panthera tigris*), disease, prey, canine distemper virus, African swine fever, health, conservation

1. Introduction

Tigers (*Panthera tigris*) now occupy just 7% of their historic distribution (Sanderson et al., 2006), and despite some recent successes, many populations continue to decline (Goodrich et al., 2022). Current estimates place the global population between 2,608 and 3,905 mature individuals, with 76% in the Indian Subcontinent (Goodrich et al., 2022). Poaching and habitat degradation have been the primary drivers of these declines and the focus of most conservation interventions. However, with remaining tigers now confined to fragmented, often isolated patches of habitat, vulnerability to disease has never been greater. As such, there is an increasing need to integrate health monitoring and disease surveillance into wider tiger conservation strategies.

Disease – the disruption of structure and/or function of living organisms – is an inherent feature of all life and an important part of the ecosystem. However, few habitats remain in their natural state, with most having been altered by anthropogenic forces that have reduced biodiversity, altered climatic conditions, and fragmented landscapes. Modified habitats create new species interfaces providing opportunities for pathogens to emerge and rapidly disseminate along global transport and trade networks, taking root in distant locations with unpredictable outcomes. This has resulted in a loss of resilience, with depleted and isolated populations now vulnerable to stochastic effects. Outbreaks of disease that were once incidental, are now capable of triggering population collapse.

Long-lived, slow-breeding species like tigers are particularly vulnerable to increases in adult mortality. Studies often use a binary classification of tiger mortality as either "human-caused" or "natural" (Goodrich et al., 2008; Singh et al., 2015; Sadhu et al., 2017), however this is somewhat reductive and discourages researchers from investigating further. In reality many so-called 'natural' disease processes are affected by human activity, whether through the introduction of exotic pathogens, new opportunities for disease transmission in modified habitats, or climate-related perturbations. In this context it is helpful to understand what disease processes are present, how they impact the tiger population and, particularly, whether they may be preventable.

The objective of this paper is to review ways in which disease can impact tiger conservation, highlighting examples that encourage researchers to focus on those of greatest potential significance. While the death of any individual tiger in a small and genetically impoverished population is important, such isolated incidents are unpredictable and difficult to mitigate against. Therefore, we have chosen to focus on disease processes that can produce declines at a population level. Pathogens which meet this criterion should be considered priorities for investigation and potential targets for intervention.

There are three fundamental mechanisms through which disease can threaten tiger populations:

1. Reducing the survival of breeding tigers–Late-maturing, slow-breeding species like tigers are sensitive to increases in mortality, particularly of adult breeding females, and populations will decline if their survival drops below 0.85 per year (Chapron et al., 2008). While most tigers die from anthropogenic causes (Goodrich et al., 2008), disease-related mortality can be additive to other factors, narrowing a population's capacity to withstand the negative effects of humans (Robinson et al., 2015). The presence of non-breeding tigers without territories may buffer against declines in a breeding population, as individuals quickly move to replace territory holders that die (Goodrich et al., 2010). However, turnover in the breeding population causes wider social disruptions and can lead to further mortality through fighting or infanticide (Goodrich et al., 2008; Gilbert et al., 2015). Cubs are dependent on their mothers until late in their second year, therefore relatively long periods of stability are required for productive breeding.
2. Reducing the productivity of breeding tigers–Population maintenance or growth, requires a steady supply of recruits into the breeding population. Lifetime productivity can be as high as 11.9 to 15.4 cubs (Smith and McDougal, 1991; Kerley et al., 2003), but many breeding females do not achieve this (Kerley et al., 2003) and many cubs will not survive to adulthood. Reproductive disease that prevents conception or causes abortion, and neonatal and juvenile conditions that result in a failure to raise cubs to independence threatens this recruitment. Repeated loss of litters can halt recruitment, effectively stalling population growth and potentially precipitating declines.
3. Reducing the carrying capacity of tiger habitat–Prey availability defines the carrying capacity of habitat, therefore any disease that reduces prey abundance places limits on tiger populations (Karanth et al., 2004; Miller et al., 2014). Epizootic waves of infection can produce temporary declines in prey density, which reduces cub survival as mothers fail to meet their energetic needs (Miller et al., 2014). Extended circulation of enzootic pathogens can impact prey abundance in the long term, reducing the number of breeding tigers that a landscape can support.

These concepts provide a useful starting point to assess the potential conservation significance of individual diseases. To be significant, pathogens must contribute to one or more of these processes and do so at an epidemiological scale that impacts population viability. This review is structured around each of these mechanisms and uses topical examples to illustrate the processes involved, priorities for research and prospects for mitigation. It must be emphasized that these pathogen case examples have been selected for illustrative purposes and are not the only pathogens with the potential to threaten tiger populations. We have elected to treat all tiger populations as biologically equivalent, as there is little evidence to suggest differences in inherent disease susceptibility between subspecies, although there may be differences in exposure geographically.

2. Literature review

To obtain a comprehensive picture of tiger health research we conducted a review of indexed literature published between 1928 and 2022 within the Web of Knowledge database using a series of relevant search strings (see Supplementary Table S1 for methodology, a full list of Boolean searches and criteria for inclusion). Overall, publications tended to focus on captive animals and on hazards that are of limited importance to the viability of wild tiger populations. Of the 280 publications considered relevant to tiger health, 256 focused on captive tigers (91.4%) and just 35 referred to wild tigers (12.5%). Publications addressing viral pathogens were most represented (40.0%), followed by non-infectious disease (26.4%), bacterial pathogens (16.8%), protozoa (11.8%), helminths (8.9%), fungi (4.6%), toxins (4.6%), ectoparasites (2.1%), prions (1.1%) and Acanthocephalans (0.7%). Among viral pathogens, more publications addressed severe acute respiratory syndrome coronavirus 2 (SARS-CoV 2) (37 papers, although only 22 of those reported on primary research), followed by canine distemper virus (CDV) (26 papers including 15 that referred to wild tigers). Studies addressing non-infectious diseases were predominantly focused on neoplasia (39 studies) or other disease of individual tigers and were not considered relevant to the conservation of free-ranging animals. An annotated account of the main health issues identified are summarized in Supplementary Table S2, and a full bibliography of papers reviewed is available https://doi.org/10.7298/rpe5-wa81.

Of the 35 publications that addressed free-ranging tigers, 27 reported primary research, while the remaining eight included reviews, textbooks, and news commentaries. Subjects covered by the primary literature sources included virology ($n = 12$), parasitology ($n = 9$), mixed pathogens ($n = 3$), dental disease ($n = 2$) and toxicology ($n = 1$). Virological studies focused on CDV ($n = 8$), feline immunodeficiency virus (FIV, $n = 2$), carnivore protoparvovirus 1 ($n = 1$) and mixed viruses ($n = 2$). In most cases, parasitological studies described incidental findings based on post-mortem examinations or fecal analysis, but in two cases the parasite was the primary cause of mortality (*Galoncus perniciosus* and *Taenia solium*). Serological surveys of wild tigers were described in eight studies (Table 1). Only one of the 17 pathogens included in the serosurveys is known to cause mortality in free-ranging tigers (CDV), a further five have caused mortality in captive tigers (feline parvovirus [FPV], feline coronavirus [FCoV], feline herpesvirus [FHV], feline calicivirus [FCV] and influenza A virus), and another (FIV) in a captive lion (*P. leo*) and a captive snow leopard (*P. uncia*). Several of these pathogens (FPV, FCoV, FHV, FCV and FIV) have been associated with reproductive failure or mortality in neonates.

3. Disease that reduces the survival of breeding tigers

Among the pathogens reported in wild tigers, only CDV has been associated with mortality in breeding adults coincident with population declines, and therefore warrants more detailed attention (Seimon et al., 2013; Gilbert et al., 2015, 2020; Kadam et al., 2022). Furthermore, the global prevalence, high morbidity and observed mortality in captive tigers suggests that SARS-CoV2 has the potential to become an emerging threat in the future. Both pathogens are discussed in the following sections.

3.1. Canine distemper virus

It is now almost 20 years since CDV was first detected in wild tigers, yet our understanding of the threat that it represents across

TABLE 1 Summary of published serological survey findings of free-ranging tigers, indicating location of sample collection.

Pathogen	Published study							
	Brown et al. (1993)	Troyer et al. (2005)	Goodrich et al. (2012)	Naidenko et al. (2018)	Naidenko et al. (2019)	Gilbert et al. (2020)	McCauley et al. (2021)	Mulia et al. (2021)
	Russia, India	Russia, India and unspecified locations	Russia	Russia	Russia	Russia	Nepal	Indonesia
CDV			15.0% (40)	17.6% (10)		37.0% (54)		42.9% (21)*
FeCoV								
FHV				5.9% (17)			45.5% (11)	
FPV			68.3% (41)	64.7% (17)			72.7% (11)	
FCV				17.6% (17)				
Influenza A virus				5.9% (17)				
Pseudorabies virus				5.9% (17)				
FeLV†			0.0% (44)	0.0% (17)			0.0% (11)	
FIV	0.0% (5)	35.8% (53)	0.0% (44)	5.9% (17)			0.0% (11)	
Toxoplasma gondii			61.9% (42)		38.9% (18)		90.9% (11)	
Trichinella spp.					72.2% (18)			
Candida spp.					50.0% (18)			
Bartonella henselae			0.0% (17)					
Mycoplasma spp.					0.0% (18)			
Leptospira spp.							54.5% (11)	
Chlamydia spp					0.0% (18)			
Coxiella burnetii					0.0% (18)			

*Eight of the nine positive tigers had been been held for periods of 6 months to 20 years in captivity.

†Enzyme-linked immunosorbent assay tests for antigen.

Results are expressed as percentage of tigers testing positive for antibodies, with sample size in parentheses. Pathogens tested include canine distemper virus (CDV), feline coronavirus (FCoV), feline herpesvirus (FHV), feline parvovirus (FPV), feline calicivirus (FCV), feline leukemia virus (FeLV) and feline immunodeficiency virus (FIV).

tiger subpopulations remains incomplete. The impact of the virus has been studied most extensively in Russia, following the death of a young female Amur tiger in 2004 and a series of subsequent cases diagnosed since 2010 (Quigley et al., 2010; Seimon et al., 2013; Gilbert et al., 2020). Death from CDV is additive to other causes of tiger mortality (Robinson et al., 2015) and a population viability model has shown that infection increased the 50-year extinction probability of small Russian populations by up to 65% (Gilbert et al., 2014). Recent tiger cases have been confirmed in Malaysia (Ten et al., 2021) and India (Kadam et al., 2022), while antibodies indicating prior infection have been detected in tigers in Indonesia (Mulia et al., 2021) and in Nepal (Bodgener et al., 2023). Although only a small number of cases have been diagnosed, the presence of infection in at least five of the 10 tiger range states suggests that all populations are probably at risk of infection.

Canine distemper is caused by an enveloped, single-stranded RNA virus in the genus *Morbillivirus* (giving rise to its contemporary common name, canine morbillivirus). The viral envelope reduces environmental stability (particularly in warmer temperatures), limiting opportunities for indirect transmission (Wilkes, 2023). However, CDV is readily transmitted during direct contact, *via* inhalation of aerosolized respiratory droplets or possibly during predation of infected individuals (Gilbert et al., 2020). Once infected, the virus replicates in immune cells (leading to immunosuppression) and then in epithelial tissue (causing respiratory and gastrointestinal disease). Tigers that survive these initial stages of infection can progress to develop severe neurological disease as the virus becomes established in the central nervous system. Mortality is high, with approximately 30% of clinically affected tigers ultimately dying, including 100% of those that develop neurological signs (Appel et al., 1994; Nagao et al., 2012; Linhares et al., 2021).[1] Survivors develop an immune response that should protect them from further infection. While immunologically naïve tigers of any age can die from infection with CDV, mortality of breeding adults has the greatest impact on population viability (Figure 1).

There are three epidemiological features, which combine to make CDV a pathogen of conservation importance for tigers: (1) high mortality, (2) high transmissibility and (3) high diversity of susceptible host species. This latter is of particular importance as it enables the virus to perpetuate in reservoirs of more abundant hosts that includes most members of the order Carnivora, which act as a continual source of exposure for tigers. In Russia, a multi-species community of wild carnivores appears to play a dominant role in the CDV reservoir for Amur tigers (Gilbert et al., 2020). However, the species composition of CDV reservoirs depends on local conditions, and in other areas large populations of unvaccinated and free-roaming domestic dogs (*Canis familiaris*) may constitute important CDV reservoirs (Acosta-Jamett et al., 2011; Belsare et al., 2014). Spillover could initiate short chains of tiger-tiger transmission, but these fade out rapidly in a species with few intra-specific contacts. Consequently, the extensive epizootics that occur in more social species are not a feature of CDV in tigers. Famously, the 1994 outbreak in Serengeti, Tanzania coincided with the disappearance of an estimated 1,000 lions (Roelke-Parker et al., 1996) and at least 68 lion cases occurred during an outbreak in Gujarat, India in 2018 (Mourya et al., 2019). Although less conspicuous, CDV in tigers can reach comparable scales. With more than a third of Amur tigers carrying antibodies that indicate prior infection (Gilbert et al., 2020), spillovers must be occurring with some regularity. In a population of between 265 and 486 tigers (Goodrich et al., 2022) the five CDV cases that have been confirmed to date clearly represent an underestimate of true mortality (Gilbert et al., 2020).

The most immediate priority for CDV research remains a risk assessment for tiger populations outside of Russia. Fundamentally, this requires two key questions to be addressed: "what proportion of tigers are exposed to CDV?," and then, "is exposure at a level that threatens population viability?." Collection of blood and preservation of serum should be routinely incorporated into tiger handling protocols (whether for research, conflict mitigation, rehabilitation, or post-mortem examination). Specimens should be archived centrally to maximize sample size and their statistical value. Commercial diagnostic kits for measuring CDV antibodies are designed for use in domestic dogs and should be considered unreliable for use in tigers without validation. Serum neutralization tests are available or have been introduced to several tiger range countries to measure titers of CDV neutralizing antibodies (Techakriengkrai et al., 2019; Mulia et al., 2021; Bodgener et al., 2023). Resulting seroprevelance estimates provide a useful means of validating population viability models based on the demography and structure of local tiger populations, which test the impact of realistic CDV exposure parameters (Gilbert et al., 2014, 2020). These could also be used to assess the impact of more frequent tiger-to-tiger contact that may occur in higher density populations outside Russia. Long-term serological monitoring would also highlight temporal variation in CDV exposure, such as the increase that occurred in Russia from 2000 onwards (Goodrich et al., 2012; Gilbert et al., 2020).

Vaccination is the only means of mitigating CDV risk to tiger populations and theoretically can be used in two ways, depending on the source of infection (Woodroffe, 1999; Haydon et al., 2002). In areas where domestic dogs are the primary source of CDV, vaccination of dogs using conventional modified live vaccines can be very effective at raising herd immunity and reducing CDV transmission to the point of achieving local elimination. However, this approach is ineffective at protecting tigers that acquire infection through contact with a sylvatic reservoir, as vaccines cannot be delivered to wildlife at the scale necessary to eliminate the virus. Under these circumstances, vaccination of tigers is the only option to reduce the threat to population viability (Gilbert et al., 2020). Captive tigers are routinely vaccinated against CDV (Sadler et al., 2016; Georoff et al., 2020), but the delivery of vaccines to free ranging animals presents additional logistical challenges and political controversy (Gilbert et al., 2020). Low coverage vaccination of tigers using injectable vaccines is feasible and would produce substantive reductions in extinction risks (Gilbert et al., 2020). Development of an oral baiting system (Budaszewski et al., 2017), could provide a less costly alternative and similar systems are already in wide use for control of rabies in wildlife.

Unraveling the structure of CDV reservoirs can be a complex undertaking and requires that multiple lines of molecular and immunological evidence be integrated from each of the populations that may be contributing (Viana et al., 2014). Considering the limited options for mitigation, a more realistic approach would attempt to

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[1] While extended convalescence may be possible in captivity (Blythe et al., 1983), this is unlikely for tigers in the wild.

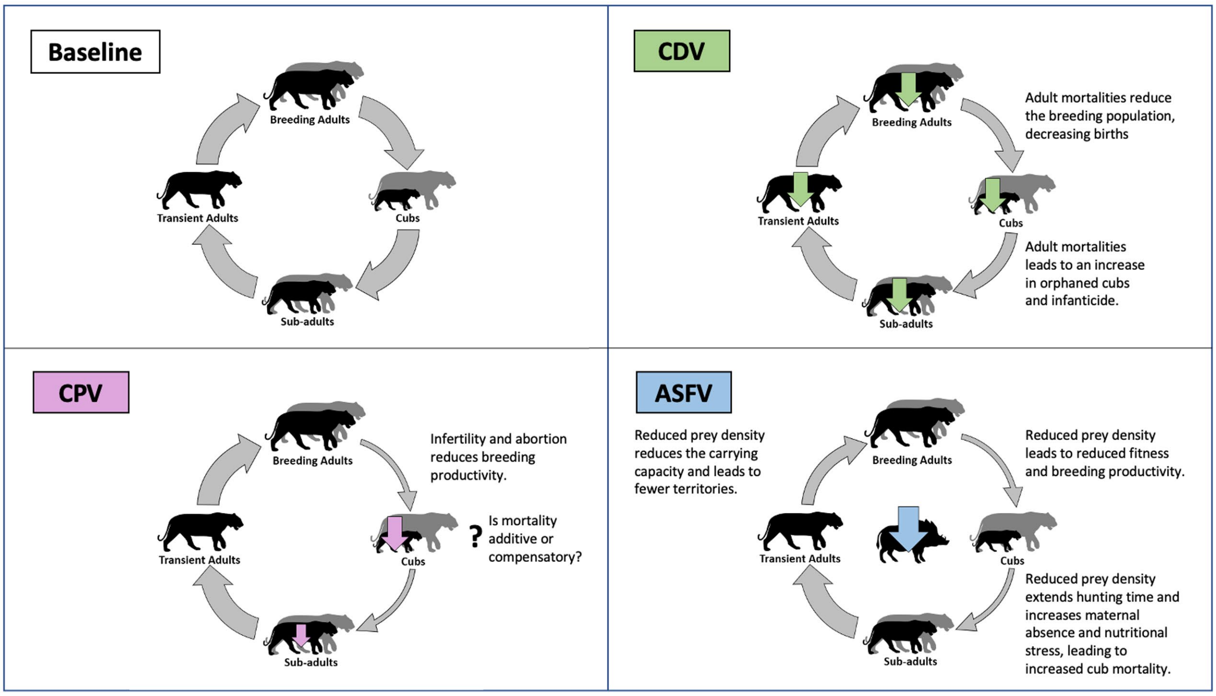

FIGURE 1
Schematic illustration of ways in which disease can threaten tiger populations compared to a baseline population where disease is absent. Populations consist of breeding adults (with territories), cubs (0–1year), subadults (1year–independence) and non-breeding transient adults (without territories). Example pathogens are used to illustrate three ways in which disease can impact tiger populations and include canine distemper virus (CDV–Reduces survival of breeding tigers), canine protoparvovirus 1 (CPV–Reduces productivity of breeding tigers), and African swine fever virus (ASFV–Reduces the carrying capacity of tiger habitat). Disease-related mortality is represented using vertical arrows (over tiger life stages, or wild boar prey) and is scaled according to relative severity. Transition between tiger life stages is represented by circular arrows, which are colored to represent transitions that are constrained by disease and scaled to indicate severity.

achieve a qualitative assessment of the relative contribution of domestic versus wild sources of virus. Viral sequence data can be used to identify transmission pathways that connect host populations, and every effort should be made to maximize this source of information from all populations. This should include the collection of tissue (a minimum of brain, lung and lymph node) for RT-PCR analysis from every dead tiger that is handled regardless of presumed cause of death, to ensure that underlying conditions or contributory factors are not overlooked. Serology can also be used to investigate tiger exposure risk to dog densities.

3.2. Severe acute respiratory syndrome coronavirus 2

The emergence of SARS-CoV2 in Wuhan, China in 2019 and the global pandemic that ensued has led to millions of human cases and deaths worldwide. In March 2020, the first SARS-CoV2 infections were diagnosed in captive tigers and lions at the Bronx Zoo, New York (McAloose et al., 2020) and numerous other outbreaks have now been reported affecting tigers, lions and snow leopards at other institutions (Fernández-Bellon et al., 2021; Mishra et al., 2021; Mitchell et al., 2021; Grome et al., 2022; Wang et al., 2022). Most cases in *Panthera* spp. present with mild and transitory respiratory signs (coughing, labored breathing, nasal discharge, malaise) that resolve after a few days or weeks (Bartlett et al., 2021). However, mortalities have been reported, particularly in older animals (Mishra et al., 2021; ProMED Mail, 2021; Madhusoodanan, 2022). Species susceptibility depends on the structure of the angiotensin I converting enzyme 2 (ACE2) that is used by SARS-CoV2 as a receptor for host entry. The amino acid composition of Felid ACE2 predicts a greater susceptibility than that of other carnivores (Damas et al., 2020). To date, in the United States there have been 53 tigers diagnosed with SARS-CoV2 using RT-PCR in 17 states and the district of Columbia (United States Department of Agriculture–Animal and Plant Health Inspection Service, 2022). With a further 52 cases in lions and 13 in snow leopards, more SARS-CoV2 cases have been confirmed in *Panthera* spp. in the United States than domestic dogs and cats (*Felis catus*) combined (101 cases). To-date, American zoological institutions have reported the death of one lion and five snow leopards that tested positive for the virus.

With SARS-CoV2 now endemic worldwide it is important to consider the risk to free-living tiger populations. The scales of our understanding of zoonotic disease weigh heavily in favor of pathogen transmission from animals to people, with comparatively little research on those moving in the opposite direction (Fagre et al., 2022). However, there are already signs that SARS-CoV2 is becoming established in free-living mink (*Neovison vison*) (Aguiló-Gisbert et al., 2021) and the detection in a dead wild leopard in India is a cause for concern (Mahajan et al., 2022). The most alarming 'spillback' into wildlife has been that affecting white-tailed deer (*Odocoileus virginianus*) in North America. Although the mechanism of initial exposure remains unknown, numerous independent human-deer transmission events with subsequent deer-deer transmission has raised the prospect of a possible SARS-CoV2 reservoir in white-tailed deer (Chandler et al., 2021; Hale et al., 2022; Kuchipudi et al., 2022). In Iowa, deer infections peaked at 82.5% ($n = 97$ deer sampled) during hunting season, soon after a surge in human cases in the state (Kuchipudi et al., 2022). Infected deer do not develop clinical signs, but they do shed virus for prolonged periods (at least 3 weeks) (Palmer et al., 2021) and the accumulation of 76 mutations in a strain detected in Canadian white-tailed deer suggest sustained transmission in deer populations with potential for generating novel variants (Pickering et al., 2022).

The susceptibility of tigers to SARS-CoV2 and its establishment in wild deer populations is concerning, but implications for tiger conservation remain unclear. While swine are poor hosts for SARS-CoV2, the deer that comprise the remainder of tiger diet are likely to be of comparable susceptibility as white-tailed deer (Damas et al., 2020) and therefore a plausible source of infection for wild tigers. However, at the time of writing transmission from deer to other wildlife has yet to be demonstrated. Furthermore, surveillance has yet to identify infection in European deer populations (Holding et al., 2022; Krupińska et al., 2022; Moreira-Soto et al., 2022) and so viral establishment in Asian deer is far from assured. Ecologically, few native deer in tiger range are as gregarious as white-tailed deer, with less extensive human contact, providing fewer opportunities for viral introduction or spread. Only chital (*Axis axis*) reach comparable densities, yet their populations are concentrated in protected areas with few settlements. Still, opportunities for contact (e.g., through hand feeding by tourists) should be avoided for this and other reasons. The limited prominence of deer hunting in most tiger range states may also hinder transmission, although the role of supplementary feeding or other hunting-related activities remains speculative (Kuchipudi et al., 2022).

If SARS-CoV2 did become endemic in Asian deer populations, the exposure of wild tigers may be unavoidable. However, the population importance of adult mortality related to COVID-19 remains debatable. Although few tigers have died from COVID-19, mortality may be higher in wild settings where animals lack veterinary care and easy meals. Just as for CDV, any wild tiger mortalities would be diagnosed through the introduction of routine post-mortem examination of all dead tigers. Any COVID-19 deaths would only become relevant at a population level if they were additive to other causes of mortality. In strict conservation terms, the loss of old or debilitated tigers would be irrelevant. However, the events since the emergence of the pandemic caution against complacency, with a virus that is adept at generating new variants and exploiting novel hosts. The virulence of SARS-CoV2 in captive settings should be monitored, with importance also placed on surveillance to detect new reservoirs in deer and other species in tiger range countries.

4. Disease that reduces the productivity of breeding tigers

Tigers are late-maturing, slow breeding species, with females producing as few as 4–6 litters in a full reproductive lifespan (Smith and McDougal, 1991; Kerley et al., 2003). Cubs face a difficult life, with 34–47% perishing within their first year from a range of causes, including poaching, starvation (e.g., following poaching of the mother), predation, infanticide and random incidents like fire and flood (Smith and McDougal, 1991; Kerley et al., 2003). Health issues could also contribute to reduced reproductive performance through failure to conceive, carry pregnancy to parturition, or disease of dependent offspring, but are poorly documented in captive or wild tigers. Most of the factors responsible for reproductive failure in domestic cats, such as management or nutritional issues, endocrine disorders, and individual pathologies (Fontbonne et al., 2020), are unlikely to affect free-ranging tigers, particularly at the population level. However, the genetic and chromosomal disorders of domestic cats could have analogs in the inbreeding depression found in small, isolated tiger populations (Smith and McDougal, 1991; Khan et al., 2021; Ning et al., 2022). Infections also have the potential for wider population-level impacts and several viral, bacterial and protozoal pathogens are known to cause reproductive loss in domestic cats (Givens and Marley, 2008; Fontbonne et al., 2020). Most prominent among these are parvoviruses and retroviruses (e.g., feline leukemia virus [FeLV] and FIV), which cause abortions and stillbirths in pregnant cats (Givens and Marley, 2008; Fontbonne et al., 2020), however, FHV, FCV, *Toxoplasma gondii* (rarely) and a variety of bacteria have also been implicated (Givens and Marley, 2008). Both FIV and FeLV are rare in captive tigers (De la Cruz-Hernández et al., 2016; Liu et al., 2022), and with only one report of FIV in a free-ranging tiger (Naidenko et al., 2018),[2] the status of infections in wild populations remains unclear. By contrast, high seroprevalence of parvovirus antibodies (65–73% Table 1) indicates that exposure is common in wild tigers and its significance warrants more detailed investigation.

4.1. Carnivore protoparvovirus 1

The highly contagious, single-stranded DNA virus carnivore protoparvovirus 1 (hereafter parvovirus) can infect a wide range of carnivores and is divided into two main genogroups: the feline parvoviruses (formerly termed feline panleukopenia virus) and canine parvovirus 2 (CPV2) (Allison et al., 2013, 2014). Both genogroups have been diagnosed in captive tigers (Steinel et al., 2000; Wang et al., 2019; Nur-Farahiyah et al., 2021; Huang et al., 2022), and CPV2 has been detected in tissues from a wild tiger in India (Shetty et al., 2020). The parvovirus genome is very small and lacks genes necessary for initiating viral replication, which is achieved through infection of rapidly dividing host cells (e.g., those found in developing fetuses or intestinal mucosa). Infection of pregnant cats can result in abortion, stillbirth, or neurological defects including cerebellar hypoplasia (that causes 'feline ataxia syndrome'), or in hemorrhagic enteritis, vomiting and leukopenia in older animals (Steinel et al., 2001; Barrs, 2019). Clinical disease is most common in young animals, typically coinciding with the decline of maternal antibodies around 3–4 months of age, or younger for those born to unexposed mothers (Barrs, 2019). Disease in captive tigers has been recorded in cubs from 5 to 10 months (Duarte et al., 2009; Wang et al., 2017).

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[2] The authors used an ELISA test that has not been validated for use in tigers (Barr, 1996; Hartmann et al., 2007).

The conservation significance of parvovirus in tigers remains unclear. The high seroprevalence in adult tigers suggests that many infections may be mild or subclinical, but more severe disease and death may go undetected, occurring during pregnancy or in early life before cubs leave the den (Figure 1). Crucially, it is unclear whether parvovirus mortalities are additive, or mainly affect weaker individuals that are likely to have succumbed to other causes (termed compensatory mortality). Addressing this question is key to understanding the conservation importance of parvovirus but is notoriously difficult to achieve. Approaches require long term datasets of sufficient detail to correlate parvovirus incidence with breeding productivity. Alternatively, interventions (such as domestic dog vaccination) that might reduce sources of tiger infections could act as opportunistic experiments, by relating exposure to reproductive output. Notably, parvovirus exposure of African wild dog (*Lycaon pictus*) packs increases with proximity to settlements, suggesting a role for domestic dogs as source of CPV2 (Woodroffe et al., 2012). Whether the same applies to tigers and their exposure to both genogroups has yet to be examined.

Several long-term studies have attempted to relate parvovirus exposure to the population ecology of wild carnivores. Packer et al. (1999) were able to demonstrate three discrete outbreaks of parvovirus in Serengeti lions that followed periods of high population density, and occurred during years of average or low cub survival, and average or low female fecundity. However, clear patterns were hard to discern during a period when the population was exposed to waves of several epizootic viruses. A clearer picture emerges in Minnesota, where parvovirus infection in gray wolves (*Canis lupus*) reduced pup survival by 70%, depressing population growth and constraining recolonization (Mech et al., 2008). Parvovirus was also implicated in the decline of gray wolves in Isle Royale National Park, Michigan, reducing the population to a level from which it was unable to recover (Peterson et al., 1998). By integrating epidemiological and ecological research, these studies go further than simple description of pathogens, instead attempting to interpret their importance, and as such should serve as inspiration for those interested in tiger conservation.

5. Disease that reduces the carrying capacity of tiger habitat

The number of tigers that can be sustained in a landscape is directly proportional to the density of available prey species (Karanth et al., 2004; Hebblewhite et al., 2014; Miller et al., 2014). Tigers prefer large prey that are sufficient to satisfy the energetic needs of hunting and raising cubs (Miller et al., 2014). In most locations, wild boar (*Sus scrofa*) and large deer (e.g., sambar–*Rusa unicolor*, red deer–*Cervus elaphus*, and sika deer–*C. nippon*) are the most important prey species (Hayward et al., 2012) with banteng (*Bos javanicus*) and gaur (*B. gaurus*) replacing boar in Western Thailand (Pakpien et al., 2017). The depletion of prey populations due to unsustainable hunting is one of the primary threats to tiger conservation (Linkie et al., 2003; Aziz et al., 2017; Goodrich et al., 2022). Historically, major epizootics have been equally capable of causing lasting declines in prey populations, with consequent reductions in large carnivores (e.g., the impact of rinderpest in Africa) (Packer et al., 2005; Dures et al., 2019). Over time a reduction in prey density leads to an increase in home range requirements to satisfy energetic needs (Fuller and Sievert, 2001). This reduces available breeding territories, thus limiting the proportion of reproductively active females in the population and raising the age at first breeding. As available biomass declines, females are unable to provision their cubs, increasing juvenile mortality due to malnutrition and predation arising from extended hunting times, as well as reducing recruitment, which limits population size and jeopardizes viability (Fuller and Sievert, 2001; Figure 1).

Domestic livestock are an important source of the pathogens that infect tiger prey species (Supplementary Table S2), and complex global trade networks provide an efficient means for exotic pathogens to gain access to naïve populations. Contemporary examples include lumpy skin disease (LSD) caused by a capripox virus of African origin, which infects cattle and buffalo and is currently spreading across South and Southeast Asia (Namazi and Khodakaram Tafti, 2021). Also, incursions of foot and mouth disease (FMD) occur with some regularity in Southeast Asia, and in 2022 the virus was introduced into Indonesia for the first time in almost 40 years (Qiu et al., 2018; Chen et al., 2022). However, despite having grave implications for agricultural output and global trade, it is unlikely that either LSD or FMD will have a major impact in tiger prey availability. Although cases of LSD have been reported in banteng and gaur (Pruvot et al., 2023), mortality is low in most species (Namazi and Khodakaram Tafti, 2021). Similarly, wildlife mortalities from FMD are relatively uncommon (Gortázar et al., 2021; Ijaz et al., 2022).

Contemporaneous with the spread of FMD and LSD, another exotic pathogen, African swine fever virus (ASFV) that is capable of decimating wild boar populations and has spread throughout tiger range in the space of just 4 years, warranting specific attention.

5.1. African swine fever

The recent and rapid advance of African swine fever (ASF) across tiger range represents an immediate and potentially profound threat to the availability of wild boars as a prey resource for tigers. With mortality of infected domestic pigs (*S. domesticus*) and wild boar exceeding 90–95% (Penrith and Vosloo, 2009; Sauter-Louis et al., 2021), this viral disease has devastated the Asian pork market, threatens food security of backyard producers, and risks far-reaching impacts on terrestrial ecosystems (Woonwong et al., 2020; Ewers et al., 2021; Luskin et al., 2021). Endemic to Sub-Saharan Africa, ASF (genotype II) was introduced to Georgia in 2007, spreading locally among wild boars and backyard pig producers into neighboring states in the Caucuses and beyond to Ukraine, Belarus and the Russian Federation (Gogin et al., 2013). Following an introduction to the northeast Chinese province of Liaoning in August 2018, the virus spread rapidly across East and Southeast Asia through 2019 (Lu et al., 2020; Mighell and Ward, 2021). Outbreaks in domestic swine reached Myamnar and Northeast India by 2020, Bhutan by 2021 and by the time of writing (December 2022) have reached the northern and southern margins of the key tiger strongholds in the Western Ghats and Central India (Figure 2). Wild boar outbreaks are heavily under-reported (Vergne et al., 2020; Cadenas-Fernández et al., 2022), with concentrations in the Russian Far East, Republic of Korea and Peninsular Malaysia hinting at the scale of wild outbreaks elsewhere (Figure 2). The population implications of ASF for wild boars in tiger habitat remains largely anecdotal, but declines of at least 90% in Sikhote-Alin Biosphere Zapovednik in Russia (Waller et al., 2022)

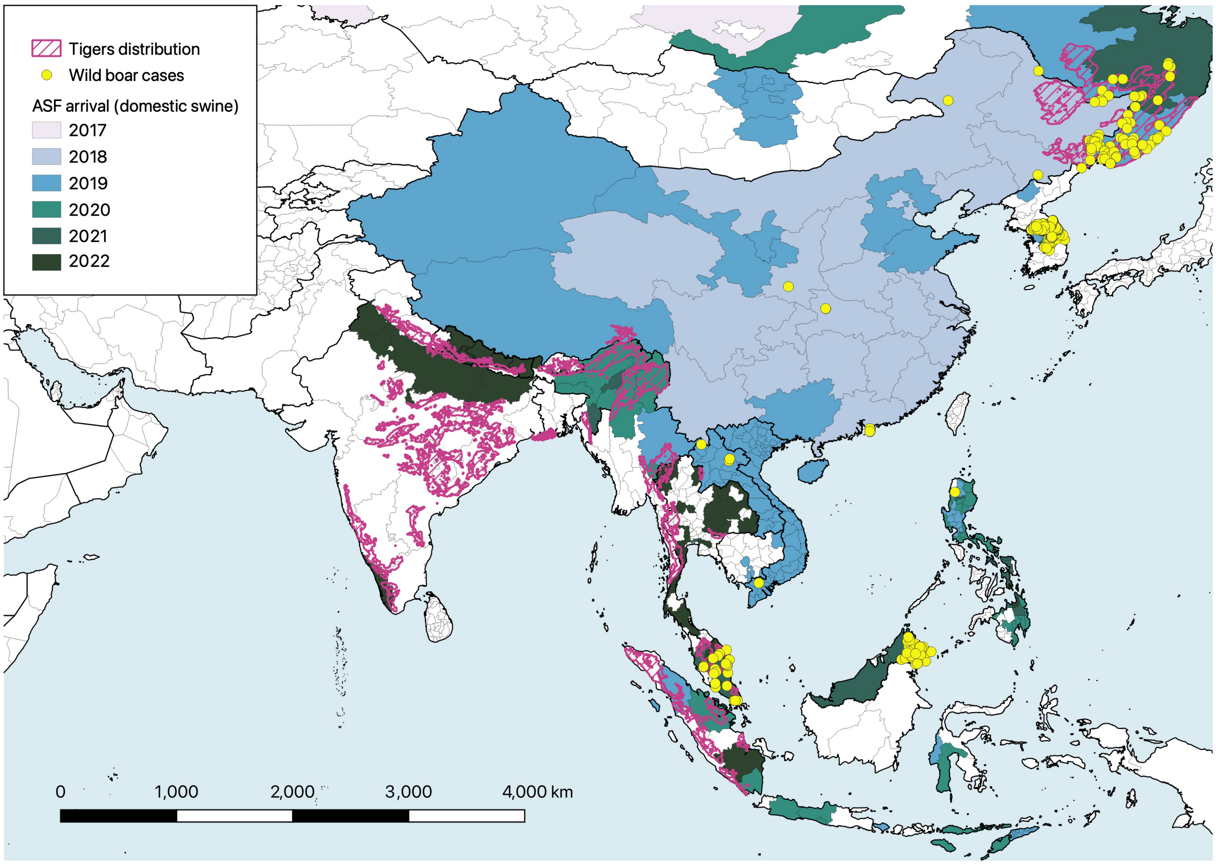

FIGURE 2
Map illustrating the spread of African swine fever (ASF) across Asia in relation to current tiger distribution (IUCN SSC Cat Specialist Group, 2022). Colors illustrate the year of first detection in domestic pigs at the province level (or equivalent) between August 2018 and December 2022. Location of ASF cases in wild boars are illustrated by yellow points. Source of ASF data: World Organisation for Animal Health - World Animal Health Information System (https://wahis.woah.org/#/event-management), accessed 6 February 2023, and Food and Agriculture Organization of the United Nations - EMPRES-i+ Global Animal Disease Information System (https://empres-i.apps.fao.org/diseases), accessed 3 March 2023.

mirrors the situation in Europe (Morelle et al., 2020; Klich et al., 2021; Schulz et al., 2021). If these reports are indicative of the threat to wild boar in other regions, the population and ecological implications could be devastating.

The disease is caused by a unique, large, double-stranded DNA virus in the family Asfarviridae that evolved to infect warthogs (*Phacochoerus africanus*) in Eastern and Southern Africa (Penrith et al., 2019). In the natural host, infections are asymptomatic, and the virus is transmitted within burrows by soft-bodied, argasid ticks of the genus *Ornithidoros*. The virus replicates more efficiently in *Sus* spp. and can be contracted with or without the involvement of tick vectors (Penrith and Vosloo, 2009). Transmission can occur during direct contact *via* oro-nasal secretions, or indirectly through oral consumption of contaminated material. The latter is aided due to prolonged environmental stability, with virions remaining viable for weeks or months in blood, tissue, or decomposing remains. Wild boars that investigate infected carcasses promote the gradual spread of local outbreaks, while human transport of contaminated products (feed, meat, offal) and fomites can introduce infection to more remote areas (Guberti et al., 2019; Sauter-Louis et al., 2021). The virus causes a hemorrhagic fever, with infected boar and pigs exhibiting a range of non-specific clinical signs including listless behavior, lack of fear, ataxia, prostration, respiratory distress, vomiting, diarrhea and reddened or hemorrhagic skin lesions (Nurmoja et al., 2017; Guberti et al., 2019; Sauter-Louis et al., 2021). Most animals die within 7–14 days post-infection.

In all likelihood, ASF is now established in all tiger range countries and there is an urgent need to assess its impact on carrying capacity within Tiger Conservation Landscapes (Sanderson et al., 2006). In northern latitudes, ASF has decimated local boar populations (Sauter-Louis et al., 2021), but it may be premature to assume that the same will happen across all of the climatic extremes that tigers occupy. However, if we are to assume a worst-case scenario where ASF becomes endemic and wild boar densities stabilize at much lower levels, there could be serious implications for tiger conservation policy. Wild boar are a key prey resource in almost all of tiger range (Hayward et al., 2012). Elsewhere, another top predator, the gray wolf has been forced to switch to alternative prey species (Klich et al., 2021), but the ability for tigers to follow suit will depend on the diversity and biomass of local ungulates. In some regions, like Peninsular Malaysia and Sumatra, where numbers of large deer have already been heavily depleted (Kawanishi and Sunquist, 2004; Sunquist, 2010), the additional loss of wild boar could restrict tigers to hunting smaller prey that would be energetically unsustainable and constrain reproductive output (Miller et al., 2014). Reduced prey densities could also drive increases in livestock depredation and the risk of retaliatory killings (Soh et al., 2014), increase the frequency of human-tiger encounters, or promote contact with domestic dogs, potentially exacerbating exposure to CDV.

The future implications of ASF for tigers will depend on the capacity of Asian wild boar populations to maintain the virus in the long term. In Eastern Europe wild boar are capable of maintaining ASFV, even at very low population densities, independent from spillover from domestic sources (Kolbasov et al., 2018; Blokhin et al., 2020; Sauter-Louis et al., 2021). However, previously the introduction of ASF into the Iberian Peninsula faded out in wild boar (Pérez et al., 1998), and viral circulation in Sardinia is only maintained due to regular spillover from local farms and free-roaming domestic pigs (Mur et al., 2016; Jurado et al., 2018). The key factor that allows sylvatic transmission cycles to persist in Eastern Europe appears to be the extended stability of ASFV in the environment (O'Neill et al., 2020). In Spain, the rapid consumption of carcasses by vultures and other scavengers reduced environmental contamination (O'Neill et al., 2020). Viral viability is also markedly reduced in the temperate Mediterranean climate. Experiments measuring the viability of ASFV in tissues estimate a half-life of 353–713 days at −20°C, 35–136 days at +4°C, and just 9–17 days at +23°C (Mazur-Panasiuk and Woźniakowski, 2020). For comparative purposes, mean temperatures in Spain vary from 6.3–23.1°C and in Lithuania from −3.3-18.3°C (World Bank, 2022). While other factors such as substrate type and moisture may also influence viral longevity (World Bank, 2022), these findings suggest that the persistence of sylvatic ASF cycles may be less likely in southern tiger range states. In these circumstances wild boar outbreaks would only continue with regular spillover from domestic pigs that are rare or absent in several key locations for tigers (e.g., Bangladesh, Bhutan, Sumatra, Peninsular Malaysia and Central/Southern India) (Gilbert et al., 2018).

The control of ASF in wild boars seeks to disrupt the cycle of viral transmission, which can be achieved in three primary ways:

a. Reduce opportunities for viral introduction – The introduction of ASFV into a landscape can occur either through the gradual progression of wild boar outbreaks from outside the area (an epidemic wave), or introduction from anthropogenic sources, such as spillover from infected pig farms, or movement of contaminated material by people. In Europe, epidemic waves travel at approximately 2–3 km/month (Guberti et al., 2019) and this can only be disrupted by reducing susceptible boar density ahead of the wave (undesirable and impractical for reasons given below). Spillover from domestic sources could be reduced through biosecurity improvements around farms to prevent contact between pigs and boars, as well as measures to discourage movement of contaminated materials from outside the area (from either agricultural or hunting sources). Programs to raise awareness among farmers and hunters are important, with benefits for rural livelihoods as well as wildlife.
b. Reduce densities of susceptible wild boars – This strategy seeks to reduce opportunities for viral transmission, such that the probability of the average infected case successfully passing the virus to a susceptible boar is less than one. Theoretically, vaccination could reduce density of susceptible animals, but currently no ASFV vaccines are available. In Czechia and Belgium local depopulation has been used to prevent the invasion of ASFV following the initial detection of cases (Guberti et al., 2019; Sauter-Louis et al., 2021). This intensive strategy requires a sensitive surveillance system to detect cases early and an efficient means of rapid depopulation to prevent epizootic spread (such as the deployment of sharpshooters). Progression to an epizootic occurs quickly, and once established, the number of infected boars increases very rapidly, and it is no longer possible to eliminate the pathogen using depopulation.
c. Reduce sources of infection – The environmental stability of ASFV is key to its circulation in wild boars. Carcasses and surrounding substrate can remain infective for extended periods and are actively visited by inquisitive boars, thus facilitating transmission (Probst et al., 2017). Early detection and disposal of carcasses is the only way to reduce the amount of virus in a landscape. However, this is a formidable task amid an epizootic when the number of carcasses is high, and many go undetected. Once the initial epizootic subsides, the number of infected carcasses declines and the task of removal becomes more manageable and promotes the likelihood of viral fade out and elimination (Guberti et al., 2019).

Clearly, strategies that rely on depopulation are counterproductive when the objective of disease control is to preserve tiger prey populations. Even in Europe, where disease control measures are motivated by economic and trade considerations, depopulation has only been used under specific circumstances to prevent the establishment of focal outbreaks. Once the virus becomes enzootic, persistence is possible due to the prolonged infectivity of carcasses, as these can continue to seed new cases even once boar densities are heavily depleted.

The establishment of ASF across Asia presents formidable challenges that can only be met through partnerships built on the common interests of the livestock, veterinary and wildlife sectors. No single agency can address pathogens like ASFV, and the wildlife sector has an important role to enhance our understanding of the virus and its management across tiger range. Existing schemes such as WildHealthNet (Pruvot et al., 2023) that take a One Health approach, integrating animal, public health and environmental bodies provide a template for expansion and adaptation in range countries. These initiatives capitalize on the field presence and ecological awareness of rangers in protected areas for the early detection of cases and connects them with veterinary authorities with the necessary diagnostic capacity and expertise in the safe disposal of carcasses. Research on the population ecology of wild boars and other key prey species should be emphasized, with results integrated into epidemiological models that inform control strategies (Bosch et al., 2017; O'Neill et al., 2020; Pepin et al., 2020). Results could also be used to design management interventions to promote the availability of alternative tiger prey as a contingency against declining boar numbers. Other priorities include an assessment of local vector communities to determine whether alternative hosts could contribute to viral spread in new environments (Karalyan et al., 2019).

Ultimately, only time will tell how ASF will affect the tiger prey base throughout the species' range. Environmental conditions and trends in domestic pig production across the wider landscape may have an important role in determining the eventual outcome for tigers. In the meantime, bleak predictions and the enormity of the challenge should not be used as grounds for complacency, as wildlife professionals have an opportunity to make critically-important contributions to an otherwise intractable One Health issue – one that could have serious implications for the long-term viability of some free-ranging tiger populations.

6. Conclusion

Despite their iconic and endangered status, we still know remarkably little about the health of free-ranging tigers. To some extent this may be explained by the suite of existing tiger conservation challenges, as long-standing politically charged questions of land tenure, wildlife conflict and indigenous rights often dominate discourse. Government officials may be reluctant to look for additional problems, like disease particularly if they are deemed to be convoluted and challenging to resolve. Equally, many established members of the conservation community may be skeptical, perceiving health as an unnecessary distraction that sits uncomfortably outside their own field of expertise. Yet, until we can reverse the declines and isolation of remaining tiger populations, disease threats are only going to become more evident. Despite all of this, there is still room for optimism. Opportunities abound to integrate wildlife health research into existing environmental management programs in ways that enhance their value to the wider community while also meeting conservation objectives.

Opportunistic sampling of tigers could (and should) be readily introduced into existing management activities with only modest financial investment. Sample collection should become part of the routine of tiger immobilizations (serum and whole blood), and all dead tigers should undergo a detailed post-mortem examination (with preservation of representative sets of tissues). While some wildlife management agencies are equipped with laboratories, these are often focused on forensic analysis or molecular research and may lack the capacity to perform the full suite of diagnostic testing required. In these situations, partnership with other agencies, or with national academic institutions should be encouraged to improve laboratory access, while also enhancing national educational opportunities and inter-sectoral communication. Given that most of the pathogens of relevance to tiger conservation are shared with domestic animals and/or humans there are mutual interests for the wildlife sector to partner with their livestock and public health counterparts. Wildlife agencies have access to species and places beyond the reach of veterinary or public health resources and can benefit from specialist assistance in diagnostics or health services, while enhancing surveillance of priority pathogens with One Health implications.

While there are many gaps to fill in our understanding of tiger health, researchers should be encouraged to focus on those issues of the greatest consequences for tigers and their prey. This should include elements of horizon scanning to be ready for the next ASFV or SARS-CoV2, as well as long term efforts to diagnose mortality causes, or changing patterns of pathogen exposure in serological profiles. This should not be viewed as distinct from traditional areas of conservation research. Instead, health research should be integrated into ongoing ecological, demographic investigations, thereby contributing to a more holistic understanding of tiger ecology and conservation. As an example, our ability to monitor and mitigate the effects of ASF will require more detailed understanding of boar ecology that will, in turn, inform our management of prey resources. Ultimately, population health is integral to the ecology of, and future for wild tigers and enhancing capacity in health research greatly enhances our ability to conserve the species.

Data availability statement

The bibliography of citations analyzed for this study can be found in the Cornell University eCommons repository: https://doi.org/10.7298/rpe5-wa81.

Author contributions

MG, ZD-R, and JB conceptualized the study. MG and ZD-R conducted the literature review. MG wrote the first draft of the manuscript. All authors contributed to manuscript revision, read, and approved the submitted version.

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Conflict of interest

The 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/fevo.2023.1135935/full#supplementary-material

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Restoring Asia's roar: Opportunities for tiger recovery across the historic range

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Wildlife conservation in the Anthropocene requires bold conservation solutions including restoration of ecosystems and species. The recovery of large carnivore populations is a conservation goal which can generate significant benefits in terms of ecosystem services, ecological functionality, and human well-being. Tigers *Panthera tigris*, Asia's most iconic species, are currently restricted to less than 10% of their historic range with recent national extinctions from a number of countries in mainland Southeast Asia. Tiger recovery through range expansion requires suitable habitat, a robust prey base, and high levels of institutional support for conservation. We explored government support for conservation to produce a ranking of the political opportunities for tiger restoration across current and former tiger range countries. We used this analysis, in combination with globally remotely sensed data-sets on human impact, to show that there is potential for significant tiger range expansion. We identified large expanses of currently unoccupied, but potentially suitable, habitat in at least 14 countries including all extant tiger range countries and four countries with extirpated tiger populations – Cambodia, Lao PDR, Viet Nam, and Kazakhstan. Thirty-two percent of expansion areas were within 50-km, and 50% within 100-km, of current tiger populations highlighting that in many landscapes range expansion could be driven by the natural dispersal of tigers provided connectivity is maintained or enhanced. The proportion of potential range within existing protected areas varied between <5% in India, Indonesia, and China, to >60% in Thailand and Cambodia. As such socially appropriate conservation approaches, in collaboration with local communities, will be necessary to support tiger recovery in many areas. We recommend that some of the areas which we have identified should be highlighted as significant for future tiger conservation by tiger range country governments. Whilst the landscapes and sites which we identify will require detailed ground-truthing, and all tiger reintroductions need extensive planning and feasibility assessments, safeguarding these areas for human-carnivore coexistence could provide significant planetary benefits and support both tiger recovery and Global Sustainable Development Goals.

KEYWORDS

restoration, landscape, tiger conservation, Asia, carnivore, protected area management, reintroduction

1 Introduction

Wildlife conservation in the Anthropocene requires bold conservation solutions. Current global conservation efforts have largely failed, and more ambitious commitments and innovations are required to stem wildlife declines (Mace et al., 2018; Bhola et al., 2021). Such innovations need to move beyond protection to the re-expansion of nature including ecosystem restoration and rewilding (Svenning, 2020). The UN Decade on Ecosystem Restoration (2021-2030) is a rallying call for the protection and revival of ecosystems and highlights that a strong connection exists between recovering nature and sustainable human development (Perino et al., 2019). Large carnivores have the potential to be leveraged as symbols for ecosystem restoration. They are amongst the most charismatic and ecologically significant animals and require large expanses of suitably managed habitat (Ripple et al., 2014; Albert et al., 2018). Restoring, then maintaining, viable wild populations of large carnivores, can act as a driver to preserve larger, better connected, and better-quality ecosystems. The majority of the world's terrestrial large carnivores are restricted to a fraction of their historic ranges and restoring carnivore distribution is a conservation goal which can also generate significant benefits in terms of ecosystem services, ecological functionality, and human well-being (Laliberte and Ripple, 2004; Wolf and Ripple, 2018). The Anthropocene extinction crisis is particularly acute in Asia and is exemplified by the state of the continent's most iconic species: tiger *Panthera tigris*. Whilst global tiger populations, if not distribution, are increasing, tigers remain the world's most threatened large cat. There are fewer than 5,000 wild tiger individuals and these are restricted to less than 10% of their historic distribution (Jhala et al., 2021; Goodrich et al., 2022). Since ~1850, tigers have been lost from at least 14 countries with three national extirpations, in Viet Nam, Lao PDR, and Cambodia, having occurred in the past 25 years (O'Kelly et al., 2012; Goodrich et al., 2015; Johnson et al., 2016). The successful long-term recovery of tigers requires both securing current source populations (Walston et al., 2010) and expanding the species' occupied range. Under the recently developed IUCN Green Status Assessment (Grace et al., 2021) tiger likely meets the criteria for Critically Depleted. Increasing the species' distribution, and the ecological breadth of places where tiger occur and are functional, is necessary to recover the species globally. Implementing actions to reverse the centuries-long decline in tiger range is an ambitious and politically relevant conservation goal. Such planning needs to be long-term and could help create proactive and inspirational conservation goals which move beyond defending current tiger space and allow tiger populations, and conservation successes, to expand.

Increases in tiger range can be driven by both natural range expansion, through dispersal from current tiger population sources, as well as planned translocations and reintroductions into parts of the historic distribution from which tigers have been lost (Chestin et al., 2017; Gray et al., 2017). Both of these processes are known to have driven large carnivore recovery in Europe (Chapron et al., 2014). Natural dispersal of grey wolves *Canis lupus* from sources in remote and mountainous strongholds, combined with specific reintroduction and translocation programs for Eurasian lynx *Lynx lynx* and brown bear *Ursus arctos*, have resulted in significant range expansion of these carnivores in recent decades (Boitani and Linnell, 2015). Strong legislative frameworks and political support for law enforcement, combined with increasing social tolerance for carnivores and rural depopulation, were significant drivers of this range expansion across Europe (Martínez-Abraín et al., 2020; Cimatti et al., 2021). Despite their appeal to many people, often distant from carnivore occupied landscapes, the conservation and recovery of large carnivores can be controversial (Hiroyasu et al., 2019; Manfredo et al., 2021; Vasudeva et al., 2021). Large carnivores can compete with people for space and resources. Human wildlife conflict, both real and perceived, can impact attitudes to carnivore recovery globally (Treves and Karanth, 2003; Miller et al., 2016). Most successful examples of carnivore range recovery occur in countries and landscapes with strong governmental policies facilitating and resourcing conservation and with support from local communities (Chapron et al., 2014). Similarly, landscapes with increasing tiger populations are often characterised by high levels of law enforcement, good management of species and their habitats, high community support, and local economies and jobs created around wildlife (e.g. tourism) (Dudley et al., 2020; Jhala et al., 2021). However, when assessing where the conditions for tiger recovery are present, less attention has been paid to the enabling political conditions which may support tiger conservation.

We explored issues linked to government support for conservation to produce a ranking of the political opportunities for tiger restoration across 30 current and former tiger range countries. We used this analysis, in combination with globally remotely sensed data-sets on human impact, to identify possible opportunities for tiger range expansion across Asia. We compared opportunities for tiger range expansion with current conservation priorities and focuses, measured through overlap with government protected areas and Key Biodiversity Areas (KBAs; Eken et al., 2004). Identifying range expansion opportunities and constraints is important to guide the future tiger conservation agenda and to proactively identify spaces for possible future tiger conservation. Landscapes and sites with opportunities for tiger range expansion are likely to require conservation interventions at all levels from national government to local communities. Protecting such future tiger space, in collaboration with local stakeholders, will ensure conservationists remain ahead of the curve on global tiger recovery.

2 Materials and methods

We mapped the historic range of tiger through identifying terrestrial ecoregions from which tiger were reported based on georeferenced historic tiger records, indicative of a breeding population, from between ~1750 and 2020. This historic resident breeding distribution (henceforth historic distribution) covered 11,792,218-km^2 in 30 countries (Figure 1). We mapped the current tiger distribution (henceforth current distribution) based on 'Extant' areas within the 2015 IUCN Red List assessment of tiger (Goodrich et al., 2015) which we modified to account for recently documented extirpations (Johnson et al., 2016; Suttidate et al., 2021). This current tiger distribution covered 673,737 km^2 in 10 countries (Figure 1; SI Table 1). Multiple factors influence distribution of tigers including habitat structure and, notably, prey abundance (Wolf & Ripple, 2016; Harihar et al., 2018). However, carnivore distribution may also be influenced by human pressures and behaviour which could be manifested in, for example, levels of retaliatory killing of tigers or elevated hunting pressures on prey species. We hypothesised that current (and future) tiger distribution is strongly influenced by human pressures and that the relationship between human pressure and probability of tiger presence differs between regions due to political, cultural, and ecological factors (Karanth et al., 2009; Sanderson et al., 2010). We used the global Human Modification Index (HMI) to establish the relationship between human impact and current tiger presence. HMI is a global 1-km^2 resolution raster data-set indicating the impact of human activity and comprising data on human settlement, agriculture, transportation, mining and energy production, and electrical infrastructure (Kennedy et al., 2019). We calculated the mean (plus-minus Standard Deviation) HMI score of polygons within current tiger distribution in each of the ten countries in which tiger currently occur and within each of three continental regions (South Asia; Southeast Asia; East-Central-West Asia).

Within each country in which tiger currently occur we identified polygons of area greater than 500 km^2, equivalent to the size of the smaller Tiger Conservation Landscapes identified by Sanderson et al. (2010), across the historic distribution with a mean HMI score below, and within one standard deviation either side of, the mean score for occupied tiger polygons within each country. For the 20 countries within the historic distribution that do not have current tiger populations we identified polygons of greater than 3,000 km^2 with HMI below, and within one standard deviation either side of, the mean score for the continental region (i.e. for Cambodia the score for Southeast Asia). We used this larger threshold size within former tiger range countries due to the likely need for large landscapes for new reintroductions (c.f. natural range expansion). In China we applied this 3,000 km^2 threshold for all habitat blocks outside the Amur Heilong Ecoregion except when within 100-km of current tiger distribution.

In addition to the direct human impact, indicated by the HMI score, the appropriateness of countries and landscapes for large carnivore recovery may be dependent upon a supportive political environment. We scored each of the 30 countries which comprised the historic tiger distribution based on perceived political support for conservation. Data we used provided information on general support to biodiversity conservation and specific information on planning for carnivore conservation. We collated data on domestic conservation funding (Waldron et al., 2013), protected area ranger density (Appleton et al., 2022), and, national governance (Kaufmann et al., 2011): all factors which may correlate with the probability of successful large carnivore conservation. Details of these data-sets are provided in Supplemental Materials. We weighted each of the above factors (domestic conservation funding, protected area ranger density, and governance) equally and ranked each country (high-medium-low; scored 3-2-1 points respectively) based on the relative mean score for each metric. For each country we summed the points for the three metrics. We also searched the literature and our personal knowledge to identify whether large carnivore reintroductions or translocations have been implemented in each country (Stepkovitch et al., 2022). Any country with a large carnivore reintroduction project was given an additional three points; any countries with tiger or other large carnivore reintroduction or translocations specifically in National Action Plans were given an additional 1.5 points. Based on this ranking the 30 countries comprising the historic tiger distribution were divided into three classes (high-intermediate-low) dependent on political support for large carnivore conservation.

To identify possible landscapes for tiger range expansion we combined the HMI polygons with the political support scores. For countries identified as likely highly supportive of large carnivore conservation all polygons with a mean HMI value smaller (i.e. less human impact) than the mean plus one standard deviation of occupied tiger polygons for the respective country or continental region (for countries from which tiger have been extirpated) were selected. For countries with intermediate levels of political support all polygons with HMI values less than the mean value for occupied tiger landscapes were selected, and for those with low support all polygons with HMI less than the mean value minus one standard deviation were selected. To identify overlap between current conservation priorities and possible tiger range expansion areas we compared range expansion polygons with current protected area coverage from the World Database of Protected Areas and the locations of KBAs (Eken et al., 2004). We compared land-cover between the current tiger distribution and predicted expansion areas based on the European Space Agency GlobCover data-set which has a 300-m resolution (Arino et al., 2012). We broadly classified land-cover as forested, human-modified, or other land-cover (SI Table 2). To identify predicted range expansion areas in which natural dispersal of tigers might be possible we extracted all range expansion areas within 50, 100, 250, and 500-km buffers of current tiger distribution.

3 Results

Our mapped current tiger distribution covers ~674,000 km^2 in ten countries (SI Table 1; Figure 1). This represents 5.7% of the historic tiger distribution (Figure 1). The mean Human Modification Index (HMI) within current tiger distribution varied among the ten extant tiger range countries (SI Table 1; Figure 2) and was highest in India, Bangladesh, and Nepal and lowest in Russia and Myanmar. The HMI of the current tiger distribution was higher in South Asia than in Southeast and East Asia, and higher in Southeast Asia than East Asia (SI Table 1). Almost three-quarters of current tiger distribution was classified as forest (SI Table 1). Lowest forest cover of current tiger distribution was in Nepal and India, where 40 and 55% of current tiger distribution respectively, was in human modified habitats (SI Table 1).

3.1 Political support indicators

Domestic conservation funding across the 30 current and former tiger range countries varied between 0 (10 countries) and 82 million USD/year (South Korea) with a mean of 13.7 million USD/year for the period for which data was available i.e. 2001-2008 (Waldron et al., 2013). Five of the 30 countries, including two extant tiger range countries, had 2019 governance scores above the global average (South Korea, Bhutan, Georgia, Malaysia, Mongolia). North Korea, and six former range states in Central and West Asia, had the lowest governance scores. Protected Area ranger densities varied considerably from >20 individuals per 100-km^2 to <1 per 100-km^2 in 8 countries (Appleton et al., 2022). We found evidence of implemented large carnivore reintroductions in five countries and formal plans for reintroductions (for tiger or other large carnivore) in an additional seven countries. Scoring for each country for domestic conservation funding, governance, ranger densities, and carnivore reintroductions are given in SI Table 3. Overall, we scored three countries (India, Thailand, and South Korea) as having strongly supportive political environments for large carnivore conservation and recovery. Ten countries were identified as having likely weak supportive political environments for large carnivore conservation. These were seven countries in the former range of Caspian tiger in Central Asia, North Korea, and two countries in Southeast Asia with recently extirpated (Lao PDR) or currently very low (Myanmar) populations of tiger. The remaining 18 countries were identified as having intermediate levels of political support for large carnivore conservation and recovery (SI Table 3).

3.2 Mapping areas for tiger range expansion

The HMI values we used to identify areas for possible tiger range expansion varied from 0.52 in India, to <0.01 for the six former tiger range countries with low levels of political support for conservation in Central and West Asia (SI Table 4). Using these thresholds, we identified 1,293,921-km^2 within 176 blocks of habitat ($\bar{x}$ 7,346-km^2; range 500 – 502,007-km^2) across the historic tiger distribution that is potentially suitable for range expansion (Figure 1). These areas (henceforth ‘expansion areas’) occurred across 14 countries (Table 1) including all extant tiger range countries (92.7% of predicted expansion area) and four countries with extirpated tiger populations – Cambodia, Lao PDR, Viet Nam, and Kazakhstan. The countries with the largest extent of expansion areas were India (612,718-km^2), China (201,656-km^2), and Russia (137,684-km^2). These countries comprised >70% of all expansion areas. No expansion areas were identified from 16 countries within the historic tiger distribution including North and South Korea and the majority of countries in central and western Asia. In total 32% of expansion areas were within 50-km of current tiger distribution and 50% were within 100-km. Four countries (Indonesia, Bangladesh, Malaysia, and Bhutan) had >50% of their expansion areas within 50-km of current tiger distribution (Table 1; SI Table 5).

The proportion of expansion areas within existing protected areas varied between <5% in India, Indonesia, and China to 64% in Thailand and 78% in Cambodia (Table 1). Overall, 188,066-km^2 of expansion areas (14%) were within protected areas. Overlap between protected areas and range expansion areas was low in the four extant tiger range countries in South Asia (4.7%) and highest in mainland Southeast Asian (30%). Just under 14% of range expansion areas overlapped KBAs (SI Table 4). Overlap with KBAs was highest in Lao PDR and Myanmar (>60%) and lowest in Indonesia (4.8%) and Russia (3.4%). More than 500,000-km^2 (41.5%) of range expansion area was in human modified habitat including large areas of low intensity agricultural and forest mosaics in India (SI Table 6). In Malaysia and Indonesia almost half of expansion area was in human modified habitats. In 8 of 14 countries, including all Southeast Asian countries apart from Malaysia and Indonesia, >90% of range expansion areas were in forest (SI Table 6).

4 Discussion

We demonstrate that there is potential for significant tiger range expansion across the species’ historic distribution with large expanses of currently unoccupied, but potentially suitable habitat, remaining in 14 countries. Whilst the global tiger population may be increasing from a nadir in the first decade of the 21st century, the species’ range contraction continues (Goodrich et al., 2022). Tigers currently occupy ~675,000 km^2, less than 6% of their indigenous range, and in the majority of the ten extant tiger range countries this distribution continues to shrink. Incorporating area-based conservation targets into global tiger recovery efforts may present

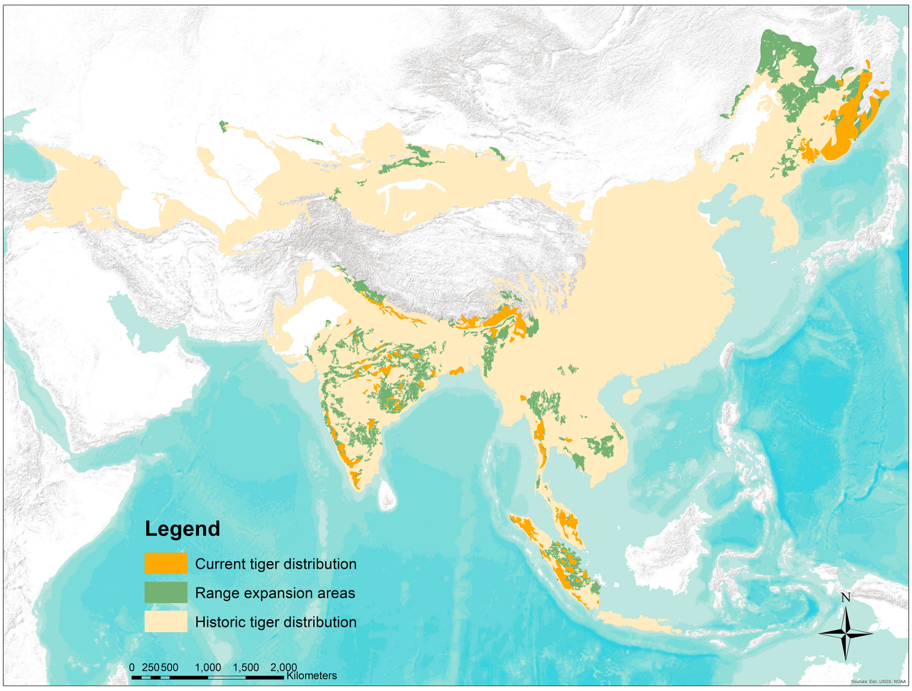

FIGURE 1
Historic and current tiger distribution and range expansion areas. Historic tiger distribution (as described in the text), current tiger distribution from Goodrich et al. (2015) amended per text. Tiger range expansion (1,293,921-km^2) per our analysis.

an opportunity to reverse this decline whilst also ensuring conservation efforts focus on some of the most important conservation wildernesses in Asia. Our expansion areas for tigers cover more than 1,290,000-km^2 in 14 countries. Safeguarding these areas for human-carnivore coexistence, through targeted conservation and land-use management interventions, could provide significant planetary benefits and support the global Sustainable Development Goals (Perino et al., 2019). We recommend that a proportion of the areas which we have identified be highlighted as significant for tiger recovery by tiger range country governments. By identifying these opportunities awareness can be raised regarding possibilities for tiger restoration and the landscapes where more detailed feasibility assessments may be required can be highlighted. Securing and increasing the protection of such areas is required to sustain tiger recovery in the long-term. Such an approach clearly fits the philosophy of the United Nations Decade for Ecosystem Restoration and may be aligned with the global vision of 30x30: a global commitment to protect 30% of the world's terrestrial and marine ecosystems as part of the 2030 Agenda for Sustainable Development (Dreiss et al., 2022). A wide range of policies, laws and regulations related to land use, forestry and natural resource management, including land tenure regulations, agricultural, forestry, environmental, rural development and climate change policies, would be needed to for integration of range expansion areas with protected area systems (DeFries et al., 2010).

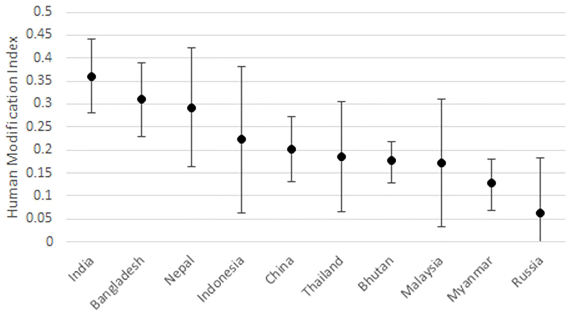

FIGURE 2
Mean (± Standard Deviation) Human Modification Index (HMI) scores for current tiger distribution in each extant tiger range country.

The expansion areas which we have identified are not a prescriptive blueprint for tiger recovery, reintroductions, or translocations. Instead, we hope that they represent some of the opportunities for future range expansion provided that the landscapes are protected, prey are sufficiently abundant, and threats are mitigated. Many of the sites identified may be worse on the ground than predicted – particularly in terms of tiger prey density, levels of effective land-use management, and community support. There is a need for country and landscape-specific ground-truthing of the expansion areas and global analyses cannot replace the need for detailed site-based assessments. Such studies, using more up-to-date and accurate information on the current distribution and status of tigers, will refine our analysis. Such country specific assessments are critical with regard to understanding habitat quality and tiger prey densities: important factors for tiger recovery but which cannot be obtained through

TABLE 1 Range expansion area (km^2) per country plus the number of discrete blocks of habitat and the percentage of expansion area within 50-km and 100-km of current tiger distribution, the percentage within Protected Areas, and the percentage classified as Forest (SI Table 2).

Country	Area (km^2)	Number of blocks	% within 50-km	% within 100-km	% within Protected Areas	% Forest
India	612,718	93	44.2	71.5	4.6	25.1
China	201,656	26	1.9	7.3	3.1 [1]	63.8
Russia	137,684	10	27.8	34.6	16.2	96.7
Indonesia	114,792	12	72.5	90.5	3.6	43.2
Thailand	94,965	19	9.3	24.3	63.9	92.9
Cambodia	70,868	2	0.0	0	78.3	90.0
Myanmar	23,688	2	26.8	65.9	17.2	97.0
Vietnam	14,501	2	0.0	0	18.6	95.2
Kazakhstan	8,617	3	0.0	0	30	0.1
Bangladesh	7,050	1	55.1	88.6	8.1	97.9
Laos	3,000	1	0.0	0	9.2	99.5
Malaysia	2,116	2	100.0	100	5.9	59.3
Nepal	1,524	2	35.2	35.2	28.9	87.4
Bhutan	742	1	100.0	100	18.5	99.4

1. Protected area coverage for China excludes the Northeast Tiger and Leopard National Park which is not yet included within the World Database of Protected Areas (www.protectedplanet.net).

remotely sensed data-sets. We hope that country specific assessments will be used to develop global goals for tiger range expansion which could be formalized as part of the revision of the Global Tiger Recovery Program (GTRP) for the next 12-years.

We demonstrate that the relationship between human activity, identified through the Human Modification Index (HMI), and the presence of tigers differs significantly between countries and regions. This relationship is likely driven by levels of anthropogenic mortality to tigers and tiger prey which in turn is linked to levels of tolerance for living with large mammals (both carnivores and ungulates) as well as the degree of enforcement of legal protection. The HMI of occupied tiger areas was higher in South Asia, particularly within India, Bangladesh and Nepal, than across the rest of the current tiger distribution. Understanding the political, cultural, and ecological mechanisms by which tigers are able to coexist with different intensities of human activity is essential for global tiger recovery. Combining HMI with political support scores adds an extra nuance to our identification of where future tiger conservation opportunities may exist. Whilst Asian countries have been identified generally as underperformers in megafauna conservation (Lindsey et al., 2017) there is significant variation in terms of conservation success, and political support for conservation, across the continent. This is exemplified across tiger range countries with more than half of the world's remaining wild tiger within a single country, India, which comprises less than 15% of the species' historic distribution (Jhala et al., 2021). We suggest there is value in incorporating measures of political support for conservation in any global analysis of conservation opportunities. Increasing both political and social carrying capacity for large carnivores is likely to expand the available area for tiger recovery globally and will be vital to the success of any range expansion goals.

We identified three of the thirty indigenous tiger range countries as being highly supportive for large carnivore conservation: India, Thailand, and South Korea. These conclusions are validated by some independent information such as India's success in tiger conservation (Jhala et al., 2021) and that Thailand supports the most significant tiger population in mainland Southeast Asia (Duangchantrasiri et al., 2016). We believe both Thailand and India have significant opportunities for tiger range expansion. South Korea has successfully reintroduced Asiatic black bears *Ursus thibetanus* (Andersen et al., 2022) but our analysis did not indicate opportunities for range expansion due to the country's high HMI in comparison with the regional (i.e. Northeast Asia) threshold. However, opportunities for big cat conservation may exist in the Korean peninsula (Jo and Baccus, 2016) and we recommend including South Korea within the family of tiger range countries. Two Southeast Asian countries were classified as having a poor political environment for large carnivore conservation: Lao PDR and Myanmar. Lao PDR is the most recent country to have lost its tiger population and is regularly highlighted as a country of concern for the global illegal wildlife trade (van Uhm and Wong, 2021). Tiger populations in Myanmar have significantly declined in the past 20-30 years and currently ~20 individuals remain in the transboundary Dawna Tenasserim and Upper Chindwin Landscapes (Goodrich et al., 2022). Whilst both Lao PDR and Myanmar remain extensively forested, with low HMI, the opportunities for proactive tiger conservation and range expansion are limited by the current political realities.

In South and Southeast Asia, the majority of range expansion areas were within 100-km of current tiger distribution: significantly less than the documented straight-line dispersal distance of tigers (Smith, 1993; Singh et al., 2013; Hussain et al., 2022). Natural dispersal into many of these areas may be possible provided that the landscape matrix allows tiger movement through both reducing anthropogenic mortality and physical barriers to dispersal. Expansion areas close to current tiger distribution may be the future frontiers of tiger dispersal and colonisation. As such they need to be the focus of conservation and land-use planning and community sensitisation to prepare for possible future tigers. To drive such tiger recovery, the protection of source populations must remain a priority for tiger conservation (Walston et al., 2010). In South Asia the majority of range expansion areas are outside protected areas and, particularly in India, comprise mosaics of low intensity agricultural cultivation and forest. There is increasing recognition of the critical role in which non-protected areas and indigenously managed land play for conservation (Garnett et al., 2018). Community-led studies are needed to understand the impact of possible tiger expansion into all areas, but particularly those outside of protected areas, and to develop supportive conservation strategies that incorporate the needs and perspectives of local communities. Such studies would need to be conducted largely at a site level, given the variation of social carrying capacity between sites, and will need to capture the heterogeneity that exists within communities and thus examine how range expansion can impact different groups. Using a rights-based approach to build partnership with local communities is of vital importance to ensure conservation investments are effective and that conservation actions benefit the local people who most often bear the highest costs (Carter et al., 2014; Hanson et al., 2019). Appropriate area-based conservation mechanisms, in collaboration with local communities, may be appropriate to secure many of these areas for tiger range expansion. Such an approach is likely to be aligned with the global vision of 30x30 and accelerate active contributions towards multiple targets of the Post-2020 Global Biodiversity Framework (GBF).

For expansion areas that are isolated from current tiger distribution, reintroductions can be considered. Large carnivore reintroductions are an increasingly widespread, and increasingly successful, conservation tool. Tiger reintroductions using wild captured or rehabilitated tigers, have been successful in a number of tiger range countries including India and Russia (Goodrich et al., 2015; Sarkar et al., 2016). Three landscapes which we identified - Ili-Balkhash in Kazakhstan, the Cardamom Rainforest and the Eastern Plains Landscapes in Cambodia – are the focus of current tiger reintroduction plans (Chestin et al., 2017; Gray et al., 2017). Those in Kazakhstan, where initial tiger releases are planned for 2025, are the most advanced. Tiger conservation efforts in China, the country with the second largest expansion area and where the vast majority of expansion areas are >100-km away from current tiger distribution, are also likely to greatly benefit from reintroduction. Such reintroductions could complement the ongoing recover of tiger populations and habitat within China (Qi et al., 2021). The possibility of using captive tigers for reintroduction and translocations within China to support range expansion should be explored particularly given evidence of inbreeding within wild populations (Ning et al., 2022). However captive tigers for rewilding must be obtained from reputable, conservation breeding programs, in no way implicated in illegal tiger trade. Gray et al. (2017) developed a framework for assessing broad scale site feasibility for tiger reintroductions. We recommend such analysis be conducted within any proposed reintroduction landscape. Effective protected area management, community support, and sufficient prey numbers are essential. In landscapes where tigers have become extinct, developing coexistence and monitoring tools with extant carnivore species such as leopards *Panthera pardus* and clouded leopards *Neofelis* spp., could pave the way to easing political support for eventual tiger reintroductions or natural recolonisation.

Across much of the tiger's historic distribution the density of tiger prey species is significantly depleted due to both legal and illegal hunting. Half of the mammalian prey species of tiger are threatened with extinction, and roughly 80% have decreasing population trends (Wolf and Ripple, 2018). This lack of prey is a major constraint to tiger recovery (Harihar et al., 2018; Steinmetz et al., 2021). The impact of prey declines on the feasibility of tiger recovery is illustrated in Cambodia's Eastern Plains Landscape where robust monitoring has demonstrated ongoing reduction in the densities of key tiger prey species (Groenenberg et al., 2020). This has delayed plans for reintroduction. In Kazakhstan increasing prey densities, through habitat manipulation and active reintroductions of prey, is a conservation focus in readying Ili-Balkhash for the return of tigers. Prey restoration in Kazakhstan includes reintroduction of Bukhara deer *Cervus hanglu bactrianus* as part of a multi-country conservation initiative which has seen recovery of the subspecies from as low as 350 individuals to over 3,500 in the past 20 years (Pereladova et al., 2020). In many expansion areas the opportunities for tiger recovery could benefit wider species conservation. In both Cambodia and Kazakhstan, plans for tiger reintroduction led to the creation of new protected areas (Souter et al., 2016; Chestin et al., 2017), and in both countries the tiger is being used as a flagship conservation initiative to support wider investment in biodiversity protection. Moreover, if they reach ecologically effective densities, tiger populations may themselves support conservation of other species, although more research into potential trophic cascades is needed (Ripple et al., 2014).

Given their large home-ranges the conservation of carnivores can compete for space with economic development, including extractive industries and infrastructure. Many areas of low human impact globally are targeted for exploitation particularly for minerals and fossil fuels. Grantham et al. (2021) found that nearly a fifth of Intact Forest Landscapes in the tropics are currently designated as some form of extractive concession. We found similar patterns across our expansion areas many of which are impacted by infrastructure and extractive industries (SI Table 7). Roads are known to impact large carnivores (Quintana et al., 2022) due to wildlife-vehicle collisions, habitat loss and fragmentation, and increased access leading to increased poaching of tiger and prey including through snaring (Gray et al., 2018). As such road expansion has been identified as a threat to tiger conservation (Carter et al., 2020). Roads occurred within the vast majority of blocks of range expansion within highest densities of roads in South Asia and Indonesia (SI Table 7). Minimising threats from roads for both expanding and reintroduced tiger populations will be important and, in some cases, there may be a need for the diversion or closure of existing roads. Extractive industries, for both minerals and fossil fuels, are impacting approximately 15% of the blocks of range expansion (SI Table 7). This impact is not evenly distributed across countries with expansion areas in mainland Southeast Asia (Cambodia, Lao PDR, Myanmar), particularly impacted. Efforts to invest in range expansion of tigers will need to consider the full added value of large carnivore recovery including social and environmental services provided by a restored and protected ecosystem. Key aspects of this would be around economic viability and sustainability and critically the economic benefits to local communities in the area. Co-benefits could include but are not limited to carbon storage and sequestration, watershed management, job creation, and ecosystem resilience (WWF, 2017). The research and articulation of these co-benefits will be vital to securing and increasing political and social support for range expansion efforts.

As with all global conservation analysis our results are impacted by the quality of the data used. Neither our current or historic tiger distributions will be completely accurate. The current tiger distribution from Goodrich et al. (2015) is relatively dated and, particularly in South Asia, a number of our predicted expansion areas may now support tiger - albeit at relatively low densities. For example, the most recent national India tiger census detected a minimum of two tigers within Cauvery Wildlife Sanctuary in Karnataka, which forms part of a large block of our expansion habitat (Jhala et al., 2019). Conversely, not all of the historic tiger distribution may form habitat or ecosystems which are suitable for tigers even at low levels of human activity. It is likely that some of the expansion areas may not be currently suitable for tigers as a result of major landscape level transformations or other socio-cultural changes. However, predicted increases in urbanisation, under a number of future development trajectories, may reduce HMI in key landscapes and increase opportunities for future tiger range expansion (Sanderson et al., 2019).

The St Petersburg Tiger Summit in 2010 and the range-wide endorsement of the Tx2 Goal have revolutionised tiger conservation and spurred unprecedented conservation efforts and investments (Jhala et al., 2021). These led to tiger population increases in many landscapes. However, tiger population increases have not been mirrored by increases in tiger distribution with a 17% loss of area occupied by tigers between 2001 and 2020 (Goodrich et al., 2022). Globally we have more tigers but in fewer landscapes and fewer ecosystems than at the beginning of the 21st century. In many sites currently occupied by tigers there are considerable opportunities to increase tiger numbers (Harihar et al., 2018) through improved site management (Dudley et al., 2020) and increasing the density of prey species (Phumanee et al., 2020). In Southeast Asia, where tiger numbers continue to decline, effective anti-poaching and community engagement are also critical (Linkie et al., 2015). Securing a viable and ecologically representative future for tigers requires both securing current populations (Walston et al., 2010) and expanding the occupied range. Effective management of current tiger populations is essential for driving natural dispersal of tigers into new areas particularly within South and East Asia (Qi et al., 2021). However, we argue there is also a need for proactive planning for future tiger range expansion. This should include both places into which tigers may naturally disperse and those which may be suitable for future reintroduction. Tiger reintroductions can galvanise conservation efforts and help protect additional habitat and support the expansion of Protected Areas and Other Effective Conservation Measures (OECMs). We identify some of the opportunities for tiger range expansion across the species' historic distribution and recommend that some of these areas be included within a tiger range expansion target which should be developed and endorsed by tiger range countries. Focusing conservation efforts on some of these places could prepare for the return of the tiger whilst also securing critical conservation landscapes and benefiting both people and wildlife.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Author contributions

TG, SC conceived the study. TG, RR, PI, DP conducted the analysis. TG, RR, GJ, PI, JY, LK, AL, MP, PC, QJ, WR, JR, SR, NS, CW wrote the manuscript. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The 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.2023.1124340/full#supplementary-material

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Using a crime prevention framework to evaluate tiger counter-poaching in a Southeast Asian rainforest

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Tigers are a conservation-reliant species, as multiple populations face the risk of local extinction due to poaching arising from the continued demand for their body parts. Preventing tiger poaching poses a challenge for the rangers responsible for their protection, particularly in Southeast Asia, where the protected areas are typically large, mountainous tropical forests guarded by small teams of rangers. Improving counter-wildlife crime tactics is hindered without robust evaluations, and inefficient approaches are perpetuated. We evaluate an eight-year project aiming to recover a tiger population in Peninsular Malaysia. Three distinct poaching problems by Vietnamese, Thai and Cambodian groups, differing by organisation, target species and tactics, were prioritised, and ranger counter-poaching tactics were tailored to reduce these. Applying a framework developed to evaluate crime prevention known by the acronym EMMIE, here we: (1) examine evidence our intervention was *Effective* in reducing the poaching threat; (2) resolve the *Mechanisms* by which our intervention caused a reduction in harm from poaching and how intervention effectiveness is *Moderated* by the three poaching types; (3) define the elements necessary for *Implementation* and the *Economic* costs involved. We found poaching incursion frequency fell 40% from baseline years to treatment years across all poaching types while poaching incursion depth declined, with disrupted incursions on average, 2.6 km (Thai) and 9.1 km (Cambodian) closer to the forest edge. However, wire snares increased from baseline to treatment years as Vietnamese poachers increased the number of snares per incursion eightfold. No poaching incursions were observed during the Covid-19 pandemic. Tiger density remained below recovery potential (0.48/100km^2 in 2014 to 0.53/

100 km^2 in 2021) but stabilised as key females survived and were detected breeding. Leopard, sun bear, muntjac and wild boar densities remained stable. Disarming active snares and seizing an increased proportion of snares before being deployed directly reduced the potential risk of mortality to medium-large mammals once a poaching incursion began. Attributing the decline in poaching attempts to our intervention is supported for Cambodian poachers via three plausible mechanisms: increased cost of reoffending by repatriated poaching team leaders; reduction of detailed knowledge sharing and imitation by peers; general deterrence at community level from increased awareness of the elevated risk of arrest and low likelihood of enjoying rewards. We found ranger performance enhancements at three critical stages of counter-poaching were instrumental in increasing arrest certainty, this was made possible by institutionalising a learn-and-adapt cycle underpinned by a dedicated site analyst. This study highlights how investing in problem analysis and going beyond simple assumptions of deterrence can greatly enhance the effectiveness and efficiency of small wildlife protection teams.

KEYWORDS

tiger poaching, adaptive management, EMMIE, crime prevention, rangers, evaluation

1 Introduction

Tigers (*Panthera tigris*) are among the world's most iconic animals and umbrella species in their habitats. However, wild tiger populations occupy a mere 7% of their historical range due to centuries of persecution. Recent estimates highlight that there are approximately one million km^2 of tiger habitat devoid of tigers - a testament to the continued poaching problem in Asia, driven by the illegal trade in tigers and prey animals (Goodrich et al., 2022). This threat is acutely realised in Southeast Asia, where vast swaths of seemingly intact forests experience hunting-induced defaunation. As a significant cause of this defaunation, indiscriminate snaring driven by the demand for bushmeat locally and in urban centres, as well as wire snares being an inexpensive and highly effective method of capturing several species of commercial importance (Gray et al., 2017), has dramatically altered mammalian assemblages, even leading to the extinction of certain tiger sub-populations (O'Kelly et al., 2012; Johnson et al., 2016; Gray et al., 2017) and range declines of other endangered carnivores such as leopards *Panthera pardus* (Rostro-García et al., 2016) and clouded leopards *Neofelis nebulosa* (Macdonald et al., 2019; Macdonald et al., 2020). In response to the crisis, range country governments and NGOs have improved law enforcement efforts; however, on-the-ground interventions that prevent poaching must be conducted and evaluated (eg. Linkie et al., 2015).

Protecting tigers in rugged landscapes can be costly and logistically challenging, and arrests of poachers are rare. Rangers tasked with protecting tigers need to be better equipped and more motivated to perform a dangerous and highly technical role (Belecky et al., 2021). Furthermore, solutions proposed to address these challenges are often simplistic and based on perceived best practices, such as increasing the number of "boots on the ground" or implementing harsher penalties with the flawed assumption that general deterrence will cause the poaching problem to decline (Moreto and Charlton, 2019; Wilson and Boratto, 2020). General deterrence theory suggests that the effectiveness of punishment depends on the certainty, speed, and severity of punishment (Beccaria, 1986), with certainty recognised as the most important (Nagin, 2013). Across conservation, impact evaluation is extremely rare. Whether in projects using behavioural change campaigns or with law enforcement interventions, systematic reviews have found that extremely few published studies either describe the impact or attempt to critically examine the causal relationship between the intervention and any decline in the threat (Delpech et al., 2021; Thomas-Walters et al., 2022). This absence of a robust evidence base prevents critical lessons about what works from being learned and shared, leading to the repetition of perceived yet ineffective approaches.

To evaluate the project's impact on reducing tiger mortality, one could use a crime prevention framework that has become the gold standard in evaluating police interventions (Johnson et al., 2015) – EMMIE. This framework stipulates that an evaluation should describe the *Effect* of the intervention (how much it caused the problem to decline by), the *Mechanism* of the intervention (how exactly did the intervention work), what factors *Moderate* the effectiveness of the intervention, how was it *Implemented* and what were sources of success or failure, and finally what were the *Economics* of the project (how much did it cost and was there evidence of cost-savings). Beyond confirming a causal relationship between the intervention and a decline in the problem, the utility of evaluations to other practitioners is boosted by identifying how and why the intervention worked and in what context.

The full impact of an intervention can only be assessed when incorporating an understanding of any crime displacement that occurred, as well as any diffusion of benefits to non-focal groups or outside the focal area. Crime displacement occurs when offenders react to an intervention by switching target, changing tactics, moving to a new location, switching to a different type of crime altogether, or by one offender group replacing another (Eck, 1993). Crime displacement in conservation is rarely considered or applied to describe unusual trends without closely examining underlying assumptions (Kurland et al., 2017). This may derive from confusion over whether a phenomenon is intentional or an artefact of sampling, and whether it is a reaction to an intervention, or an independent innovation. Criminals innovate new techniques, exploit new places and markets independently of any interventions. However, interventions may accelerate and direct the nature of these innovations, and crime displacement was found to occur in 25% of studies examined, the same rate as studies reporting diffusion of benefits from an intervention (Guerette and Bowers, 2009).

Here, we used EMMIE to evaluate the effectiveness of protection efforts to conserve wild tigers, focusing on the impact of key structures and processes developed to control tiger poaching in a mountainous protected area in northeast Peninsular Malaysia. We also examine the challenges and limitations of our approaches and suggest ways to improve or strengthen them. Overall, our findings can contribute to developing more effective conservation strategies for wild tigers and help ensure the long-term survival of this iconic species in the region.

2 Materials and methods

2.1 Background

In Peninsular Malaysia, poaching for the illegal wildlife trade has been identified as the most critical threat to the Malayan tiger subspecies (*P. t. jacksoni*) (Clements et al., 2010), with the population plummeting from an estimated 3,000 in 1954, to 200 by 2020 (Ten et al., 2021). The Kenyir Core Area (hereafter known as Kenyir), comprises 1,200km^2 of mountainous tropical forest in Taman Negara, a globally recognized source site embedded in a priority tiger landscape (Sanderson et al., 2006; Walston et al., 2010), Kenyir State Park (gazetted 2018) and permanent forest reserves in Terengganu state (Figure 1). In 2014, in line with Malaysia's National Tiger Action Plan (Department of Wildlife and National Parks Peninsular Malaysia, 2008) and Panthera's Tigers Forever Protocol (Goodrich et al., 2013), Malaysian NGO Rimba, in partnership with Panthera and Woodlands Park Zoo, initiated a project with the Department of Wildlife and National Parks (DWNP) to recover Kenyir's tiger population by 50% by 2024.

2.2 Problem analysis and poaching type moderators

Between 2015-2023 poaching sign observations detected by patrols were categorised by poaching type and stored and managed in Spatial Monitoring And Reporting Tool (SMART; www.smartconservationtools.org). A poaching incursion was defined by nine key activities including entry of the poaching team to the site, camping, harvesting wildlife and departing (Figure 2). During an incursion, poaching teams leave sign with distinct characteristics. Poaching sign was aggregated to a specific incursion through the age of the sign, geographical proximity, and unique identifiers such as litter, tree markings, camp and snare signatures.

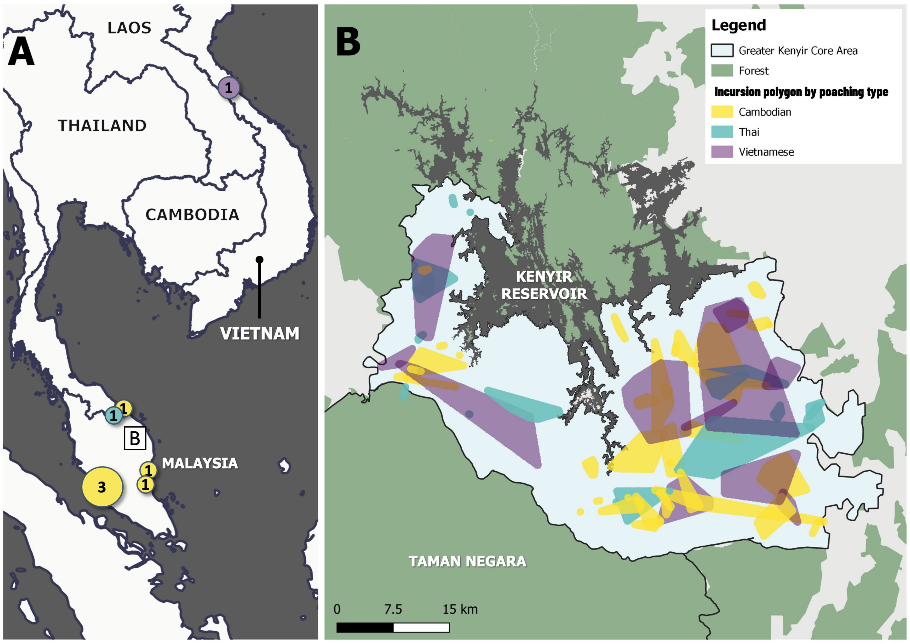

FIGURE 1
(A) Location of the Kenyir Core Area within Peninsular Malaysia. Bubbles indicate district of origin of Thai, Cambodian and Vietnamese poaching teams where known. Bubble size indicates the number of known poaching incursion attempts made from each district; **(B)** The Kenyir Core Area in detail indicating the extent of poaching incursions detected.

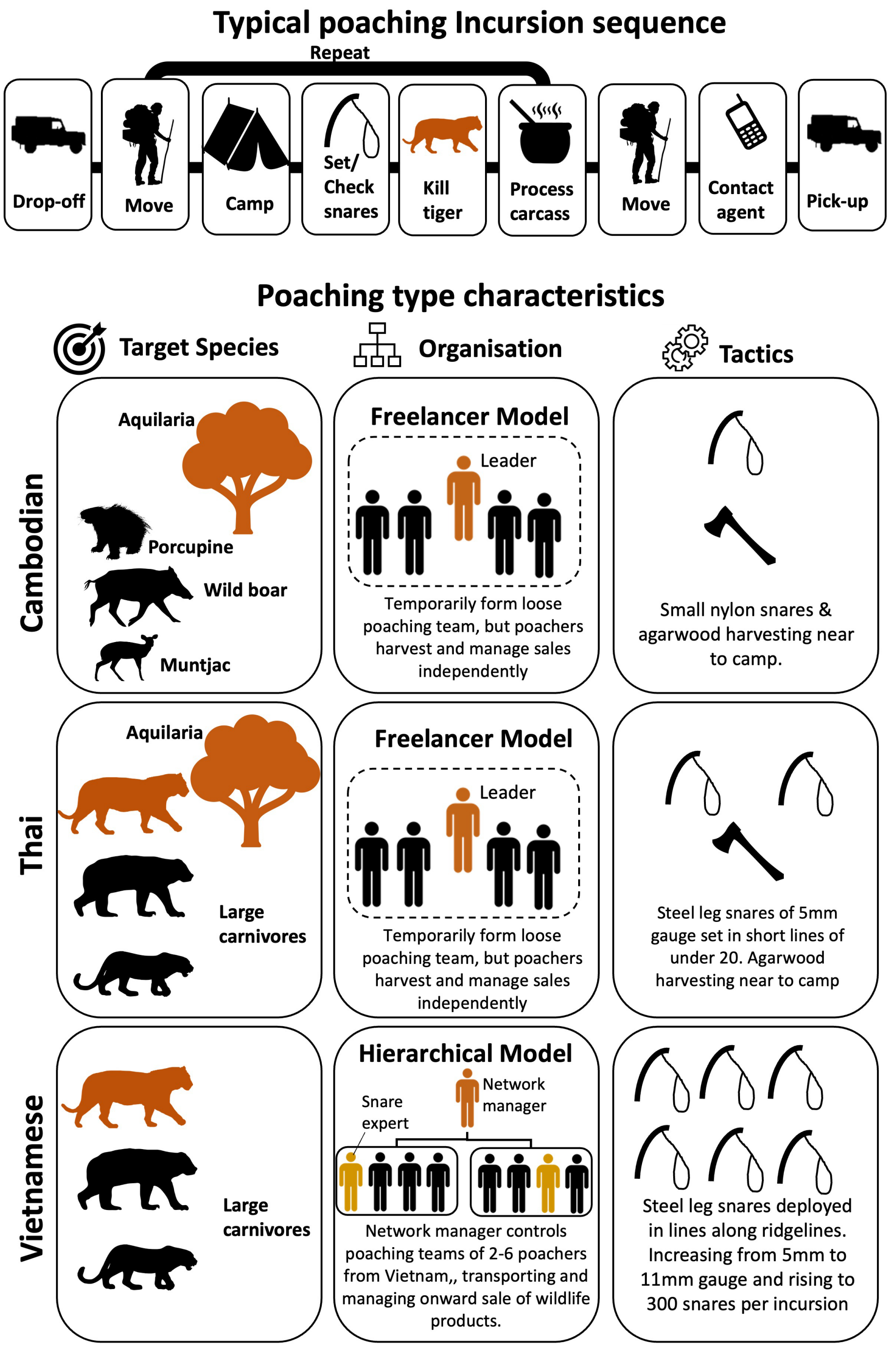

FIGURE 2
A typical poaching incursion sequence and characteristics distinguishing the three poaching types in the Kenyir Core Area.

Following the patrol debrief, all observations attributed to an incursion were tagged with an incursion-unique reference number to enable spatial querying. From 2016 onwards, DWNP Investigating Officers began asking questions in post-arrest interviews regarding poaching team organisation and decision-making within the landscape. From 2016-2019, seven interviews took place. This was complemented with by-catch data from tiger survey cameras, and poacher cameras deployed at the forest edge.

Investments in problem analysis and institutional learning were instrumental in developing this intervention. The team adopted a problem-oriented wildlife protection approach (Lemieux and Pickles, 2020). Increasing the granularity of threat from 'tiger poaching' or 'snaring' to resolve specific poaching problems provided sharper focus and mission objectives. Analysis of snare volume by poaching type conducted in 2016 identified non-Malaysian poachers as a priority threat to address, sharing similarities including living far from the site, operating for multiple months deep inside the forest, and being supported by vehicle transportation by a third party (Lam, 2018). Disaggregating this poaching threat revealed three distinct nationalities: Vietnamese, Thai and Cambodians, differing in target species, organisation and methods (Figure 2). Vietnamese and Thai poaching incursions involved wire leg-snares set for large carnivores (tiger, leopard and sun bear), to sell body parts to traditional Chinese medicine markets. Tiger carcasses were flensed and skeletons boiled in large pots over several days to create bone glue, while sun bear gall bladders, claws and canines, and leopard claws and canines were removed and dried (Lam and Mat, 2020). Cambodian poaching teams were recorded using rope or nylon snares for argus pheasant, mouse deer, porcupine, muntjac and boar for consumption inside the forest. Cambodian teams almost primarily harvested valuable agarwood from Aquilaria trees, for perfume markets in the Middle East.

Analysis of non-Malaysian poaching types informed a revised protection strategy in 2018. Our strategy assumed three mechanisms to reduce poaching and recover the tiger population. First, counter-poaching performance improvements would lead to earlier detection and arrest of Vietnamese, Thai and Cambodian poaching teams, resulting in fewer snares deployed and less immediate harm to tigers. Second, awareness of the increased risk to poachers would spread within poaching communities and dissuade other poaching teams from targeting Kenyir, resulting in a decline in poaching incursion attempts. Third, understanding that there are different roles within a poaching team, the impact of any arrest on subsequent poaching attempts would depend on the role and experience played by a poaching team member arrested (Duijn et al., 2014). Apprehending a poaching team leader or experienced snare setter was judged to have a greater disruption impact on subsequent poaching attempts than a porter, cook, or junior member. Maximising arrests within a poaching team was therefore prioritised before conducting a snare sweep. DWNP and NGO partners Rimba and Panthera developed a specialisation in deep-forest counter-poaching operations (DFCPO), synthesising tracking and search and rescue theory. The NGO partners maintained civilian scout teams, detecting active incursions and guiding arrest teams. DWNP ranger teams could detect incursion alerts but were also instrumental in conducting arrests. In 2017, DWNP formed the Special Protected Areas Response Team (SPARTA) unit as a deep-forest specialist counter-poaching unit.

2.3 Evaluation approach

This evaluation covers eight years from January 2015-January 2023, in which we compare Baseline years (2015-2016) with Treatment years (2018-2019) following the implementation of the revised strategy. We examine the COVID-19 pandemic years (2020-2021) and post-COVID years (2022) separately. We use EMMIE (Johnson et al., 2015) as our overarching framework and have structured the methods and results accordingly (Figure 3). First, we establish the impact (Effect) of the intervention on the poaching problems and tiger recovery, using Eck's (Eck, 2017) Four Point Test to examine the evidence for causation. We then examine how the intervention may have worked (Mechanism) by testing a theory of change using a logical framework (Stewart et al., 2020) and assessing 15 indicators (Table 1). We contrast the three poaching types to identify where the intervention appears to have worked best (Moderators). Finally, we examine how the intervention was conducted, the main challenges overcome (Implementation), and the costs (Economics).

2.3.1 Effect of the intervention

2.3.1.1 Did the poaching problems decline?

The size of each poaching problem was assessed using four dimensions. Starting at the community level, we used post-arrest information to identify the number of different communities poaching teams were coming from, and to examine the cessation of poaching activity by specific communities (Indicator 7). We measured the success of poaching incursion attempts in Kenyir each year (Indicator 8) by classifying incursions as 'successful' if the ranger team did not intercept. Poaching incursions were classified as 'failed' if there was an apprehension, or a ranger team seized or destroyed essential equipment and rations, forcing the poaching team to abort. We assessed the change in maximum penetration depth of incursions (Indicator 9) by first estimating the likely drop-off point direction from the overall distribution of sign. Potential access routes including recent logging roads, plantations and minor roads were digitised from satellite image data by students from the University of Montana's Geography Department, and the symmetrical difference operation was performed using QGIS 3.16.9 to exclude road segments within Kenyir. Closest potential vehicle drop-off point to the deepest point for each incursion was determined using the 'st_nearest_feature' from the 'sf' package (Pebesma, 2018) in the R Statistical Software v4.2.1 (R Core Team, 2021) and Euclidean distance between the deepest point of each incursion and potential drop-off point was calculated using the "st_distance' function from the 'sf' package (Pebesma, 2018). Boxplots were generated using the 'ggplot2' package (Wickham, 2016) for each poaching type for baseline and treatment years to assess change in incursion depths. We quantified the extent to which the project mitigated harm to tigers from snares by classifying snares based on status when found and scoring them based on their kill potential (Indicator 10). All snares used in Kenyir involved the same basic construction involving a wire noose was attached to a sapling spring pole and held under tension, lying on a small platform above a pit approximately 30cm deep. The snare was activated by an animal placing its foot on the platform, pushing it into the pit, and releasing the spring pole, which drew the noose tight. These construction elements allowed snare placements to be detected over a year later. For all snares and poaching signs detected, the 'date of last use' was estimated by experienced trackers based on weathering characteristics. Ageing stands of discards and sign commonly found in a poaching incursion were maintained at the field station for comparison, and refresher training was regularly conducted. This technique allowed us to avoid snare counts being highly sensitive to current patrol efforts, as snares could be detected by a patrol in 2020 but backdated to an incursion in 2019, for example.

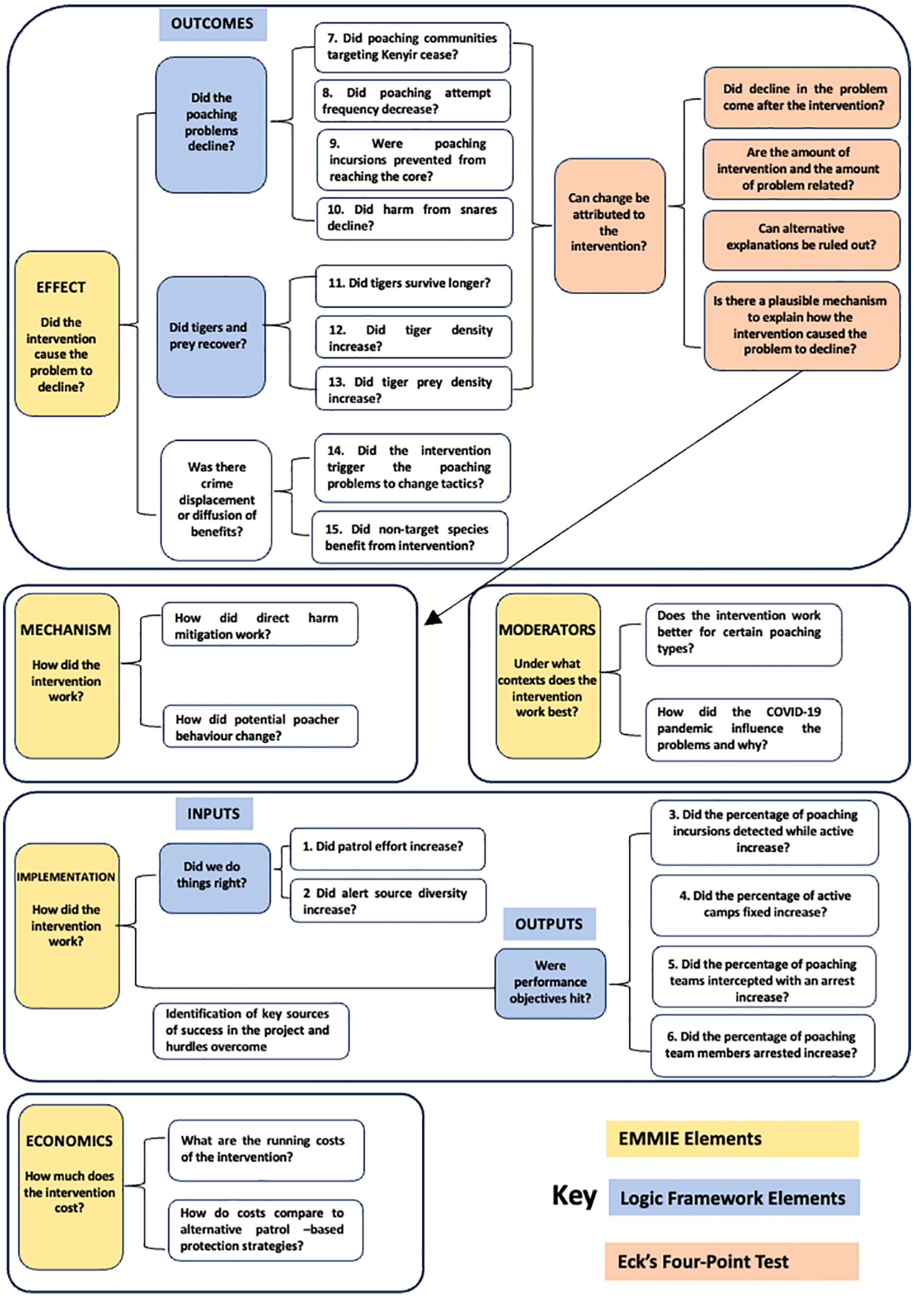

FIGURE 3
Assessment methods used in the evaluation of the counter-poaching intervention in Kenyir and specific indicators used. The arrangement of questions corresponds to the flow of this publication.

2.3.1.2 Did tigers and prey recover?

Large-scale camera trap surveys were conducted in 2014, 2017 and 2021 with camera traps deployed in a 2.5 x 2.5km array covering a monitoring area of 600 km^2 in the centre of Kenyir. Surveys were conducted from May to November when conditions were dry. PantheraCam V4, V5 and V7 units (Oliff et al., 2014) were placed on ridgelines and places with tiger signs to maximise detection. For the years not covered by systematic surveys, *ad hoc* cameras were placed in high detection stations to maintain awareness of focal individual tigers. Individual tigers were manually identified by their stripe pattern and tracked across survey years to estimate persistence (Indicator 11). Next, we used spatially explicit capture-recapture (SECR) to estimate tiger density using the maximum likelihood approach (Indicator 12). All analyses were done with packages "secr" (Efford, 2018), "rgdal" (Bivand et al., 2015), "wiqid" (Meredith, 2020), and "nimble" (Ghoting et al., 2011) in Rstudio (RStudio Team, 2020). We calculated an index of tiger prey density using the space-to-event (STE) method (Moeller et al., 2018), which uses the spatial distribution of animal detection events. STE is a method for estimating population density; however, since we employed cameras that targeted tigers, we interpreted the

TABLE 1 Indicators used to evaluate success of counter-poaching operations.

Indicator	How measured
1. Protection Effort	Foot patrol hours inside the Kenyir Core site.
2. Alert Source Diversity	Ratio of alerts of poaching incursions from patrols, cameras and community contacts
3. Poaching incursions detected while active: Missed incursions ratio	An 'active' incursion was defined by the evidence for the alert estimated at under three weeks old (including ground signs, a report from the community, or camera trap image). Incursions for which the evidence was older than three weeks were classed as 'missed'.
4. Active poaching camp fixed: Camp missed ratio	A 'fixed active camp' was defined by a ranger team having direct sight of the poaching camp following a search operation and confirming that it was still in use. Search operations that failed to locate the active poaching camp were classed as 'missed'.
5. Interdiction successful: Interdiction failed ratio	An interdiction was classed as a success if at least one member of a poaching team was arrested.
6. Poachers arrested: Poachers escaped ratio	The total number of poachers in a team was estimated by a mix of evidence after an interdiction attempt including counting hammocks, identifying personal effects and through post-arrest interviews.
7. Cessation of activity of poaching communities	Communities of origin of poaching teams were assessed during post-arrest interviews.
8. Poaching incursions attempts and success	A poaching incursion was considered to have 'failed' if the patrol team had made an interdiction attempt and either the poacher was apprehended and/or the ranger and critical equipment were seized, forcing the team to abort. All other poaching incursions which were not disrupted were classed as 'successes'.
9. Maximum poaching incursion penetration depth	Euclidean distance between most central observation of an incursion and nearest potential vehicle access point on edge of Kenyir.
10. Snare Harm Mitigation	Snares were classified as prevented, disarmed or missed. A 'prevented' snare was removed by a ranger team before it could be deployed, either taken from a poacher's camp, or an uncut reel of steel wire in which potential snares were calculated based on a rule of 3m per snare. A 'disarmed' snare was removed by a patrol while still capable of trapping an animal. 'Missed' snares were no longer capable of trapping an animal due to age and weathering. Removal of missed snares had no harm mitigation effect.
11. Individual tiger persistence	The percentage of each cohort of tigers detected in a survey that had been redetected since the previous survey.
12. Tiger density	Densities of tigers were estimated using spatially explicit capture-recapture from camera trap images in a 600km^2 central monitoring zone.
13. Prey density	Density indices of wild boar and muntjac. were estimated using the space-to-event method from camera trap images in a 600km^2 central monitoring zone.
14. Crime displacement	Evidence appraised that two observed phenomena were (a) intentional, (b) a reaction to the intervention and (c) weakened the effect of the intervention.
15. Diffusion of benefits to non-focal species	Densities of leopard and clouded leopard were estimated using spatially explicit capture-recapture. Density indices of Malayan tapir, sun bear were estimated using the space-to-event method from camera trap images in a 600km^2 central monitoring zone.

density estimate as an index of density since the model relies on a random camera placement design. For the analyses, we applied an occasion definition of 5 seconds every 30 minutes, where simultaneous species detection across all camera trap stations was tabulated. The viewshed was kept constant throughout the years and stations, and the analyses were conducted with the package "spaceNtime" (Moeller and Lukacs, 2021) in Rstudio (RStudio Team, 2020). Using this index, we assessed the trends of tiger prey with sufficient detections: the southern red muntjac (*Muntiacus muntjac*) and wild boar (*Sus scrofa*) (Indicator 13).

2.3.1.3 Did our intervention cause the problems to decline?

To examine whether any decline in the poaching problems could be attributed to our intervention, we applied Eck's (Eck, 2017) four-point test. This asks: 1) the decline in the problem occurs after the intervention; 2) the amount of intervention and the amount of problem are related; 3) alternative explanations are rejected; and 4) there is a plausible mechanism to explain how the intervention caused the problem to decline. We assessed the evidence for points 1 and 2 by comparing annual incursion frequency estimates

(Indicator 8) against patrol hours inside Kenyir as a proxy measure for the combined intervention. We tested possible alternative explanations by developing predictions if they were true, and testing these using information from patrol observations, post-arrest interviews, online searches and interviews with subject matter experts. The evidence for plausible mechanisms by which the intervention caused the problems to decline is described below.

2.3.1.4 Was there crime displacement or diffusion of benefits?

We examined the evidence for crime displacement caused by the intervention using available patrol data, debriefings, and post-arrest interviews. It was not possible to test for geographical displacement due to changes in detection efforts outside Kenyir between baseline and treatment years. Trends detected in shifts in tactics or offenders were examined, and the evidence appraised that these were: a) caused by the intervention; and b) intentional decision-making by the potential poachers. Two possible crime displacement phenomena were detected: (1) an increase in the number of snares per Vietnamese incursion; (2) a decrease in the number of poachers per Cambodian poaching team. As snaring indiscriminately affected multiple medium to large ground-dwelling mammal species at our study site, we wanted to determine if our tiger-specific intervention conveyed benefits to non-target species. We estimated clouded leopard density (*Neofelis nebulosa*) using the maximum likelihood approach for SECR and tracked individual persistence across survey years. Melanistic leopard (*Panthera pardus*), detections did not allow individual identification with our Xenon flash camera traps. Hence, we implemented the Spatial Count (SC) (Chandler and Andrew Royle, 2013) model with priors from Hedges et al. (Hedges et al., 2015) to estimate leopard density. For two other species of high conservation value, Malayan tapirs (*Tapirus indicus*) and sun bears (*Helarctos malayanus*), we followed the same protocol as for tiger prey to develop a density index (Indicator 15).

2.3.2 Mechanism & moderators of the intervention

We investigated the mechanism by which the intervention may have caused the poaching problems to decline in two ways. First, we used a logical framework to map a theory of change by which our inputs would deliver intermediate results (outputs) and ultimately desired problem decline and population-level outcomes (Figure 4). We then measured indicators 7-10 to test this theory of change, conducting separate analysis for Vietnamese, Thai and Cambodian poaching types.

Second, we conducted a post-hoc interrogation of the mechanism by which elevated risk of arrest may have led to a reduction in incursion attempts to Kenyir. This combined opportunistic details of poacher decision-making from interviews with poachers, community members and subject matter experts in enforcement agencies, contextualised with wider open-source reporting. This was conducted separately for each poaching type and the reasons for differences examined.

2.3.3 Implementation & economics of the intervention

We use the logical framework (Figure 4) to detail how the intervention was implemented, including measuring input changes in personnel, patrol effort (Indicator 1) and poaching alert source diversity (Indicator 2). We then conduct a process evaluation using indicators 3-6 to examine improvements in counter-poaching operation performance at critical steps. We place this in a narrative identifying key sources of success and failure points overcome, to facilitate replication by other teams. We calculate annual operating costs for the team where costs were available. We then compare unit protection costs of our intervention against alternative ranger-based protection models recommended.

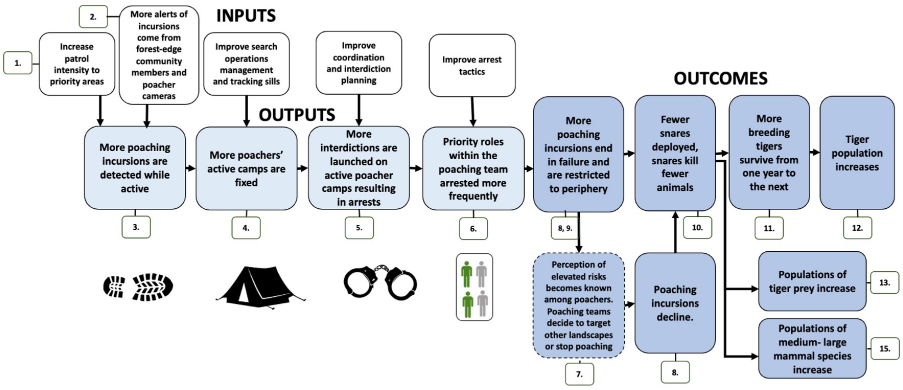

FIGURE 4
Theory of change for how the intervention was considered to lead to a tiger population increase. Numbers refer to the indicators used to measure progress and evaluate the mechanism (Table 1).

3 Results

3.1 Effect of the intervention

3.1.1 Did the problem decline?

Ninety-six poaching incursions of all nationalities were detected between 2015 and Feb 2023 inside Kenyir. Location data on the origins of poaching teams was only available for eight incursions (Figure 1; Supplementary Material). Thai (n=1) and Vietnamese (n=1) poaching teams initiated from their home countries and travelled overland to Malaysia before entering Kenyir. All Cambodian poaching teams intercepted (n=6) were residing in Malaysia and initiated the incursion from their home community. In each case, all poaching team members were from the same community. The first three Cambodian poaching teams apprehended in 2017-2018 were from Petaling District, Selangor, totalling 23 individuals. Subsequent Cambodian incursions in 2019-2023 were exclusively from east coast districts. It is possible that incursions from Petaling District were missed; however it also indicates potential cessation of poaching activity by Petaling District Cambodians.

Poaching incursion frequency declined by 40% from baseline years (n=34) to treatment years (n=20) across poaching types. Poaching incursions were absent during COVID-19 and low during post-COVID years (n=3) (Figure 5). Among the poaching types, Thai and Vietnamese incursions each recorded a decline of 34% and 13% in successful incursions. Success rates for Cambodian poaching incursions fell by 40% from baseline to

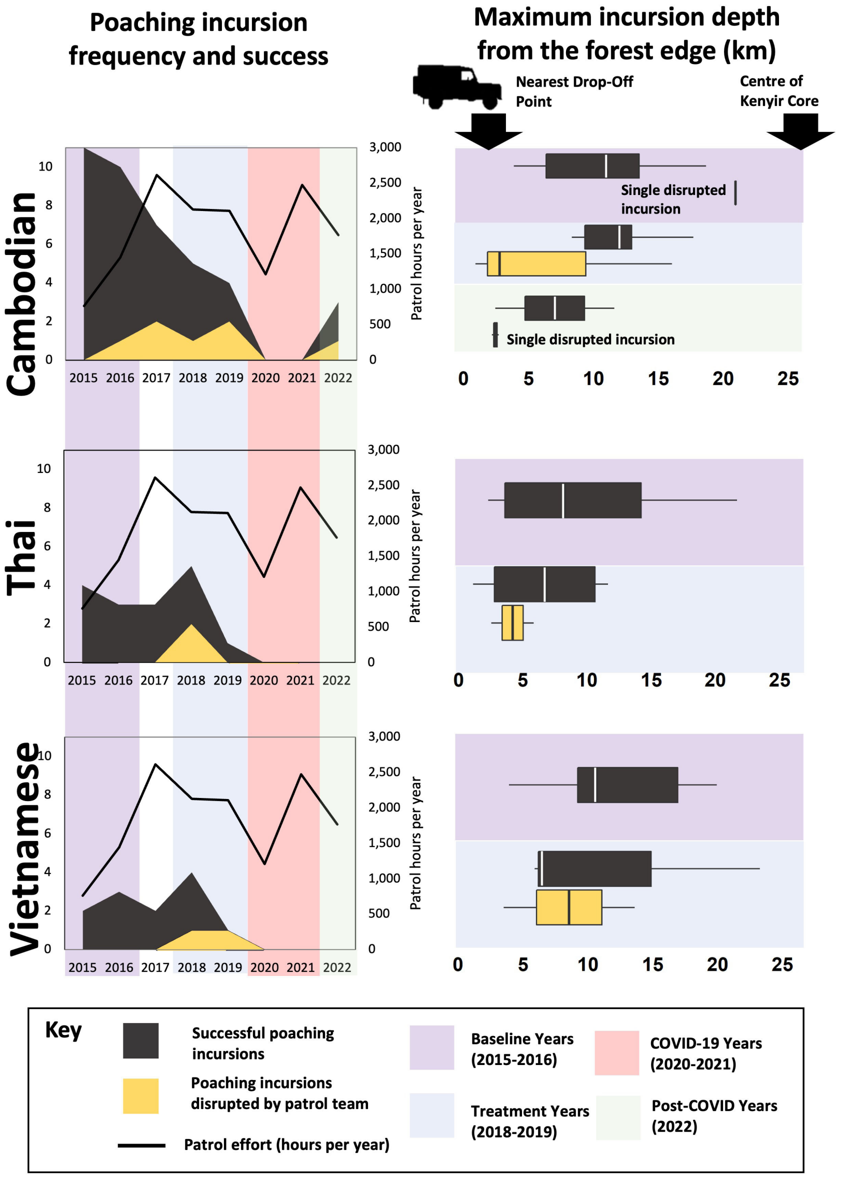

FIGURE 5
Declines in poaching incursion attempt frequency, and poaching success (left) and declines in penetration depth of poaching incursions (right) in the Kenyir Core Area for each poaching type.

treatment years. Vietnamese and Thai poaching incursions remained constant until 2018, then declined in 2019. From 2020-2023 no Thai or Vietnamese incursions were detected inside Kenyir, though incursions were detected on the surrounding landscape.

The depth of poaching incursion penetration into Kenyir decreased for all poaching types from baseline to treatment years (Figure 5). However, this was more marked when comparing successful and disrupted incursions during treatment years. Disrupted incursions were on average, 2.6 km (Thai) and 9.1 km (Cambodian) closer to the forest edge, respectively. No difference was detected for Vietnamese incursions. Maximum depth continued to decrease for successful and disrupted Cambodian incursions during the Post-COVID period. In each case, the effect was found to not be statistically significant due to low sample sizes. The overall effect of this spatial shift was a reduction in the proximity of poaching incursions from some of the most high-quality tiger habitat in Kenyir, whose central lowlands included higher prey densities, and two breeding females were detected here.

The number of wire snares detected inside Kenyir during treatment years was over four times higher than in the baseline years (Figure 6). Despite this, harm mitigation efforts improved. The proportion of wire snares disarmed before reaching full kill potential increased fourfold, with 10% of all snares entering Kenyir in treatment years seized before deployment. Between 2015 and 2019, patrols identified 44 animals trapped by snares, over half of which occurred during the 2019 mass snaring event. One Indochinese leopard and five sun bears were detected as target species, while bycatch of Asian tapirs and wild boar accounted for 18% and 38% of known catch mortality, respectively. Harm mitigation from snaring improved notably

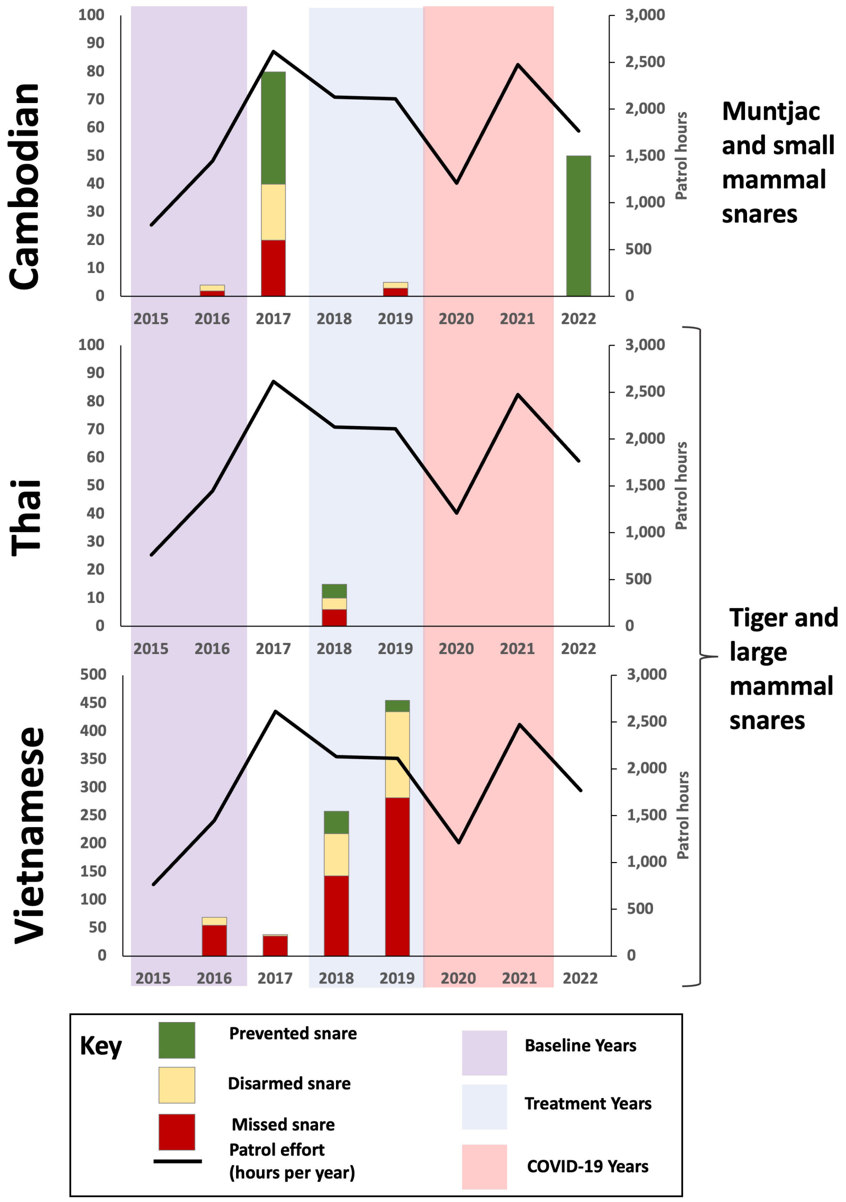

FIGURE 6
Mitigation of harm to wildlife from snares removed in the Kenyir Core Area for each poaching type.

against Cambodian poachers using rope and nylon snares for small and medium mammals.

3.1.2 Did tigers and prey recover?

Persistence of individual tigers was low throughout the study period. In the 2017 sampled population, 50% of the tigers detected were first-year detections, while first-years comprised 60% in 2021. A small core of three resident female tigers survived mass snaring events and were detected for seven years in Kenyir. Four breeding events were detected from these females during the study period. Eleven offspring were observed, with 10 classified as subadults, surviving the initial high mortality cub stage. Two offspring were redetected as adults; the female was detected breeding in one case. Mean tiger density fluctuated from 0.48/100 km2 (CI 0.22-1.04) in 2014 to 0.15/100 km2 (CI 0.04-0.52) in 2017 before stabilising to 0.53/100 km2 (CI 0.24-1.19) in 2021, well below the possible recovery range (Figure 7). Of the prey species in Kenyir, the Sumatran serow and sambar deer were detected at extremely low frequencies, and we could not compute density indices. Density indices for wild boar and southern red muntjac indicated steep

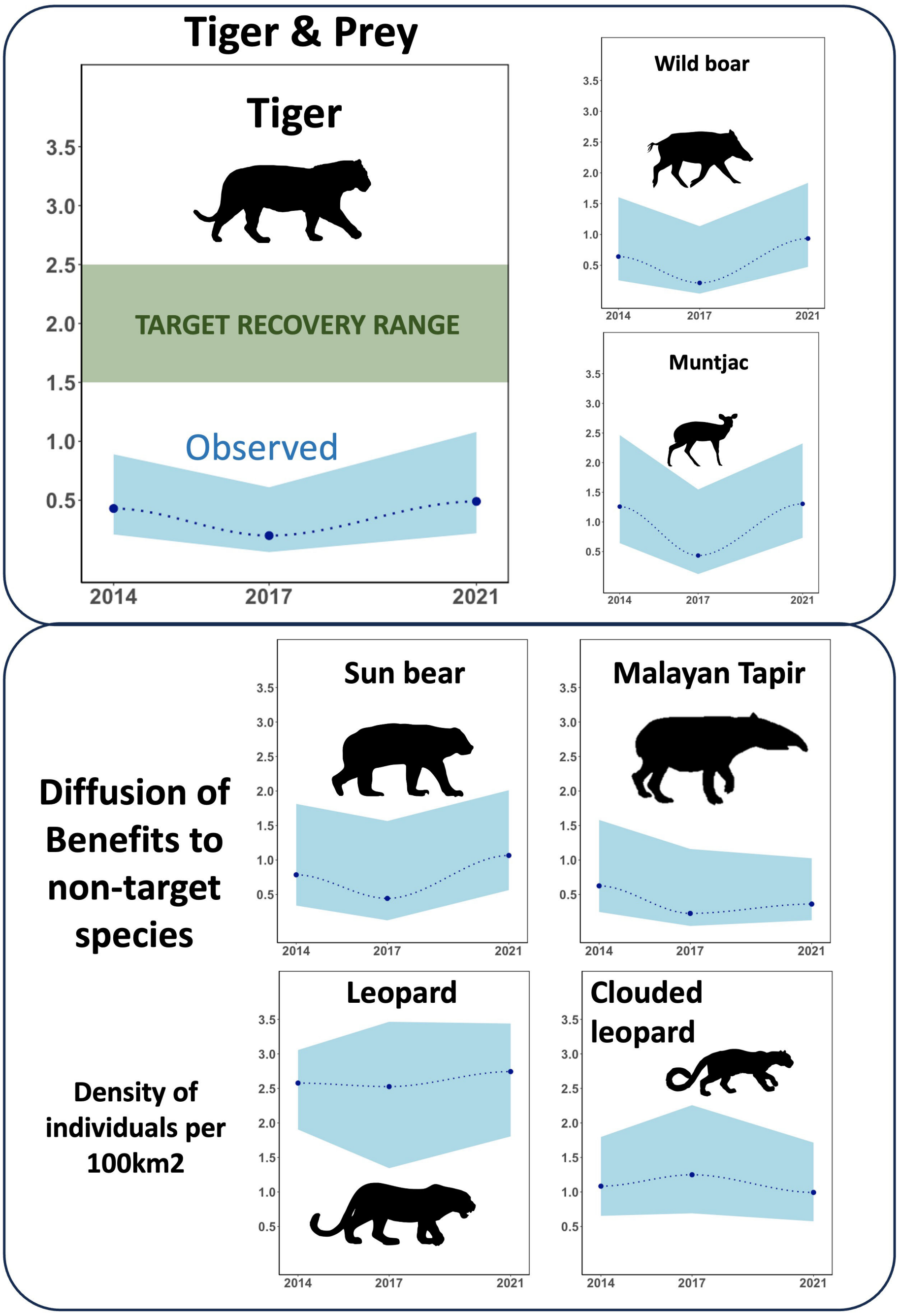

FIGURE 7
Density changes of tigers and prey and diffusion of benefits to non-target species in the Kenyir Core Area.

declines from 2014 to 2017 before stabilising around 2014 levels in 2021 (Figure 7).

3.1.3 Did our intervention cause the problems to decline?

There is reasonable support that the intervention was responsible for the decline in Cambodian poaching incursion attempts, passing all four of Eck's criteria (Table 2). The infrequent incursions and comparatively lower risks experienced by Vietnamese and Thai poaching teams mean there is insufficient support for the intervention causing the drop in these poaching types.

3.1.4 Was there crime displacement or diffusion of benefits?

While the frequency of Vietnamese poaching incursions was the same in baseline and treatment years, the number of snares deployed per incursion rose by more than eight times. This trend was associated with an observed switch in the snare wire gauge from 4-6 mm during baseline to 11mm during treatment years. A single catastrophic Vietnamese incursion was responsible for all 330 snares deployed in 2019. From 2019 until Feb 2023, at the time of writing, no wire snares were detected inside Kenyir. The trend in intensive snaring corresponded with a decline in agarwood harvesting by Vietnamese poaching teams. This was evidenced by reduced tree felling, sign of wood processing at camps, and the absence of agarwood chisels in arrests. While this trend correlates with the increased success of the ranger teams, the hypothesis that this was a response by poachers to the increased risk of arrest has insufficient support (Table 3) and more likely represents independent innovation to increase capture success innovation to increase capture success in a depressed carnivore population. Counts of sleeping spaces in nine Cambodian camps revealed a steadily declining trend in team size that began before the pandemic. No teams larger than ten were detected from 2018 onwards. Evidence is weak to support the hypothesis that Cambodians were adaptively switching to smaller team formations to avoid patrol detection (Table 3). The decline in poaching team size corresponds with the wider decline in Cambodia incursion frequency and supports the hypothesis for decreased recruitment at community level. Of the four non-target, high-conservation value mammal species, leopard density was stable from 2.58/100 km^2 (CI 1.90-3.06) in 2014 to 2.53/100 km^2 (Cl 1.34-3.46) in 2017 and 2.74/100 km^2 (Cl 1.81-3.44) in 2021 (Figure 7). Clouded leopard density remained broadly stable, from 1.08/100 km^2 (CI 0.66-1.80) in 2014 to 1.25 (CI 0.69-2.26) in 2017 and 0.99/100 km2 (CI 0.58-1.72) in 2021. The Malayan tapir and sun bear displayed the same declining trend in 2017 as tigers, with tapirs showing only marginal recovery by 2021. Sun bears, by contrast, stabilised to above 2014 levels.

3.2 Mechanism & moderators of the intervention

The mechanism of direct harm mitigation from snare removal, and preventing poaching teams from reaching priority areas of the site is described in 3.1.1. and is well supported by the available data. The reduction of Cambodian incursions can be explained by three possible mechanisms that complement and reinforce one another—triangulating from the limited data available. The pattern of change in the community of origin of poachers, reduction in poaching team size, and post-arrest testimony, offer partial support for all three of these.

TABLE 2 Appraisal of evidence in attributing decline of Cambodian poaching incursions in the Kenyir Core Area.

Test	Evidence & Conclusion
1. Decline in the problem comes after intervention	Pass. The year-on-year decline in Cambodian incursions followed a trebling of patrol effort and increase in arrests in 2017.
2. The amount of intervention and amount of problem's decline are related	Pass. Following the initial drop, sustained counter-poaching performance increased the risk of a poaching incursion failing to 1 in 2, this was associated with sustained decline in incursion attempts.
3. A clear mechanism by which the intervention caused the decline	Pass. The intervention may have caused the decline via three plausible mechanisms. There is circumstantial evidence to support all three. 1. Increased effort and costs of re-offending after arrest. 2. General Deterrence within small communities. 3. Reduced imitation by peers.
4. Alternative explanations are rejected	Pass. Four alternative explanations were examined and are unlikely to have caused the decline in Cambodian incursions in Kenyir. 1. Decline in international agarwood value 2. Deterrence or incapacitation of poachers by immigration sweeps 3. Voluntary repatriation of Cambodian agarwood harvesters 4. Agarwood stocks in Kenyir became depleted From 2016-2019 agarwood's value remained high; there were no actions, policies or initiatives which would have curtailed agarwood traders' ability to launder illegally harvested wild agarwood through licit channels; there were no notable immigration sweeps until 2020 or voluntary returning home of Cambodian nationals. Interviews with Cambodian poachers in 2023 indicated there were still perceptions of high agarwood stocks in Kenyir.

TABLE 3 Assessing the evidence for two hypotheses of crime displacement in Kenyir.

Displacement Hypothesis	Expected	Evidence	Conclusion
Tactical Displacement. Cambodians adaptively shrank team size to reduce likelihood of detection and arrest.	Cambodian poacher behaviour becomes increasingly covert.	Rejected. No other covert behaviour or countermeasures to detection observed by patrols.	Crime displacement unlikely. More plausible that the change reflects reduced recruitment to poaching.
	Smaller poaching teams carry lower risk of being detected. Individual poachers have lower risk of arrest.	Rejected. Small poaching teams were detected and camps fixed by patrol teams at the same frequency as large teams. Arrest rates were actually higher within smaller teams.	
	If solely a tactic to reduce risk, the frequency of incursions by poaching teams would not change.	Rejected. Number of poaching teams launching incursions declined at a similar rate to the number of individuals per poaching team	
Tactical Displacement. Vietnamese increased the number of snares per incursion to reduce the time needed to obtain carnivore body parts and reduce risk of detection and arrest.	Vietnamese poaching incursion duration shrinks.	Rejected. Poaching teams deploying larger snare arrays spent up to 5 months inside Kenyir.	Crime displacement unlikely. More plausible that the change was intended to increase likelihood of capture of remaining individual carnivores in a heavily depressed population
	Risk of detection and arrest for Vietnamese poachers reduced over time.	Rejected. The larger 2019 snare line enabled the patrol team to locate the camp faster and make arrests.	

3.2.1 Poacher repatriation increased the effort and costs of re-offending after arrest

Repetition of signature tree carvings across different incursions, and details shared in interviews with offenders indicate that the same poachers returned to Kenyir to conduct subsequent incursions, guiding teams with new members. Repeat victimisation occurs because a target is particularly attractive or vulnerable to offenders (the “flag” explanation), or specific offenders gain knowledge about the target from experience and use this to re-offend (“Boost” explanation) (Weisel, 2005). Offenders learn how to navigate the area, where and when security is and is not present, and what targets to return for. Interviews with burglars found that up to 75% of offenders had robbed a property twice or more (Ashton et al., 1998). Arrested Cambodian poachers received sentences ranging from 3 months to 1 year for illegal agarwood harvesting on failure to pay a fine. Most of the poachers were undocumented migrants whose work visas had expired, and they were routinely repatriated to Cambodia. Repatriation increased the costs and effort of an individual poacher attempting a subsequent incursion. Cambodian poaching teams did not have a strong hierarchy, and the incursion was instigated by one person in the team who would fill the team leader role, engage co-poachers and contract a transporter. While it was challenging to identify who the leader was in a poaching team, the increased percentage of team members arrested during the treatment years increased the likelihood that the leader was arrested. This mechanism is suspected of being weaker for Vietnamese and Thai poachers due to the low number of individuals arrested.

3.2.2 Repatriation reduced knowledge sharing and imitation by peers

In interviews with Cambodian poachers, interviewees described selecting the target location following advice and detailed descriptions from another team. For instance, “*I knew it was against the law to take things out of the forest, but I was willing to take the risk as I’d heard about success stories from other people who’d been to Area X*” (Interviewee 5). This suggests arresting and repatriating Cambodian poachers prevented them tempting peers to imitate their success. Second, it reduced the transmission of detailed information about Kenyir’s terrain and security with peers in their community or to guide in new poachers. Reduced temptation and landscape awareness would have reduced the likelihood of another poaching team targeting Kenyir. But, again, this mechanism is suspected of being weaker for Vietnamese and Thai poachers due to the much lower number of individuals arrested.

3.2.3 General deterrence from increased awareness of the elevated risk of arrest and low likelihood of enjoying rewards

Certainty of arrest for a poacher rose significantly in Kenyir during the study period. Poachers escaping made heavy financial losses as they were forced to leave behind equipment and harvested wildlife products. From post-arrest interviews, Cambodian poachers invested approximately $170 each in rations and travel costs to embark on a poaching incursion and saved up in the months before. Post-arrest interviews with Cambodian poachers (n=9) revealed that many worked part-time, low-paid jobs. Awareness of the risk of arrest and potential financial losses could have been shared with potential Cambodian poachers within their community, from escaped poachers or from arrested poachers’ families.

The Cambodian and Vietnamese poaching types offer contrasting examples of how effectiveness of a deterrence mechanism is moderated by risk awareness and rational choice (Figure 8). Interviews suggest Cambodian poachers operated a freelancing model with flexible group membership, conducting agarwood poaching as an income side-line. Nothing indicates coercion or impaired judgement, and individual poachers were responsible for the up-front costs of rations and travel

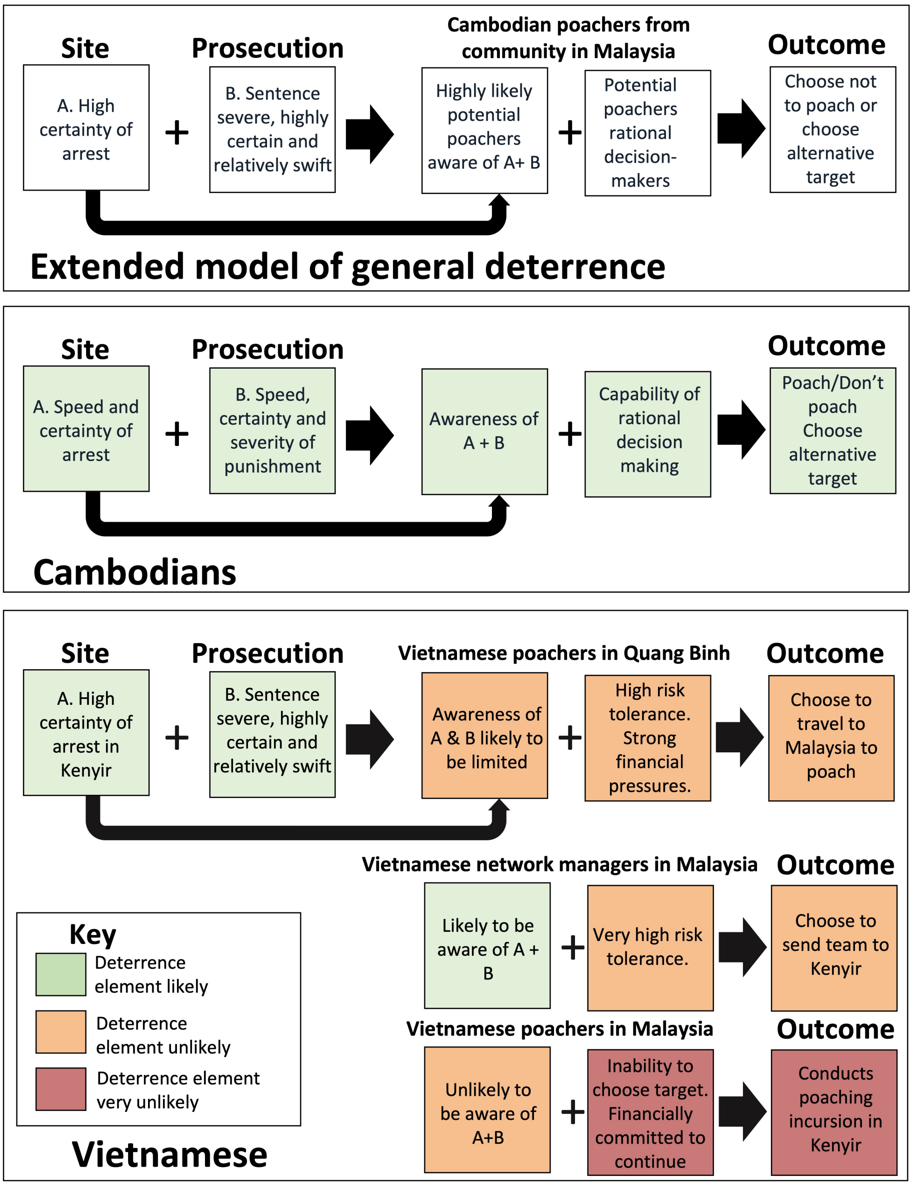

FIGURE 8
Contrasting perspectives for how the increased certainty of arrest in the Kenyir Core Area would influence Cambodian and Vietnamese poacher decision-making.

arrangements. Interviews suggest they could weigh costs and rewards to make an economically rational decision. As Cambodians were long-term residents of Malaysia, they were more likely to have a broad awareness of forest landscapes within Peninsular Malaysia. They could also choose an alternative target landscape or elect not to poach in response to locally elevated certainty of arrest. During interviews with Cambodian poachers from Pekan District arrested in 2023 without the usual small nylon snares used for trapping small animals, interviewees (n=2) indicated awareness of sanction severity "*Other people told me not to take wildlife because the penalty is very heavy*" (Interviewee 5). Still, they did not know anyone arrested for poaching or had any awareness of the elevated risk of arrest in Kenyir. After speaking to others from their community who had returned with a good agarwood harvest, the poachers were incited to attempt the incursion. In each of the six cases for which we have data, all poaching team members were from the same community in Malaysia. Given the large distance between Cambodian communities, knowledge about targets and risks may be relatively low, which could localise deterrence to a specific community.

Interviews with the two Vietnamese poachers arrested in 2019 provided a different insight into the limitations of deterrence. Both poachers had travelled to Malaysia specifically for a poaching expedition after being recruited by an agent in Vietnam supporting a Vietnamese network manager in Malaysia. Both poachers described raising personal and family debts to fund the $500 travel expenses. Two days after arriving in the country, they were taken to the forest edge with rations to begin a five-month incursion. This style was identified as a hall-mark of Vietnamese specialist poachers from community interviews, other prosecution cases and subject matter experts from the Wildlife Department (Lam and Mat, 2020). The Vietnamese hierarchical model involved tight control of multiple groups of Vietnamese poachers by a Vietnamese network manager living in Malaysia. In multiple cases, the poachers were contained inside safe houses until deployment and, in some instances, had their passports withheld by the network manager (Wildlife Justice Commission, 2021). Once inside Malaysia, Vietnamese poachers had limited ability to learn about relative risks across the peninsula or select a target. After committing expenses to arrive, there would be immediate pressure to generate income, increasing risk tolerance. The network manager living in Malaysia would be more likely to be aware of relative risks, but this person's risk tolerance would differ from that of poachers. While a network manager may lose potential earnings from the arrest of a poaching team, interviews suggested the poachers purchased their rations and equipment themselves, meaning very little actual financial loss fell on the network manager. As there was no immediate risk of arrest for the network manager, they may tolerate the poaching team being subject to even higher risks than the team itself would tolerate. Interview work conducted in Quang Binh suggests some awareness of general risks in poaching operations in Malaysia but also considerations that those caught were unlucky (Dan Tri Online, 2021). Therefore, reducing Vietnamese incursion attempts through general deterrence was found to be complex and unlikely.

3.2.4 COVID-19 effect

The abrupt absence of poaching incursions coinciding with the onset of the COVID-19 pandemic suggests national travel restrictions were the most significant moderator of the intervention across all three poaching types. All non-Malaysian poachers apprehended in Kenyir had entered the country legally. Malaysia closed its national borders to foreign tourists and workers for two years, from March 2020 until April 2022. Vietnam, Thailand and Laos also enacted similar border closures, severely limiting international travel options. Peninsular Malaysia enforced interstate travel restrictions by police roadblocks for three months in 2020 and one month in 2021. Non-Malaysian poachers found it challenging to enter the country and move to Kenyir. Concurrently, undocumented migrant workers were targeted by Malaysian Immigration during the pandemic (David, 2020). This may have reduced motivation for embarking on risky poaching incursions. The ability to move wildlife products out of Malaysia and into Vietnam appears to have been disrupted by reduced transport options and enhanced border screening (VOA News, 2020; Wildlife Justice Commission, 2020). Supply bottlenecks may have led to reduced orders and poacher recruitment. Interviews with members of the Vietnamese expatriate community in Malaysia during this time indicated that poaching network managers returned to Vietnam, removing the nucleus controlling Vietnamese poaching operations.

3.3 Implementation & economics of the intervention

Conducting arrests in the deep forest is exceptionally challenging. Three main failure stages were identified during the arrest process following failed arrest attempts in initial years. First, incursions had to be detected while there was still a window of time to conduct an arrest; we used three weeks as a cut-off for 'active incursions'. Second, the poachers' active camp had to be 'fixed' requiring a visual confirmation of the camp location and a DWNP enforcement team had to be guided to the location. Third, an ambush had to occur at the camp. To succeed, this required coordination, planning and clarity on the number of poachers and the camp's layout. Earlier attempts to snatch-arrest poachers moving in the forest had very low success rates due to the ease of escape, while rangers were also at risk from active poachers as each person carried a *parang, or machete*. Counter-poaching operations improved substantially during the study.

Improvements in operations were introduced in 2017. First, a risk map specific to the poaching types was used for tasking patrols (Lam, 2018), improving patrol scheduling to priority areas (Lam et al. In Prep). Incursion alerts doubled and diversified from scout team detections in baseline years, with nearly half of all alerts coming arising community members and camera traps in treatment years (Figure 9). Combined patrol effort of NGO scouts and DWNP rangers measured in active hours inside the forest doubled from baseline to treatment years to over 40,000 hours. This led to the detection of active poaching incursions improving by a factor of three from baseline to treatment years.

Enhanced search operation management and tracking were adopted, drawing from Search and Rescue (SAR) principles and providing guidelines for ranger teams coordinating with base support. Post-arrest interview questions intended to understand poacher decision-making and modus operandi were introduced and used to build search profiles for the three poaching types, improving ranger teams' ability to interpret signs and predict poacher behaviour. The patrol captain's influence was instrumental in maintaining team morale and leading ranger teams during extended and gruelling search operations. These enhancements led to doubling the proportion of active camps 'fixed' from baseline to treatment years.

Due to the risks in conducting arrests, a minimum ranger-to-poacher ratio of 2:1 was considered essential, with 3:1 preferred. Specific improvements included modifying the time of interception, enhanced reconnaissance by the ranger team, and improving raid planning. Once the camp was fixed, successful apprehensions resulted in all cases in treatment years. The odds of a poaching team member being detained shortened from 1 in 32 in baseline years to 3 in 7 during treatment years. The increase in risk was pronounced at an individual level within a poaching team (Figure 9). Once a ranger team fixed the active camp and initiated the apprehension, odds of escape shortened from over 5 to 1 to under 2 to 1.

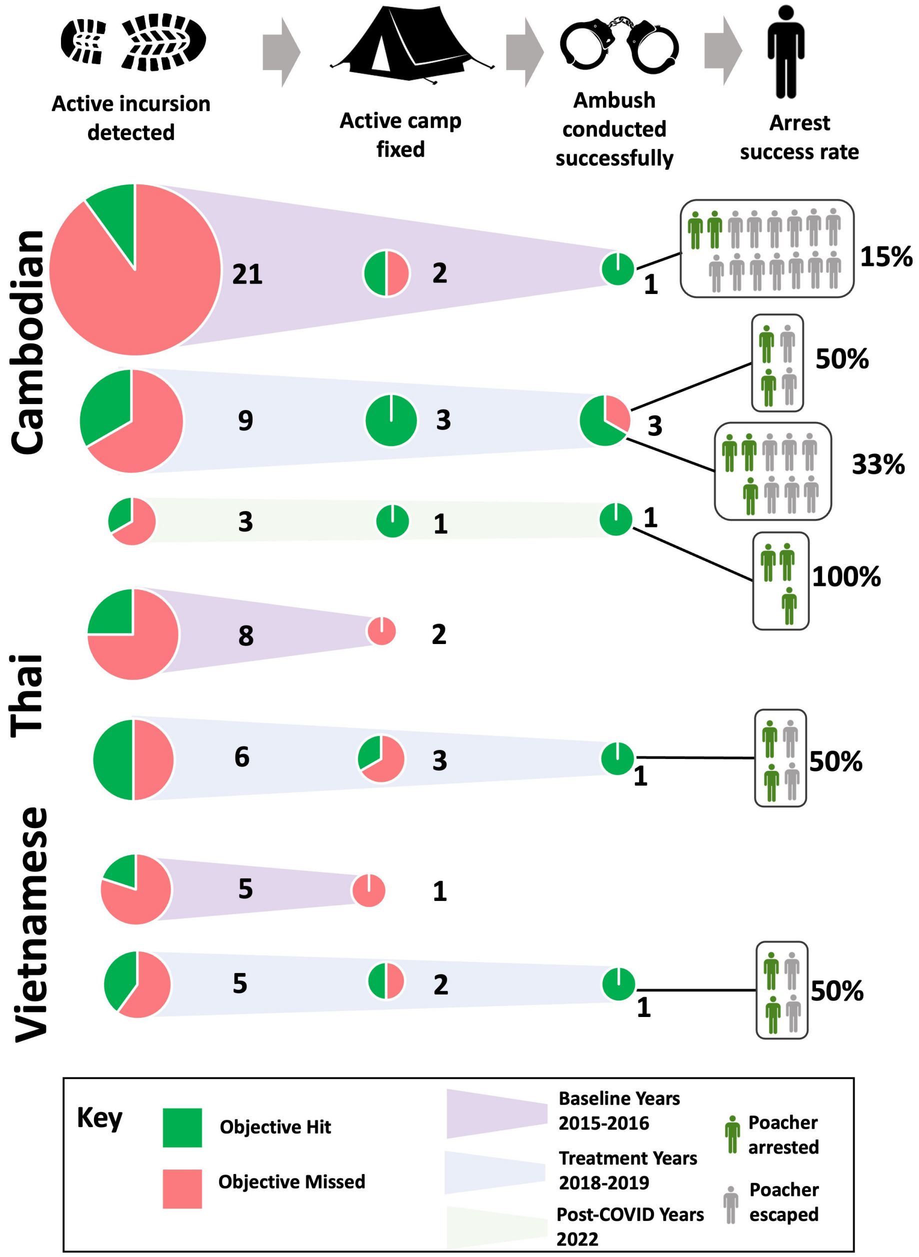

FIGURE 9
Attrition of success, and performance improvements at key stages of deep-forest counter-poaching operations in Kenyir, for each poaching type.

A key source of success was the institutionalisation of an adaptive management cycle designed to learn from failures and adapt tactics and was a key source of success. Each counter-poaching operation was followed by rigorous examination of patrol data, group debriefs and focal interviews with key staff. This process enabled the analyst and patrol captain to pinpoint specific failure points during the operation and identify improvements. Due to hesitance within the ranger team to change habits, a stage of consensus on tactical revisions involved trialling new approaches which were either sustained or rejected. Once there was agreement, updated standard operating procedures would be formalised, and training needs clarified to ensure staff were competent in the revised way of working.

While this intervention shows promise for certain poaching types, it may not be as successful if replicated elsewhere. This was developed to counter poachers spending extended months operating inside a forested landscape and would need modifying for other poaching types. Kenyir has very low footfall from other forest users, making detecting poaching incursion easier. In high-footfall landscapes, incursion analysis and search operations may be more complicated. Due to the hardship in traversing Kenyir carrying heavy packs, poachers follow predictable least-cost paths- ridgelines or riverbanks, which increased the likelihood of an incursion being detected. Detection of incursions is likely to be harder on flat homogenous terrain. Last, Thai, Cambodian and Vietnamese nationals are recognisable as outsiders, attracting interest and may be more likely to be reported on by rural Malaysian community members than local poachers.

Accurate costs were only available for the NGO scout team for the study years and staff salary costs. Scout team size increased from 20 to 21, and annual operating costs rose 2.5% from $175,000 in baseline to $180,000 in treatment years. This price rise was due to the changes in team composition with the recruitment of analysts, community engagement staff and a patrol captain, and comprehensive medical insurance for the scout team. Staff regularly patrolling decreased from 20 to 17. Routine patrols were conducted by all-NGO scout teams initially, although 2018-2019, joint NGO/DWNP regular patrols became more common. Logistics and consumables for a typical four-man, five-day patrol cost $108 for a vehicle deployment or $453 for a deployment by boat across the lake. At one ranger per 75 km^2, Kenyir falls far short of recommended ranger densities by the IUCN (one ranger per 5 km^2) or Appleton et al. (one ranger per 26 km^2; Appleton et al., 2022). If we followed IUCN recommendations, Kenyir would require 240 patrollers, with an associated annual staff budget of between $200,000 and $250,000 compared to the current $180,000 total annual operating budget.

4 Discussion

This is the first study to use a crime prevention framework to assess the effectiveness of counter-poaching operations on a large mammal in Southeast Asia. Our evaluation indicates the intervention did not succeed in recovering Kenyir's tiger population, but it did enable key individuals to survive and reproduce until COVID-19 travel restrictions made poaching by non-Malaysians extremely difficult. Breaking down the threat of tiger poaching into specific problems allowed us to apply specific tactics tailored to the problems. We were then able to measure incremental performance improvements and track outputs to have confidence in the impact of the intervention. Challenging the assumption of causality gave us a clearer understanding of the processes by which the intervention worked, or not, attribute causality with higher confidence, and know in what contexts it would be likely to produce similar results. Lastly, testing hypotheses of poacher adaptation to our intervention, while examining cascading benefits to non-target species falling under the umbrella of tiger protection provided a more complete understanding of the impact of the intervention. This study offers protected area managers working with challenging poaching problems a template for evaluating patrol-based interventions (Table 4). Despite the data limitations of this study, it illustrates how to

TABLE 4 Summary of EMMIE elements from the intervention in the Kenyir Core Area.

EMMIE element	Details
Effect: Impact on the problem	1. Reduction in potential harm to tigers caused from snares 2. Reduction in incursion attempts by Cambodian agarwood poachers 3. Persistence of key individual tigers and reproduction 4. Stabilisation of non-target carnivores and tapir populations
Mechanism: How it works	1. Harm control by snare removal, and interception before poaching teams could reach sensitive areas. 2. Increased effort and costs of re-offending after arrest. 3. General Deterrence within small communities. 4. Certainty of reduced rewards of offending. 5. Reduced imitation by peers.
Moderators: Where it works	1. Poachers conducting extended incursions. 2. Low footfall landscapes where poachers leave sign. 3. Landscapes with well-defined topographical features and limited access points. 4. Poachers are outsiders, with most forest-edge locals not benefiting from the poaching activity and are easily identified. 5. Poachers come from limited number of small stable communities with knowledge of the wider landscape. 6. Poachers are prevented from returning to the same community after arrest.
Implementation: How to do it	1. Analyst embedded within the ranger team. 2. Strong manager on site 3. Post-operation dissections and rigorous tactical reviews and revisions. 4. Strong coordination among ranger teams. 5. Scenario development and tactical experimentation and refinement. 6. Training, retraining, 7. Good wage and health insurance. 8. Performance incentives 9. Centralised barracks and operations room 10. Strong and experienced patrol team leaders
Economics: How much it costs	$180,000 annually to maintain a 21 person team including scouts, analysts, community liaison staff, patrol captain and project coordinator and all operational expenses. $108 for a typical five day/four man patrol by vehicle deployment $453 for a typical five day/four man patrol by boat deployment

triangulate from different source types to infer indications of how behavioural change mechanisms may work.

4.1 The limits of deterrence

Deterrence is either an explicit or implied intended mechanism for reducing wildlife crime using enforcement. However, vague use of the term weakens protection teams' ability to develop, and adequately evaluate this mechanism. Deterrence theory, as it was initially conceived, involves three elements to work: Punishment is swift, certain and severe (Beccaria, 1986). From the perspective of site protection, deterrence through the criminal justice system requires both speed and certainty of arrest combined with speed, certainty and severity of the sentence. Research indicates that the most important of these three factors in deterring crime is the certainty of arrest and punishment (Wilson and Boratto, 2020), which is most often chronically lacking in protected areas. However, if the certainty of being arrested is high, but the population of potential poachers is unaware, they cannot be deterred (Paudel et al., 2018). Even when there is broad awareness of true risk, potential poachers must be capable of rational decision-making and weigh the relative likelihood of risks and rewards to make an informed judgment (Clarke and Felson, 1993). Where potential rewards are extremely high, offenders may tolerate a high level of risk (Epper et al., 2022), judgement is impaired by alcohol, learning disabilities or acute need (Walters, 2015). The perception of those that were caught as being the ones who 'just got unlucky' or 'didn't know what they were doing' can be an essential factor in inhibiting offender decision-making away from continuing with the activity, particularly when contrasted with the highly visible success stories of the lucky few who made it. The support for deterrence of Cambodian poachers found here is caveated by the fact that this appears highly localised to specific communities, but also that non-deterrent mechanisms reducing poaching opportunity structures may have been involved in the decline.

4.2 Patroller quality over quantity

The causal relationship between enforcement officer numbers and decline of crime incidents is context specific and nuanced. In Nepal, Chitwan's success in recovering its rhino population following intensive counter-poaching work and heavy sentencing for wildlife crime is often used as a model for others to follow (Mahatara et al., 2018), leading to calls from NGOs to increase 'boots on the ground'. However, interviews with poachers in Chitwan suggested the general deterrence effect is overestimated (Paudel et al., 2018). Evidence is mixed that increasing police officer numbers cause crime to decline (Bradford, 2011), while increased officer numbers do not always increase perceptions of risk of arrest among offenders (Kleck and Barnes, 2014), or presence of armed guards deter rhino poachers in South Africa (Barichievy et al., 2017).

In other landscapes, large ranger teams formed from indigenous and local community members can provide an essential source of local employment. In such instances, general deterrence may be a less important mechanism of poaching reduction than occupying potential poachers' time with patrol work or providing an alternative income source to poaching. Understanding this is important for tailoring interventions to be more effective. Yet, the mechanism by which an intervention achieved a decline in the problem is rarely critically examined in publications (Delpech et al., 2021).

Rangers perform various essential roles preventing wildlife crime, aside from counter-poaching operations (Stolton et al., 2023). Simple and attractive policy goals such as an optimum patroller density can become counterproductive when the supporting infrastructure of management, analysis, training and equipment are secondarily and insufficiently factored into budget planning. Larger protection teams bring added complexity in management and resourcing. The hardship and risks associated with patrolling necessitate a high degree of training and support from strong management and incentives, which is often lacking (Belecky et al., 2021). Failure to provide sufficient wages, a strong professional approach and tight management oversight risks ranger effectiveness declining and rangers becoming vulnerable to corruption solicitations, a problem many protected areas face (Felbab-Brown, 2017). Elevated ranger numbers in guard posts can create blind spots of assumed deterrence while facilitating localised poaching (Jenks et al., 2012). For example, between 2009 and 2021, 42 staff from Kruger National Park in South Africa were dismissed for alleged involvement in rhino poaching (Keir, 2021), with up to 40% of staff estimated to be involved in corruption (Rademeyer, 2023). With limited budgets, heavy focus on enforcement-based interventions can draw resources away from community-based crime prevention measures (Cooney et al., 2017; Duffy et al., 2019).

Investment in limited resources was prioritised here over employing larger numbers. In Kenyir, scout numbers decreased slightly from the baseline to treatment years, but an increase in analysts compensated for this. The strong problem focus taken by the team, backed up by stronger analysis guiding patrols, led to a clearer mission and better scout team deployment, which increased the frequency of incursion alerts from patrol teams. The innovation of the federally deployable SPARTA unit proved highly effective. Based in Kuala Lumpur, with members in different states, the team could deploy to any forest patch in 24 hours to support a counter-poaching operation. This made maximal use of limited workforce. The close working relationship between experienced SPARTA officers and Panthera staff led to the formalisation of deep-forest counter poaching operations doctrine in a training guide and structured scenario-based course. A further key development was the tracking skills of teams.

In four key tiger landscapes in the Peninsular, NGOs provide civilian scout teams. These employ a large number of staff to augment government rangers, mostly from indigenous Orang Asli ethnic groups. The traditional field skills of veteran Orang Asli were recognised in 2019 when DWNP created the "VetOA" regiment. Orang Asli are a marginalised people within Malaysia and have suffered extensive land dispossession, including from Kenyir when the hydroelectric lake was created in 1985. In Kenyir, over half of the scout team comprised Orang Asli patrollers. Traditional skills were developed and enhanced with modern search and rescue techniques and combat tracking techniques. Under this process, senior patrollers were provided additional training and mentoring in instruction techniques to lead internal refresher trainings and run trainings for other teams. Early recognition of the value and adoption of traditional indigenous skills was instrumental in developing the team.

While more eyes and ears increase the likelihood of detecting a poaching incursion, these do not need to be salaried rangers. Indigenous people and local communities have a substantial role to play as front-line protectors of forests and wildlife (Roe et al., 2017), ranging from sharing alerts of a poaching incursion (Risdianto et al., 2016), to collaborating on joint community initiatives to reduce incentives for poaching (Jones et al., 2020), to forming organised community teams to patrol and protect the natural resource (Kragt et al., 2020). A major aspect of the Chitwan model was also the increased informal guardianship among the bordering communities, with a willingness to provide alerts due to benefits accruing in the communities from the rise in tourism (Mahatara et al., 2018). In Kenyir, the poaching problem conducted by non-locals operating far from their community of origin constrained our ability to directly engage with those poaching communities. However, relationships with forest-edge locals through recent cattle-predation reduction has led to increased poaching incursion alerts being shared. Engaging communities as partners to prevent poaching can offer a more cost-effective way of dealing with the problem than expanding an enforcement team. However, this requires analysis of the conditions for informal guardianship in the communities to find approaches that work alongside traditional practices and cultural beliefs (Viollaz et al., 2022).

4.3 Analysts and decentralised learning

The early investment in analysts based at sites trained in skills in wildlife crime problem analysis was a second crucial factor. Analysts have become more common in policing yet remain rare in wildlife protection. As the analysts in the Kenyir team consolidated a deeper understanding of decision-making and the modus operandi of the focal poaching types, this drove substantial improvements in the deployment of routine patrols to detect incursions, the speed of a search operation to locate the camp, and the tactics used to improve arrest effectiveness. However, not all teams have succeeded with analysts in policing or wildlife protection. Cultural constraints and budget cuts were identified as reasons for preventing analysts from being incorporated into the heart of policing, exacerbated by managers inadequately tasking analysts or being perceived as academic outsiders (Belur and Johnson, 2018). Key ingredients of success in Kenyir involved the analysts being well embedded in the protection team, able to go on patrols, engage in debriefs and encourage patrol members to challenge their interpretations. This helped legitimise their presence in the group and increased the likelihood that their recommendations would be adopted. This was driven and facilitated by a project manager with prior experience working as an analyst and a deep understanding of what was needed from the analyst to inform decision-making. Adopting a productive and self-critical culture within the team was significant, with failures being interrogated in an environment that encouraged participation and the identification of solutions. The post-operation dissection reports became a vital reference library on which to base tactical and procedural changes, with testing and consensus gained from the team before formalisation, training and implementation. This was essential for engaging the team in identifying and backing solutions to failures in operations. Rather than passively accepting orders, rangers were encouraged to voice opinions and be part of a refinement process. Despite their deep understanding of threats, the terrain, and their capabilities, rangers rarely engage in this way (Moreto and Charlton, 2019).

Within conservation, adaptive management has been promoted by which managers adaptively make and implement resource and tactical decisions based on an updated understanding of the state of the environment to achieve conservation goals. However, within the conservation literature, this more commonly focuses on regional or national policy settings, with relatively few examples of how the process should work at the level of a protected area (Lee, 1999). Furthermore, tight centralisation of performance and threat metrics and implementation of national-level tactics can impede the ability to solve complex problems at the local scale (Game et al., 2014). By contrast, empowering local teams and leaders to be creative in how they innovate ways to reduce priority problems within a knowledge-producing environment can be more productive (Moffat, 2002; Uhl-Bien et al., 2007).

4.4 Conclusion

This project aimed to increase the tiger population by 50% in ten years. By 2024, ten years after beginning the project, with a near-stable density and improved persistence of tigers, we are not yet on track to achieve this. The tiger population of Kenyir, as in other landscapes in Malaysia, has suffered an onslaught of poaching, leading to tigers falling below a national estimate of 200. Recovery becomes significantly more complicated once a species is extirpated from a landscape (Harihar et al., 2018; Miquelle et al., 2018), so a focus on counter-poaching operations was driven by the urgency of preventing extirpation of Kenyir's remaining tigers. The COVID pandemic gave us breathing room and the ability to review tiger protection investments, including this evaluation. This study illustrates the benefits and limitations of site protection in reducing a wildlife crime problem and a template for a more rigorous evaluation of counter-poaching investments. While we have compelling evidence that the investment reduced threats to tigers, and delivered diffusion of benefits to other felids and non-target species, we assess the intervention is unlikely to have been responsible for declines in incursion attempts by Thai or Vietnamese poachers. The increased understanding of offender decision-making from post-arrest interviews has highlighted options to prevent poachers from beginning the process of preparing to embark on an incursion at the level of their community of origin. These need to be explored further, particularly where wildlife trafficking overlaps with worker exploitation and human trafficking.

Data availability statement

The datasets presented in this article are not readily available because: data sharing will take place selectively on a case by case basis following agreement with partner data owners from PERHILITAN involved in this study and following careful review of the request. Requests to access the datasets should be directed to RPICKLES@PANTHERA.ORG.

Ethics statement

Ethical review and approval was not required for the animal study in accordance with the local legislation and institutional requirements because this study did not involve any invasive approaches. Data collection involved passive camera trap surveys. The research was conducted under permit by the Government of Malaysia.

Author contributions

LWY was responsible for leading the strategy, developing and institutionalising the problem analysis and evaluation presented. CCP and CPS played key roles both in analysing and interpreting the poaching and enforcement data presented. ZAM, HJ and AS were instrumental in developing the tactics, all three provided expert opinion and context to the findings to interpret poacher decision making. FAZA was responsible for analysing PERHILITAN's data. MKYC led the analysis and interpretation of the wildlife data. NAWO, SS and AKAH were responsible for overseeing PERHILITAN's tiger protection operations in Kenyir. They reviewed and provided expert opinion to the study. MDB led tactical trainings and was integral to the tactical refinement and Kenyir strategy formation. He provided expert opinion in the study. AH provided technical support to the project, shaping the strategy, and was integral to the development and refinement of the evaluation approach and writing up of the study. GRC initiated the Kenyir project and was integral to the development and refinement of the strategy, ideas discussed in the manuscript, reviewing and refining the study. RSAP provided technical and analytic support to the project, providing support in the writing and application of crime prevention frameworks in this study. All authors contributed to the article and approved the submitted version.

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Conflict of interest

Authors MB and AH were employed by the company Panthera Corporation. 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.2023.1213552/full#supplementary-material

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Planning for megafauna recovery in the tropical rainforests of Sumatra

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Human-induced forest loss has had devastating impacts on biodiversity. Mammal populations in the tropics have been hit particularly hard by the resulting habitat loss, fragmentation and degradation, as well as by overhunting which often goes hand-in-hand. While declines in these populations are generally well documented, few studies offer a pathway for their recovery. Here, we test the association between changes in forest habitat and occupancy trends of Sumatran megafauna (elephant and tiger) and key tiger prey species (wild boar and sambar) in the Leuser Ecosystem: a large forest landscape on the Indonesian island of Sumatra. For elephant and tiger, we develop additional occupancy models to predict their respective spatial distribution under different scenarios of forest loss and gain (through restoration and increased connectivity) to provide a blueprint for avoiding future species loss and assisting with their population recovery. From 2000 to 2019, 254,722 ha (6.7%) of natural forest was converted, primarily to plantations and shrubs. The species-specific responses over the study period revealed that the occurrence of elephant declined along the west, with a range shift to the northeast of Leuser, whereas wild boar underwent a dramatic widespread decline and although sambar experienced losses around the forest edge, it remained widespread in the interior forest, while tiger occupancy remained stable. Modelling habitat loss and fragmentation led to an unsurprising demise of Sumatran megafauna, whereas strategic investments that reconnected several forest patches provided disproportionately large benefits for their recovery through the recolonization of former parts of their range. Indonesia has achieved six consecutive years of declining forest loss rates, and our study's findings can build off this conservation success by supporting improved provincial spatial planning and field-based restoration efforts that avoid declines of threatened megafauna species and act as a catalyst for rewilding a landscape of global importance.

KEYWORDS

large mammal conservation, occupancy, tiger, tropical forest loss, landscape connectivity, extinction risk, rewilding

1 Introduction

Tropical forest loss along with the overexploitation of species, invasive alien species, and climate change, are driving down levels of global biodiversity at an alarming rate (Morris, 2010; IPBES, 2018; Harvey et al., 2022). As tropical forest landscapes are degraded, in particular by expanding settlements, farmlands and plantations, they lose their size, intactness, and biodiversity, which makes them less resilient to edge effects, climate change, and other pressures (Kinnaird et al., 2003; Senior et al., 2019). Forest habitat fragmentation can be especially harmful to wide-ranging species because it potentially limits their ability to migrate, disperse, find mates, feed, and therefore complete their life cycle (Tucker et al., 2018). Furthermore, the expansion of human activities into previously inaccessible forest areas has led to greater human presence, and increases the risk of human–wildlife conflicts and diseases spillover (Corlett, 2007; Inskip & Zimmermann, 2009; Symes et al., 2018; Vora et al., 2022).

Forest conversion has had an acute impact on mammalian assemblage, functional diversity, and the structure and composition of natural habitats (Ahumada et al., 2011; Vynne et al., 2022). It has led to a general decline in mammal populations that has raised concerns over the loss of key roles that certain mammals play in maintaining healthy ecosystems, such as through seed dispersal for forest regeneration, and mesopredator and ungulate control (Seidensticker, 1986; Kinnaird et al., 2003; Linkie et al., 2006; Gaveau et al., 2009; Luskin et al., 2017). The recent calls for rewilding (Fernández et al., 2017; Perino et al., 2019), especially of large-bodied mammals, is therefore seen as one way to restore ecological integrity and ecosystem health (Vynne et al., 2022).

Rewilding can be achieved through the reintroduction of individuals from extirpated populations to well-managed areas, such as the bison (*Bison bison*) in North America, or through reconnecting patches of natural habitats to facilitate recolonization by extant populations, such as the grey wolf (*Canis lupis*) across continental Europe (Sanderson et al., 2008; Szewczyk et al., 2019). Numerous studies have shown the positive impacts of rewilding and its positive feedback on forest regeneration and ecosystem health, more generally (Corlett, 2007; Budiharta et al., 2014; Crouzeilles et al., 2016; Omeja et al., 2016; Derhé et al., 2018; Acevedo-Charry & Aide, 2019).

A rewilding approach holds great potential for a country like Indonesia. It hosts globally important populations of threatened large mammal species and, despite having had high rates of forest change, it has maintained a trend of decreasing forest loss rates for six consecutive years (MoEF, 2022). While safeguarding the area and integrity of the remaining forest remains a priority, along with protecting its resident wildlife from poaching, these recent forest trends allow for greater consideration to be given to mapping out a pathway for species recovery, particularly in landscapes surrounding the better protected national parks (Luskin et al., 2017).

In this study, we investigate the association between forest change patterns and the population status of several threatened mammal species in the Leuser Ecosystem. We map and quantify temporal trends in forest cover change from 2000 to 2019 and use these data to assess the spatial drivers of forest loss. From this, we estimate the change in species occupancy for two of the national government's priority species — Sumatran elephant (*Elephas maximus ssp. sumatranus*) and Sumatran tiger (*Panthera tigris sumatrae*) — and the principal prey of tiger — wild boar (*Sus scrofa*) and sambar (*Rusa unicolor*) — using field survey data collected in 2009 and 2019. We develop a spatially-explicit predictive model to explore how future patterns of forest loss and gain would influence the occurrence of elephant and tiger in the wider landscape.

2 Materials and methods

2.1 Study area

The 2.6 Mha Leuser Ecosystem is one of the most important intact rainforests in Southeast Asia. Located at the northern end of the Indonesian island of Sumatra, the ecosystem straddles the provinces of Aceh and North Sumatra. The forest of the Leuser Ecosystem has a unique biodiversity richness due to its geological divisions that consist of: lowland forest, montane forest, freshwater swamp forest, mangrove forest, and peat swamp forest (Baukering et al., 2009). The Leuser Ecosystem is the only place on Earth where the Sumatran tiger, Sumatran rhino (*Dicerorhinus sumatrensis*), Sumatran orangutan (*Pongo abelii*), and Sumatran elephant, all critically endangered, coexist (IUCN, 2023). Due to its outstanding biodiversity and cultural values as well as the essential ecosystem services it provides, the Leuser Ecosystem has been globally recognized as a top priority tiger conservation landscape (Dinerstein et al., 2006), a UNESCO Tropical Rainforest Heritage Site (UNESCO, 2004), and currently on the "in danger" list (Setyawati et al., 2021). In Indonesia, it is considered a National Strategic Area for its Environmental Protection Function under Indonesian law (Government regulation No. 26/2008). Most (80%) of the Leuser Ecosystem is protected through its designation under Gunung Leuser National Park (GLNP, 31%), Forest Management Units (FMUs, 46%), and Singkil Wildlife Reserve (SWR, 3%).

The integrity of the Leuser Ecosystem is threatened by habitat conversion, primarily to smallholder farmland, and wildlife poaching. A network of 10,415 km of official and unofficial roads encircles the Leuser Ecosystem and, in key places, cuts into it, thereby providing direct access to the forest edge and sections of its interior (Sloan et al., 2018). These roads increase the likelihood of poaching for high-value wildlife species, such as tiger and elephant, or for subsistence hunting by local people (Figel et al., 2021). As consequences, dramatic declines of tiger prey, such as wild boar and sambar have been observed, while wild boar populations have been heavily impacted by the spread of African swine fever (ASF; Luskin et al., 2021). This prey base reduction provides one explanation for a recent increase in the frequency of human–tiger conflict incidents (Lubis et al., 2020).

2.2 Datasets

2.2.1 Mapping forest cover change

Sumatran elephants and tigers require good quality forest habitats to thrive (Gopala et al., 2011; Goodrich et al., 2022), so we mapped forest cover change from land use and land cover (LULC) data published by the Indonesian Ministry of Environment and Forestry (MoEF) from 2000 to 2019 (Figure 1). The LULC dataset consists of 23 land cover classes that were generated by MoEF using visual interpretation of Landsat satellite imagery, with a mapping unit of 6.25 ha (MoEF, 2018a). For our analysis, we grouped the LULC data into five broader land cover classes: forest (FOR); plantation (PLT); cropland (CRP); shrubland (SHB); and non-vegetation areas (NON; Table S1). The forest class included six MoEF-defined forest types (primary dryland forest, secondary dryland forest, primary mangrove forest, secondary mangrove forest, primary swamp forest, and secondary swamp forest). We define habitat loss as when forest is converted to plantation (industrial plantation forest or plantation under MoEF's LULC definition), cropland (dryland agriculture, mixed dryland agriculture, paddy field), shrubland (savanna, shrub, shrub swamp, and swamp), or non-vegetation area (settlement, cloud, bare land, water, fishpond, airport, transmigration, and mining). Habitat gain occurs when non-forest habitat (PLT, CRP, SHB, NON) returns to forest (FOR). The land cover change analysis was conducted using ArcMap 10.4.1 and R 4.2.1 (R Core Team, 2017).

2.2.2 Species data collection

The Sumatra-wide Tiger Survey (SWTS), led by MoEF in partnership with several NGOs, was conducted in two time periods (2007–09 and 2018–19) in 21 landscapes encompassing 12.9 Mha, including the Leuser Ecosystem. The survey was designed to primarily collect data on Sumatran tiger, but also collected data on other mammalian species, namely Sumatran elephant, sambar, and wild boar. The survey's aim was to determine species occupancy in the two time periods, population trends, and the environmental and anthropogenic factors that influence species

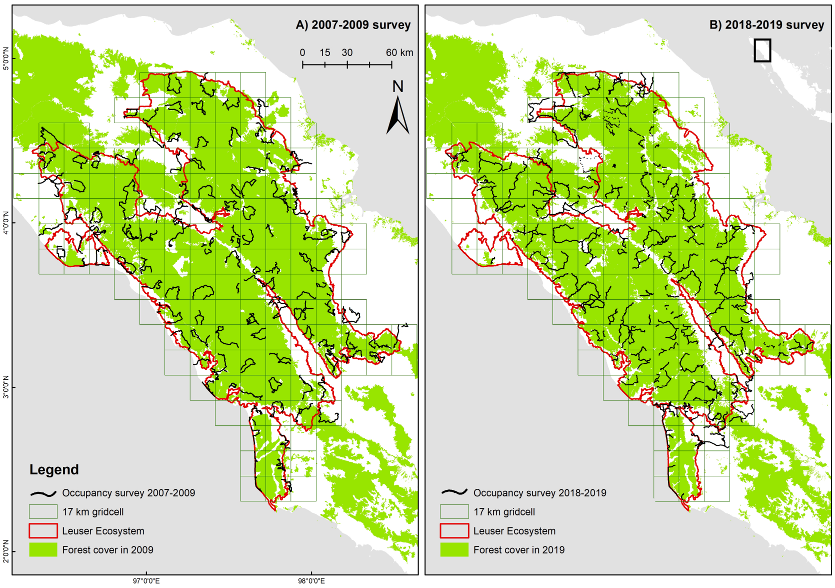

FIGURE 1
Occupancy survey design for the Leuser Ecosystem and transects surveyed in **(A)** 2007–2009 and **(B)** 2018–2019.

occurrence (Chandradewi et al., 2019). In Leuser Ecosystem, the first survey was conducted between May 2007 and February 2009, whilst the second survey was conducted from October 2018 to December 2019. For each survey, species detection and non-detection data were collected along transects in a network of 17 × 17 km grid cells (Figure 1), an area based on the putative home range size of an adult male Sumatran tiger (Wibisono et al., 2011).

To address logistical and cost challenges, whilst incorporating a random sampling element, we conducted detection/non-detection surveys along continuous transects, following the methods outlined in Hines et al. (2010), Karanth and Nichols (2010), and Wibisono et al. (2011). This was done by creating random smaller quadrants (2.12 × 2.12 km) within each of the larger grid cells. Each field team had to create routes, which were mainly along the ridges that pass through these smaller random quadrants. The number of random quadrants varied from one to four depending on the percentage of forest cover. So, for example, a grid cell with 10%–35% of forest cover would be allocated one random cell, 36%–65% and 66%–85% of forest cover for two and three random cells, whereas a grid cell with > 85% forest cover would receive four random cells to be surveyed. The transect length (survey effort) was proportionate to the extent of forest habitat in a grid cell, and ranged from a minimum of 4 km for 10% forest coverage in a cell and up to 40 km for 100% forest coverage (Pinondang et al., 2018).

Transects were walked by 4–5 trained field staff searching for any sign of the target species such as pugmarks, footprints, and feces. Covariates such as habitat types were also measured along the transects. Similarly, the presence of poaching activity, such as snares, or signs of illegal logging (tree stumps, logged over trees, logged over spots, and processed woods) were collected during the surveys. Field teams were trained and equipped with a standardized field survey manual that was developed solely for this survey to minimize observation errors (Royle & Link, 2006). Survey effort, as measured in distance travelled, was calculated three dimensions by incorporating topography variability (z values) in the transect length walked in each 17 × 17 km grid cell using track2dm package in R (Lubis, 2021).

2.3 Data analysis

2.3.1 Estimating rates and drivers of forest habitat change

We calculated habitat loss and gain in four periods (2000–2006, 2006–2009, 2009–2014, and 2014–2019) and presented the trends of habitat conversion as a Sankey diagram (Figure 2; Schmidt, 2008). To understand the drivers of forest change in our study area, we used a logistic regression analysis to investigate which combination of environmental predictors explained the presence or absence of forest loss (Table S2). First, we created geospatial information systems (GIS) layer over our study site depicting forest change between 2000 and 2014 with four classes (forest loss, forest gain, and remaining forest habitat and non-forest habitat). We randomly assigned 10,000 points over our study area and only selected 398 points that fell on forest cover class (N = 345) and forest loss class (N = 50) with minimum distance of 5 km between points. We then combined points from forest loss and forest cover habitat to be used as presence and absence of habitat loss for the habitat loss modelling. We used the same number of points for forest loss and forest cover. For example, we used 50 points of forest loss and randomly select 50 points over forest cover classes from 2000 and 2014 GIS map for model calibration/training. Similarly, we used 35 forest points and 35 forest loss points from 2014 and 2019 GIS map for model validation.

We used six environmental predictors based on our prior assumptions of drivers of tropical forest loss (Table S2). These included a terrain ruggedness index (tri), distance to village (dist. to village), distance to roads (dist. to road), distance to river (dist. to river), distance to forest edge in 2000 (dist. to forest edge), and distance to large oil palm plantation (dist. to oilpalm). The tri was generated based on an algorithm developed by Riley et al. (1999) that express the difference in elevation between adjacent cells using digital elevation data (Jarvis et al., 2008). The dist. to village, dist. to road and dist. to river layers were generated using village points, road networks, and river networks, respectively, from the Indonesian Geospatial Agency (BIG). Dist. to forest edge was calculated from 2000 forest cover data (MoEF, 2018b). We used the extent of oil palm plantation published by Danylo et al. (2021) to generate the dist. to oilpalm predictor variable. We only used large plantation (>100 ha) established between 1985 and 2014 across the study area to create the GIS layer. All GIS variables were standardized using z-scores transformation $((y-)/SD_y)$. All raster calculation were performed using ArcMap 10.4.1 and R 4.2.1 (R Core Team, 2017).

We fitted the model using a logistic regression, using 50 present and 50 absent forest loss points for 2000 and 2014 as our response variable. This model explains the likelihood of forest loss based on the above predictor variables. We measured the presence of multicollinearity among the variables and avoided using variables that have high correlation coefficient (Pearson's $r > |0.6|$; Figure S1)

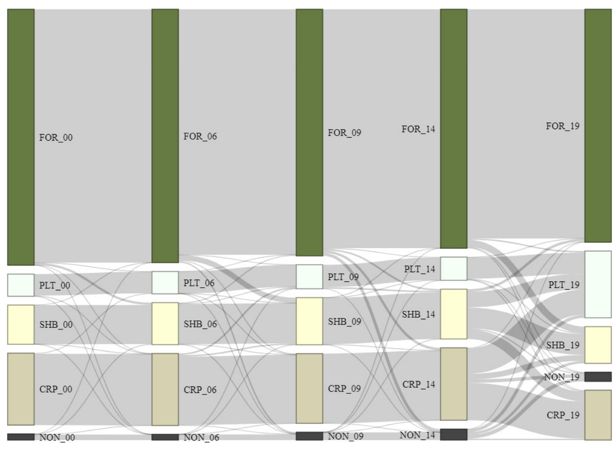

FIGURE 2
Land use changes in the Leuser Ecosystem between 2000 and 2019, where forest (FOR_00), plantation (PLT_00), shrub (SHB_00), croplands (CRP_00), and non-forest (NON_00) were generated using MoEF land use land cover data for the year 2000, and then the years 2006, 2009, 2014 and 2019.

in the same model. The top ranked model was chosen based on the lowest small sample size corrected Akaike's Information Criterion value (AICc; Akaike, 1998). In addition, we assessed model accuracy by comparing the spatial prediction of habitat loss from each candidate model with 70 independent points generated from 2014 and 2019 GIS map and calculated the receiver operating characteristic (ROC) curve (Hanley and McNeil, 1982). The logistic regression analysis was performed using R software and the AUC values were calculated using pROC package (Turck et al., 2011) in R.

2.3.2 Spatial and temporal patterns of mammal occupancy

We applied a single species hierarchical occupancy model (MacKenzie et al., 2002) to estimate the detection probability and occupancy value for each of the study species (elephant, tiger, wild boar, and sambar), and extended this model to incorporate the correlated detection model (Hines et al., 2010) for each SWTS survey period (2007–2009 and 2018–2019). In our modelling framework, we applied different grid cell sizes for different species based on their different home range size. We used 17 × 17 km grid cell to estimate the occupancy of tiger and elephant that have a large home range (Linkie et al., 2008; Wibisono et al., 2011). We used 8.5 × 8.5 km grid cell (subdividing 17 km grid cell by four) for smaller species such as wild boar and sambar (Gopalaswamy et al., 2012). For each grid cell size (17 × 17 km and 8.5 × 8.5 km), we extracted spatial replicates at three lengths; 1 km, 3 km, and 5 km. Detection and non-detection data from the four study species were extracted from each spatial replicate. To avoid misidentification of these species, we only used specific signs of the species such as pugmarks and direct observations for tigers, and used footprint, feces, and direct observations for elephants and sambar, and including nest for wild boar. We only used signs with high certainty noted by the field observers. We used track2dm package (Lubis, 2021) in R software to extract detection and non-detection data for each species including survey covariates (e.g., habitat type) in various replicate lengths and grid sizes for both SWTS survey periods (2007–2009 and 2018–2019).

The detection and non-detection data for each species were fitted using a single species, single season occupancy framework that accounted for spatial correlation of detections (Hines et al., 2010). For each species and each survey period, four key parameters were estimated: probability of species presence (ψ), probability of detecting a species (p) in a spatial replicate conditional on presence, probability of species presence in a segment if the site is occupied and the species was absent in the previous segment (θ_0), and probability of species presence in a segment if the site is occupied and the species was present in the previous segment (θ_1). The latter two parameters were developed to account for a Markov process that assumes a strong correlation exists between successive spatial replicates (Hines et al., 2010).

Based on priori information (Table S2), we hypothesized that species occupancy (ψ) was associated with environmental covariates, such as elevation, slope, total area of forest cover (fcover_area), number of forest cover patches (fcover_patches), human disturbance (disturbance) and, for tiger only, prey occurrence (prey). The detection of a species (p) was hypothesized to be influenced by proportion of forest habitat (forest_hab) collected directly during the surveys. Elevation and slope were generated using elevation data (Jarvis et al., 2008), which were used to estimate species occupancy in both survey periods, whilst fcover_area, fcover_patches, prey, disturbance, and forest_hab layers were specifically created for each survey period. For example, to estimate species occupancy in 2009, we used MoEF's forest cover map in 2009 (MoEF, 2018b) to create fcover_area and fcover_patches layers. Whilst prey, disturbance, and forest_hab layers which were the proportion of prey species (including wild boar and sambar) and human disturbance (including the signs of illegal poaching, illegal logging, encroachment, and non-timber forest product extraction), and forest habitat respectively, detected along the transect lines during 2007–2009 occupancy survey. A similar approach was used to create fcover_area, fcover_patches, prey, and disturbance to estimate species occupancy and forest_hab to account for detectability using 2018–2019 data. All predictor variables were extracted for each grid cell for each species using ArcMap 10.4.1 and R software.

We assessed the robustness of each replicate length (1 km, 3 km, and 5 km) by creating a null model (without covariates) and a global model (with all non-correlated covariates) for each species in each survey period and compared their AICc values. From all species and in both survey periods, our preliminary analysis revealed that 5 km replicates had the lowest AICc values and were therefore used in the subsequent analyses.

In the second step, we developed ~10 models for each of the four species with different combination of elevation, slope, fcover_area, fcover_patches, prey, and disturbance covariates to the occupancy component, and only used forest_hab for the detection component (Tables S3, S4). The candidate models were built with a maximum of two covariates for and one covariate for p, while keeping θ_0 and θ_1 with no covariates. We avoided using models with covariates that had a correlation coefficient of more than 0.6 (Figure S2) to avoid overfitting. We dropped any model that failed to converge and selected the top-ranked model based on lowest AICc values to generate point estimates of probability of species occurrence (ψ) and its corresponding detectability (p) from the two survey periods. We note that the RPresence package we used in this analysis does not facilitate any goodness of fit test for the correlated detection model (Hines et al., 2010). So, in order to measure the uncertainty for ψ and p, we used a non-parametric bootstrap technique by randomly selecting the detection and non-detection data with replacement, re-fitting the model (using the top-ranked model), extracting mean ψ and mean p, and repeating this 1,000 times to produce 1,000 mean ψ and 1,000 mean p as bootstrap distributions (MacKenzie et al., 2006; Kéry and Royle, 2015). We then generated 95% confidence intervals for ψ and p by selecting the 2.5% and 97.5% percentile from the bootstrap's distribution.

2.3.3 Mapping occupancy change

We developed spatial predictions of species occupancy in each survey period using the top-ranked model's regression coefficients with a "predict" function from the raster package in R (Hijmans et al., 2017). We used a threshold of 0.5 to convert the probability map into a binary map that consists of unoccupied (< 0.5) and occupied (≥ 0.5) cells. We then compared the species occupancy change between seasons using spatial matching, where for each grid cell, we evaluated whether the occupancy status for each species had changed between the two survey periods. For this, we created a new raster layer based on these two spatial predictions of species occupancy. This new raster layer had four categories; 0 if a cell remained unoccupied in both periods, 1 if the occupied cell became unoccupied (locally extinct), 2 if an unoccupied cell became occupied (recolonized), and 3 if the cell remained occupied in both periods. We created a single raster layer for each species and calculated the areas (in hectares) for each category.

2.3.4 Modelling forest management scenarios

We developed scenarios for forest gain and loss and modelled the effects of this habitat change for Sumatran elephant and Sumatran tiger, since these two subspecies are critically endangered and require large forest areas for their survival. We used the occupancy estimates of elephants and tigers from 2018–2019 data (Table S5) with the forest habitat variable to extrapolate species occurrence to forest connected to the Leuser Ecosystem in the provinces of Aceh to North Sumatra. We developed 10 scenarios for future forest habitat ranging from worst to best scenarios. We used the predicted model of habitat loss generated from the top-ranked model's regression coefficients (Table 1) where the forest near the forest edge in 2000, particularly in areas with less rugged terrain, were more prone to undergoing changes.

For the forest loss scenarios (#1–5), we disaggregated predicted habitat loss into five classes based on the interquartile range of the predicted probability of forest loss: 20%, 40%, 60%, 80%, and 100% (Figure S3). For the forest gain scenarios (#6–10), we predicted that varying amounts of degraded forest would be recovered, and reforestation strategies would be implemented to reconnect forest patches. We used a global study on mapping reforestation potential to prioritize areas for forest restoration and reforestation to mitigate climate change impacts and improve ecosystem functioning (Rayden et al., 2023). Using the reforestation potential map, we developed five habitat gains scenarios by splitting the raster data into five equal areas ranging from low to high values of potential areas. This allowed us to predict what would happen to elephant and tiger occupancy if 20%, 40%, 60%, 80%, and 100% of this potential habitat was restored (Figure S3).

Predicted areas (as a percentage) from the forest loss and forest gain scenarios were calculated by multiplying the probability of occupancy generated from top-ranked model for both elephant and tiger with the total area for each grid cell. For instance, if a cell had $\psi = 0.7$, the occupied area for that cell would be $0.7 \times 28{,}900$ ha, which is 20,230 ha, i.e., equal to 70%.

2.4 Study limitation

We recognize several limitations in our study that warrant consideration. Firstly, each survey period extended between 14 to 22 months, potentially violating the closed population assumption, particularly for highly mobile animals like tigers, which have large home ranges and may exhibit movements during the survey period (Tilson and Nyhus, 2010; Priatna et al., 2012; Simcharoen et al., 2014). Although dynamic occupancy models, accounting for changes in occupancy over time with colonization and extinction probabilities, were considered to address this issue (MacKenzie et al., 2003), their application was constrained due to the low density of tigers and limited species detections. Moreover, the positive correlation between local occupancy of successive segments, which should be considered in dynamic models (Hines et al., 2014), may inflate occupancy probability estimates (Emmet et al., 2021).

Secondly, the future predictions of our forest habitat models were based solely on regression estimates from the top-ranked occupancy model, using data taken only from 2018 and 2019. As a result, these predictions lack empirical validation using data from other periods, potentially affecting the reliability and generalizability of our findings. Additionally, while the importance of forest habitat to the survival of both megafauna species was found to be similar in 2009 and 2019 (Table S5), the study lacks a dynamic model approach, which might provide a more nuanced understanding of the relationships between forest cover loss and megafauna occurrence, by explicitly identifying parameters associated with the extinction process. Thus, future research should endeavor to incorporate data from multiple time periods and employ dynamic modeling techniques, effectively addressing the challenges posed by species mobility and utilizing more comprehensive datasets for validation purposes.

3 Results

3.1 Spatio-temporal patterns of forest change

From 2000–2019, forest cover in the Leuser Ecosystem remained largely intact. The 2.4 Mha of forest in 2000 underwent

TABLE 1 Regression coefficients (± SE) for models within four delta AICc units (supported models), model weight (AICc Wt) and area under the curve (AUC) of the operating plot, depicting the association between forest loss and environmental predictors in the Leuser Ecosystem.

Model ID	Intercept	Tri	Distance to forest edge	Distance to road	Distance to river	AICc Wt	AUC
1.1	0.29 (0.36)	−2.07 (0.45)	−3.68 (1.58)	–	–	0.5	0.94
1.2	−31.98 (7.26)	–	–	−47.03 (10.44)	–	0.3	0.93
1.3	−41.33 (13.51)	–	–	−47.64 (10.72)	−13.66 (15.80)	0.1	0.93

an average annual loss of 0.3% (or 13,406 ha). Forests were mainly converted to shrubland (2.9%), followed by plantation (2.4%), and cropland (1.1%). Plantation expansion (11.5%) was most substantial during 2014 and 2019 where 6.4% of croplands, 3.9% of shrubland, 0.8% of non-forest, and 0.4 of forest were converted to plantation (Figure 2). The conversion of forests around Leuser Ecosystem mainly occurred at the habitat edges especially along roads or at lowland areas.

Based on our top-ranked model (Tables 1; Table S6), forest loss was more likely to occur in areas that were less rugged and closer to the forest edge (Figure S4). This model had a high predictive accuracy (AUC = 0.94) as compared to an independent land use type dataset for the years 2014–2019. The residual of the selected model was not affected by spatial autocorrelation (Moran's *I* = −0.03, P > 0.1). Sub-setting the predicted habitat loss model with 2019 forest edge data revealed patches of lowland forest that were both important for biodiversity and at a high risk of clearance (Figure 3). This highlighted the two largest intact peatlands of Singkil WR and Kluet (inside GLNP) as being particularly susceptible to future conversion.

3.2 Species occupancy trends

The occupancy survey conducted in the first period (2007–2009) had a sampling effort of 4,483 km in 119 17 × 17 km grid cells (average of 37 ± 15 km per cell). In the second period (2018–2019), the total survey effort increased by 25% to 5,639 km in 109 grid cells (average of 51 ± 28 km per cell; Figure 1). Comparing across the two sampling periods, signs of elephant occurrence were found in 34 grid cells (naïve occupancy = 0.29) in the first period and then 19 grid cells (0.17) in the second period. Signs of tiger occurrence were found in 50 grid cells (0.42) in the first period and then 37 grid cells (0.34) in the second period. For tiger prey, using smaller grid cells (8.5 × 8.5 km), naïve occupancy decreased for each species: wild boar (193 to 50 cells, or 0.57 to 0.15); and sambar (188 to 91, 0.55 to 0.28; Table 2).

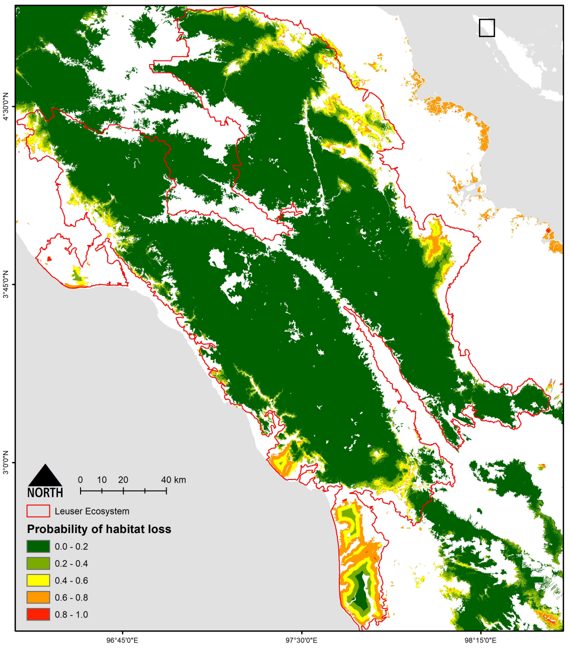

FIGURE 3
Probability of habitat loss in Leuser Ecosystem.

The mean occupancy estimate for each species, except tiger (1.4% increase), declined over the two time periods. This reduction in mean occupancy was most pronounced for wild boar (−59.5%), elephant (−18.2%), and sambar (−9.7%), although sambar still maintained a high level of occurrence in the study area ($\psi = 0.84$; Figure 4). Changes in detection probability were observed for each species and the differences were statistically significant (Table 2). We found for all species in both periods that even using 5 km transect lengths as replicates, the probabilities of a species being present in a 5 km transect was higher when that species was also detected in the previous 5 km transect (θ_1; Table 2).

In the 2008–2009 survey, forest cover area and disturbance were positively correlated with the occurrence of elephants and tigers. Disturbance was positively associated with wild boar especially at lower elevation. Sambar occupancy was associated with areas of flatter slope and in a more fragmented forest (higher number of forest patches). In the 2018–2019 survey, elephant occupancy was higher in areas with more intact forest and higher disturbance. For tigers, in addition to higher forest cover area, this species was found in areas with a higher proportion of wild prey species. Wild boar preferred less rugged areas and more fragmented forests. Sambar showed a positive association with forest cover (Figure 5; Table S5).

Tiger and sambar had high levels of occupancy (78.4% and 72.3%) in both survey periods but had strong predicted patterns of local extinction along the forest edge, with 21.6% and 27.7% of grid cells that were occupied by tiger and sambar in 2009 being no longer occupied in 2019 (Figure 6). Elephants had limited distribution in the study area, due to the unsuitable rugged terrain located in the interior areas, as reflected by their absence in most (73.4%) grid cells in both survey periods. The local extinction and colonization patterns were mixed, with elephant decline along the west side of the Leuser Ecosystem and shifting their range in the northeast forest patch. Wild boar experienced dramatic occupancy changes, where occupied areas in 2009 (72.3%) were extinct in 2019. Only a small percentage (25.9%) of areas were occupied by wild boar in 2019 and these were mostly (21.2%) in lowland forest located near the forest edge (Figure 6).

3.3 A pathway for Sumatran megafauna recovery

Forest cover was found to be the single most important predictor of elephant and tiger occupancy in 2019, followed by human disturbance and, additionally for tiger, wild prey. Based on this result, we were able to explore how future forest cover change could impact elephant and tiger populations. A 20% decline in forest habitat, for example, was predicted to result in an occupancy decrease by 2–3% for elephant and 10–12% for tiger, whilst a 20% increase in habitat led to an occupancy increase of 2–4% for

TABLE 2 Survey effort and parameter estimates of single season occupancy from 2009 and 2019 surveys with correlated detection from the top-ranked model for each species.

Species	Grid size	Grids surveyed	Grids with a detection	Naïve	ψ (95% CI)	p (95% CI)	θ_0	θ_1
2009 survey								
elephant	17km	119	34	0.29	0.33 (0.25–0.53)	0.73 (0.36–0.98)	0.46	0.62
tiger	17km	119	50	0.42	0.72 (0.52–0.82)	0.47 (0.30–0.74)	0.41	0.61
wild boar	8.5km	341	193	0.57	0.79 (0.70–0.88)	0.80 (0.61–1.00)	0.47	1.00
sambar	8.5km	341	188	0.55	0.93 (0.85–0.97)	0.43 (0.38–0.77)	0.53	1.00
2019 survey								
elephant	17km	109	19	0.17	0.27 (0.17–0.64)	0.34 (0.16–0.87)	0.43	0.99
tiger	17km	109	37	0.34	0.73 (0.45–0.92)	0.25 (0.11–1.00)	0.41	0.36
wild boar	8.5km	327	50	0.15	0.32 (0.22–0.68)	0.47 (0.21–1.00)	0.39	0.95
sambar	8.5km	327	91	0.28	0.84 (0.62–0.91)	0.59 (0.21–0.87)	0.23	0.82

Naïve occupancy is the total number of grid cell where the species is detected at least once divided by total grid surveyed, ψ is the probability of species presence, p is the probability of detecting a species, θ_0 is the probability of species presence in a segment if the site is occupied and the species was absent in the previous segment, and θ_1 is the probability of species presence in a segment if the site is occupied and the species was present in the previous segment.

elephant and 5–10% for tiger (Figure 7). Under the most progressive habitat gain scenario (#1), connecting the western and eastern forest patches in Leuser Ecosystem (Figure 7) resulted in an occupancy increase of 67% for tiger and 23% for elephant. In this scenario, elephants mainly benefitted from increased lowland habitat, while tiger benefitted from increased interior forest habitat that was more rugged (Figure 7).

4 Discussion

Our study provides the first assessment of occupancy trends for Sumatran elephant and Sumatran tiger, as well as scenarios for population recovery under different landscape management plans. Our findings suggest a stable population trend for tigers with a declining population trend for elephants and the wild prey of tigers, especially wild boar. Our hypothesis on the positive correlation between forest cover and species occupancy especially for tiger and elephant was confirmed, although the effect of forest cover loss on elephant occupancy in the interior of the Leuser Ecosystem was lower as this large mammal prefers lowland habitats, which are primarily located at its periphery (Rood et al., 2010; Gopala et al., 2011).

We found that signs of human activities (disturbance) were positively associated with elephant and tiger occupancy. This may be an artefact of both people and large-bodied animals using similar trails to traverse the rugged interior of the Leuser Ecosystem, which would be very difficult otherwise. A study from the north of Leuser, in the Ulu Masen forest area, also found elephants to occupy habitat patches close to human-dominated landscapes (Rood et al., 2010), and several studies have shown the high overlap between people and tigers in the Leuser Ecosystem (Lubis et al., 2020) and Bukit Barisan Selatan NP in southern Sumatra (Pusparini et al., 2017). While tigers may be able to survive in human-modified landscapes,

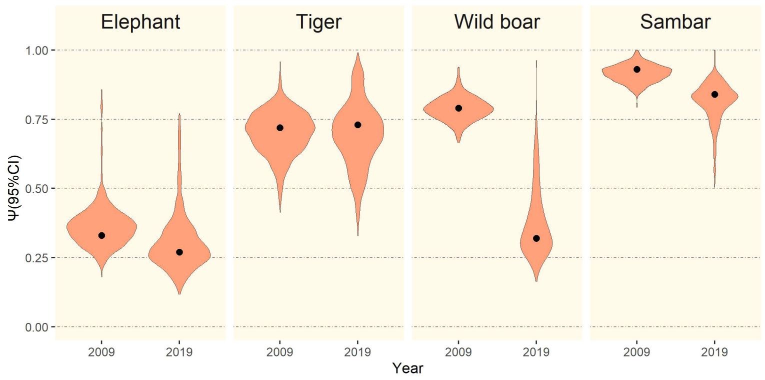

FIGURE 4
Mean occupancy estimates (black dots) with 95% CI (violin plots) of elephant, tiger, wild boar, and sambar in Leuser Ecosystem in survey periods 2009 and 2019.

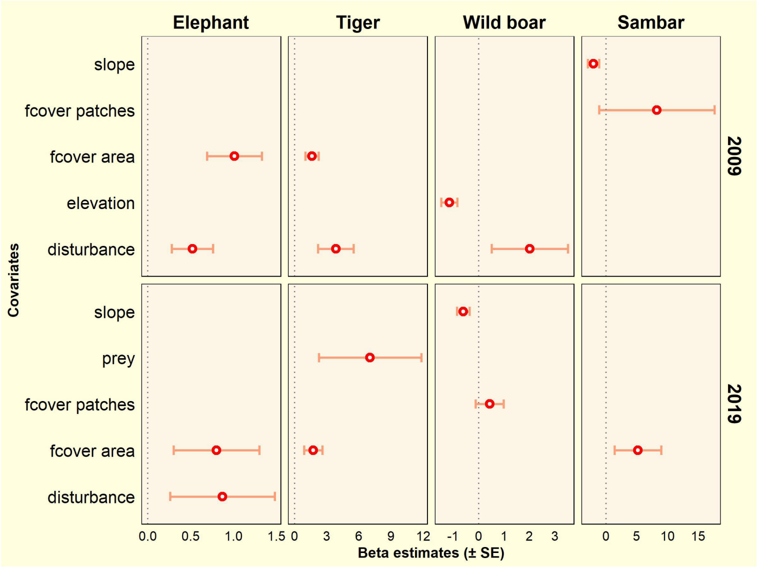

FIGURE 5
Covariate effects on occupancy estimates based on the top-ranked model for tiger, elephant, wild boar, and sambar in the Leuser Ecosystem from two survey periods (2009 and 2019).

it is a precarious existence that relies on a having sufficient wild prey base and not relying on livestock, and avoiding the perils of poaching and retaliatory killings due to conflict with people that are often heightened in these edge environments (Karanth et al., 2011; Amir et al., 2022).

Our study revealed a declining trend in the size of the forest areas occupied by tiger prey, especially wild boar. This lower occurrence of prey, along with habitat loss, are predicted to have a detrimental impact on Sumatran tiger population viability (Karanth et al., 2004) and might have caused an increase in human–tiger conflicts in the Leuser Ecosystem (Lubis et al., 2020). Another study, which used camera trap data from GLNP in 2010, 2013, and 2017, found a stable tiger density but a substantial decline in wild boar occupancy (WCS unpublished data), which is of great concern because this species alone provides the highest prey biomass for tigers in Sumatra (Hayward et al., 2012; Allen et al., 2021). The presence of African swine fever (ASF) in the Leuser Ecosystem offers one possible explanation for the alarming decline of wild boar in this landscape (WCS unpublished data). The ASF virus has rapidly spread across Asia, including Indonesia, having a devastating impact, with 100% fatality to infected domestic pigs and wild boar (Luskin et al., 2021). As a pertinent example near to our study area, from 2019 to 2020, around 1,007 ASF cases were reported by the Department of Food Security and Animal Husbandry of North Sumatra Province and Medan Veterinary Centre in 17 districts, including Langkat and Deli Serdang, which form part of the Leuser Ecosystem (Primatika et al., 2022). A recent mass death of pigs occurred in November 2022, where approximately 2,000 domestic pigs were found dead, with symptoms suggesting ASF (Karouw, 2022). A large, but unquantified, number of these pig carcasses were disposed of in nearby rivers and may have ended up in close contact with people and/or wildlife, leading to further ASF transmission and infection (Tambunan, 2022). While it remains unknown how a presumed loss of wild boar has impacted tiger population density or changed prey selection, particularly towards livestock, the outlook is certainly dim (Hayward et al., 2012; Miquelle et al., 2018).

Assessing the spatial occurrence of species over time is important for formulating appropriate conservation management actions. In our study, areas where species were predicted to have gone locally extinct (occupancy change category 1; Figure 6), we would recommend, as an initial step, allocating increase ranger patrol effort to secure this forest patch from poaching and habitat loss (Linkie et al., 2015; Dancer et al., 2022; Adhiasto et al., 2023). Our newly developed tools (e.g. track2dm R package; Lubis (2021)) used data from regular patrols to enable near real-time monitoring of species and poaching threats. Additionally, within the Leuser Ecosystem, our spatial model identifies where habitat restoration, such as reforestation, should be prioritized to improve habitat quality and allow species to naturally recolonize former parts of their range. Improving the quality and quantity of habitat in these areas should also provide more suitable candidate sites for releasing suitable conflict tigers back into the wild (Goodrich and Miquelle, 2005). Where one of our target species could naturally recolonize (occupancy change category 2; Figure 6), securing these areas through threat removal remains key, and anticipating the effects of increased tiger occurrence near the forest edge would require conflict mitigation measures that reduce the opportunities for encounters between tigers and people, such as improved livestock husbandry involving keeping goats penned in at night (Goodrich et al., 2011). These efforts require active collaboration between stakeholders (e.g., GLNP, FMUs, SWR, and local governments) from planning to field implementation activities.

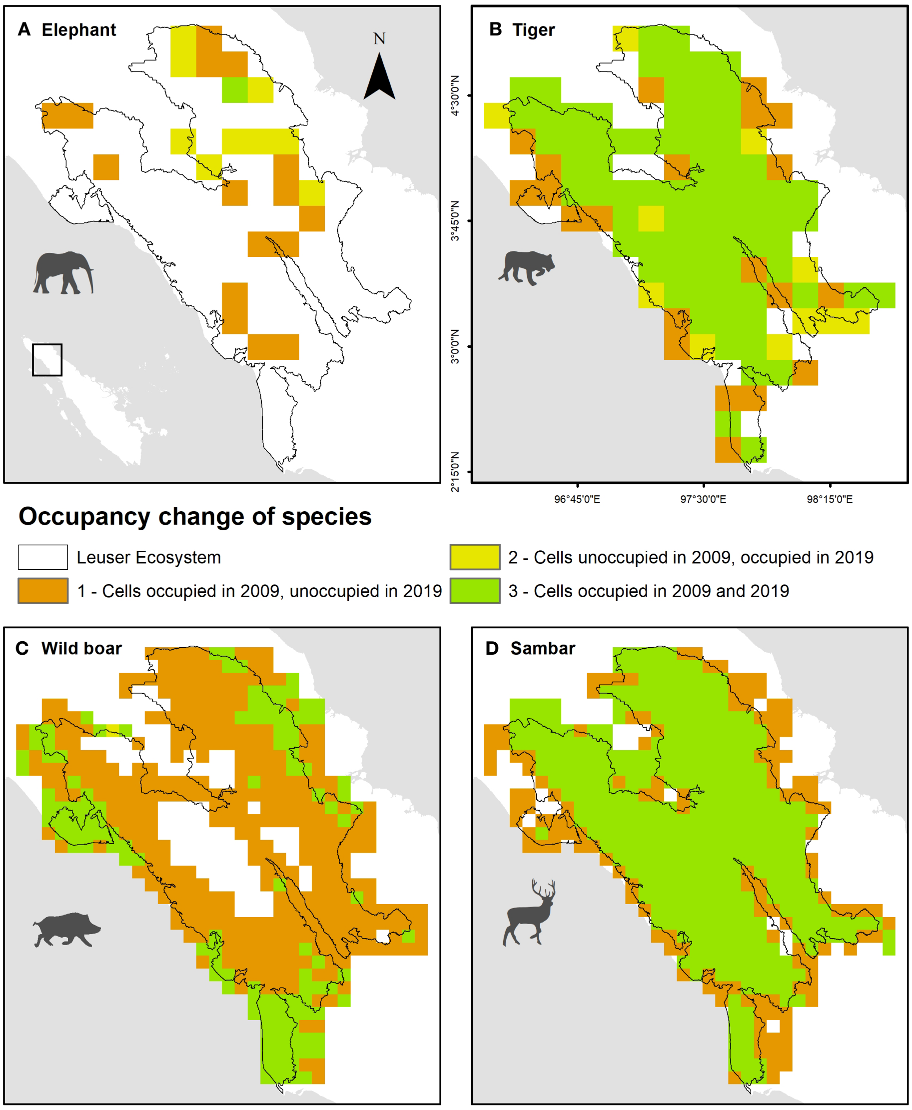

FIGURE 6
Spatial occupancy change of **(A)** elephant, **(B)** tiger, **(C)** wild boar, and **(D)** sambar in Leuser Ecosystem between 2009 and 2019.

We were able to extend our predictive model beyond the Leuser Ecosystem to include connected forests spanning the provinces of Aceh and North Sumatra. However, our extrapolation could only be based on the predictive model using forest cover because the other important predictor variables of human disturbance and wild prey were not available for areas outside of the Leuser Ecosystem. Still, forest cover was the single most important variable, and we assume that the levels of human disturbance and wild prey available would not markedly vary based on our knowledge of the other areas, so the final results should be reasonably accurate and provide important insights. Our spatial predictions should help conservation managers prioritize areas for habitat recovery and directly estimate the associated consequences on species' occupancy. Habitat enrichment or restoration should be conducted to connect fragmented and distant habitat patches. This is feasible because, for example, habitat restoration has become a government of Aceh priority approach, as stipulated under local law (*Qanun*) Aceh No.11/2019 (DLHK Aceh, 2019), and our spatially-explicit map could be used as a science-based way to guide efforts towards more strategically achieving this conservation goal.

5 Conclusion

Monitoring programs that assess wildlife populations and their distributions, along with associated habitats, are crucial for adaptive wildlife conservation management. With effective forest habitat management, through forest restoration and reforestation, issues related to decreasing wildlife populations can be addressed in the following ways: 1) reducing the risk of further isolating highly threatened species that are already low in numbers and isolated in distinct habitat patches (Smith et al., 2018); 2) re-populating areas by connecting source sites with a larger forest habitat (Linkie et al., 2006; Walston et al., 2010); and, 3) reducing

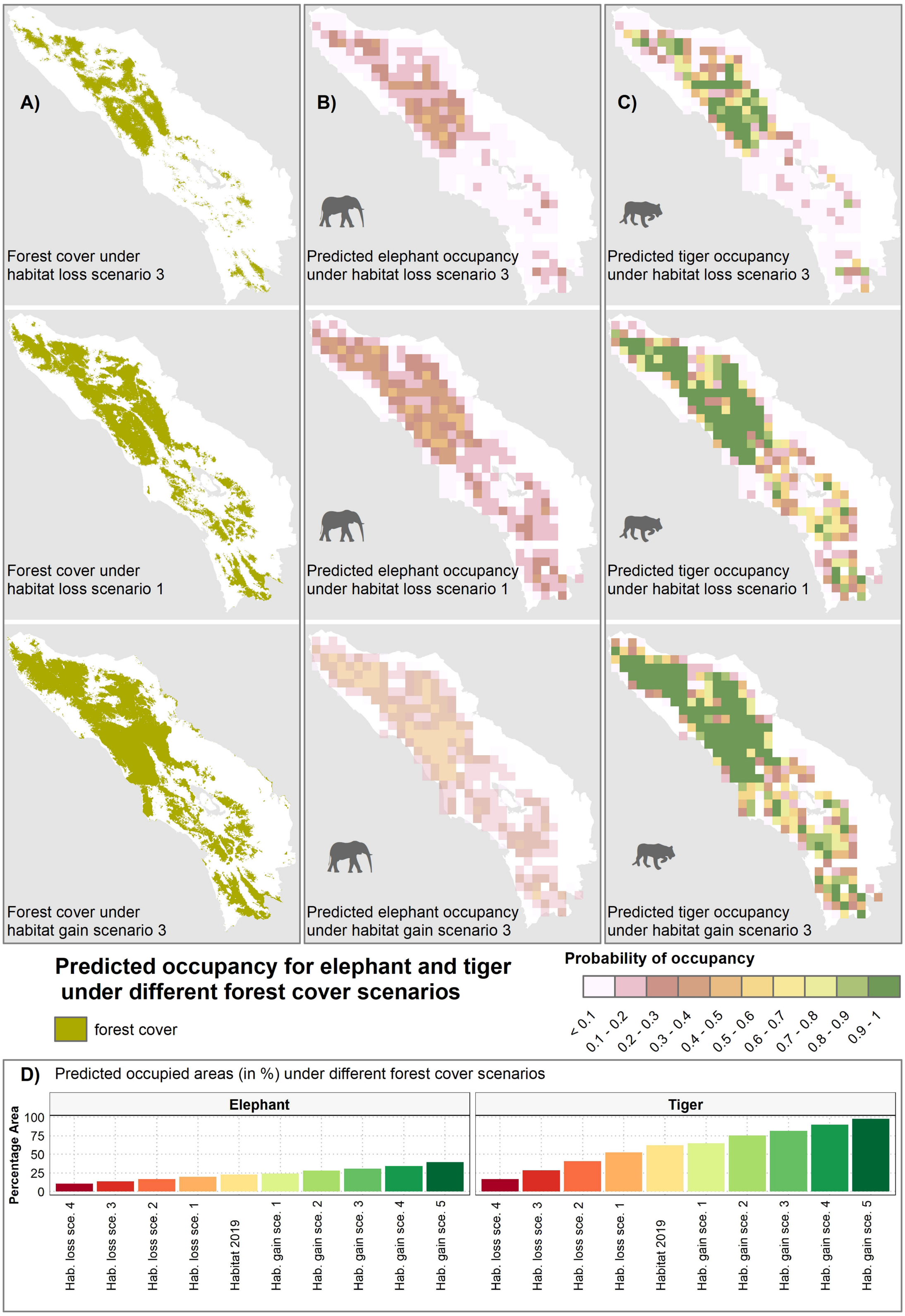

FIGURE 7
Predicted occupancy for elephant **(B)** and tiger **(C)** under various forest habitat loss and gain scenarios **(A)**, with illustrations included for three habitat changes scenario including habitat loss scenario 1 & 3, and habitat gain scenario 3. Bar plot **(D)** shows predicted occupied areas (in %) under different forest cover scenarios.

the accessibility of the forest for perpetrators and thus reducing the poaching risk.

Data availability statement

The datasets presented in this article are not readily available because the raw dataset is owned by the Indonesian Ministry of Environment and Forestry (MoEF). Requests to access the datasets should be directed to the MoEF.

Ethics statement

Ethical review and approval was not required for the study of animals in accordance with the local legislation and institutional requirements.

Author contributions

The authors confirm contribution to the paper as follows: MIL, ML, T, WM, NA, ER, and DY planned and designed the study. UR and AT provided permission letter to conduct the study. MI, T, ER, and RA organized the field works. MIL, A, SS, DM, ER, AT, and RA managed and cleaned the field data. MIL analyzed the data. MIL, ML, JL, and KJ wrote the manuscript. All authors reviewed and approved the manuscript for publication. All authors contributed to the article.

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Conflict of interest

The 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.

The handling editor TG is currently organizing a Research Topic with the author ML.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2023.1174708/full#supplementary-material

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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

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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.

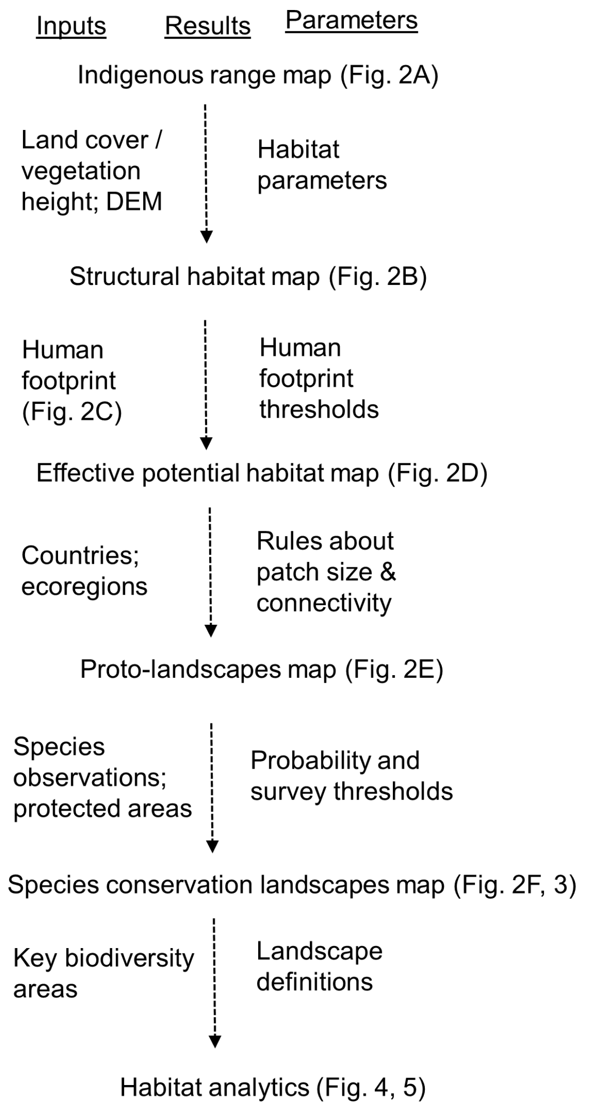

FIGURE 1
Schematic of analysis of the Species Conservation Landscapes including inputs and parameters.

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

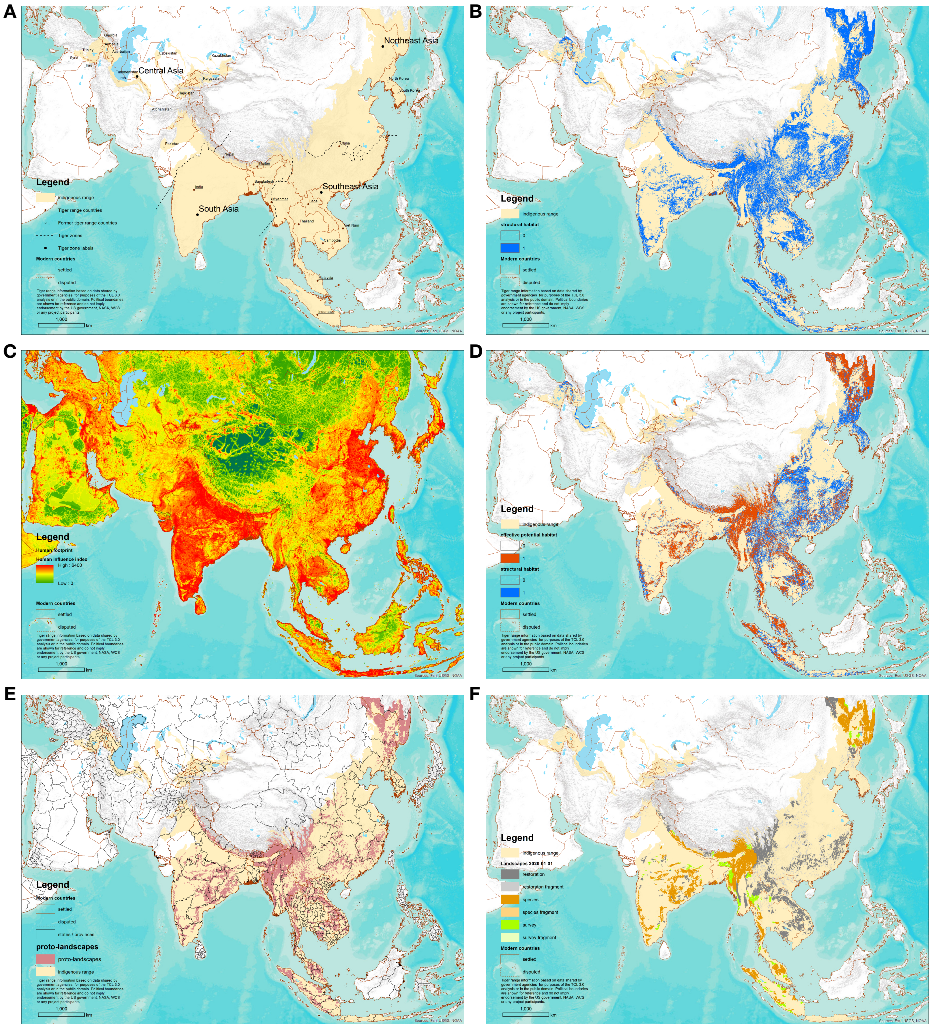

FIGURE 2
Species Conservation Landscape Mapping process, with application to tigers (*Panthera tigris*) for 1 January 2020. **(A)** Map of the likely resident indigenous range, with zone boundaries (dotted lines). **(B)** Map of structural habitat as revealed by land cover, elevation, and vegetation 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

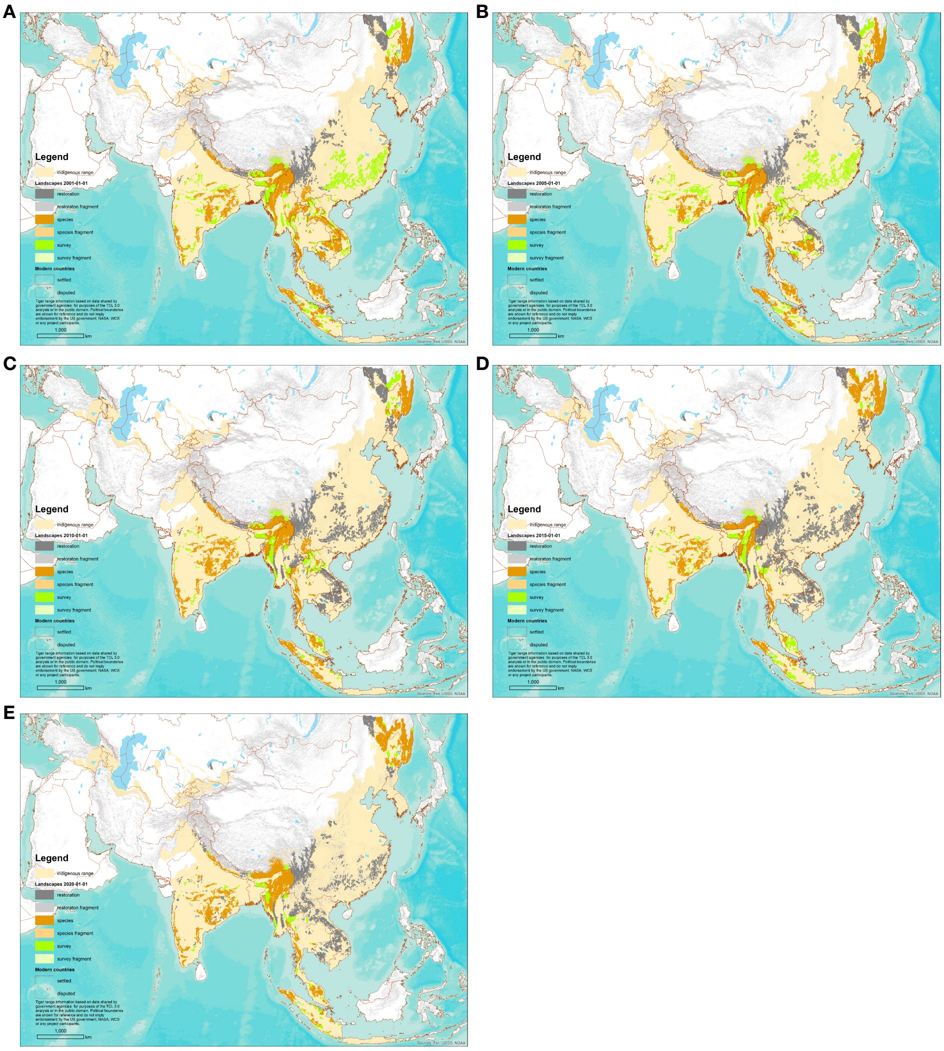

FIGURE 3
Map of Tiger Conservation Landscapes on five dates. Note: Figures 2F and 3E are the same. **(A)** 1 January 2001. **(B)** 1 January 2005. **(C)** 1 January 2010. **(D)** 1 January 2015. **(E)** 1 January 2020.

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.

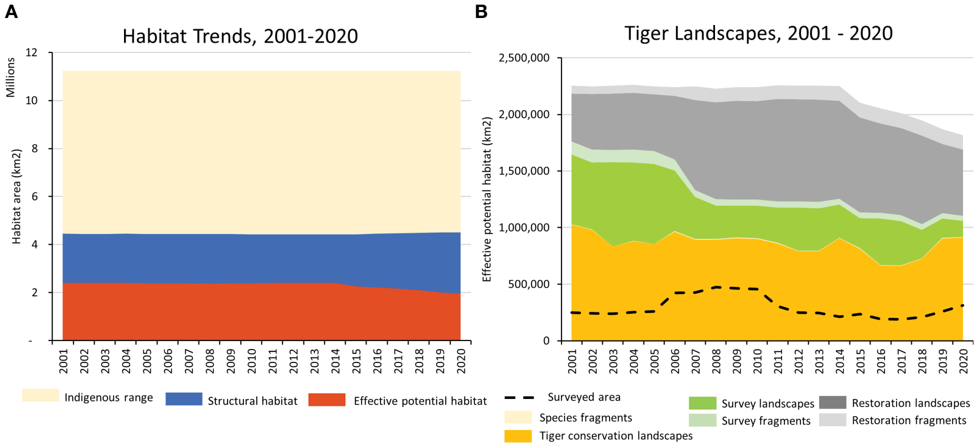

FIGURE 4
Range-wide trends. **(A)** Trends in structural habitat and effective potential habitat within the tiger's likely resident indigenous range, 2001 - 2020. **(B)** Trends in Tiger Conservation Landscapes, Survey Landscapes, and Restoration Landscapes, fragmented landscapes, and estimated surveyed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

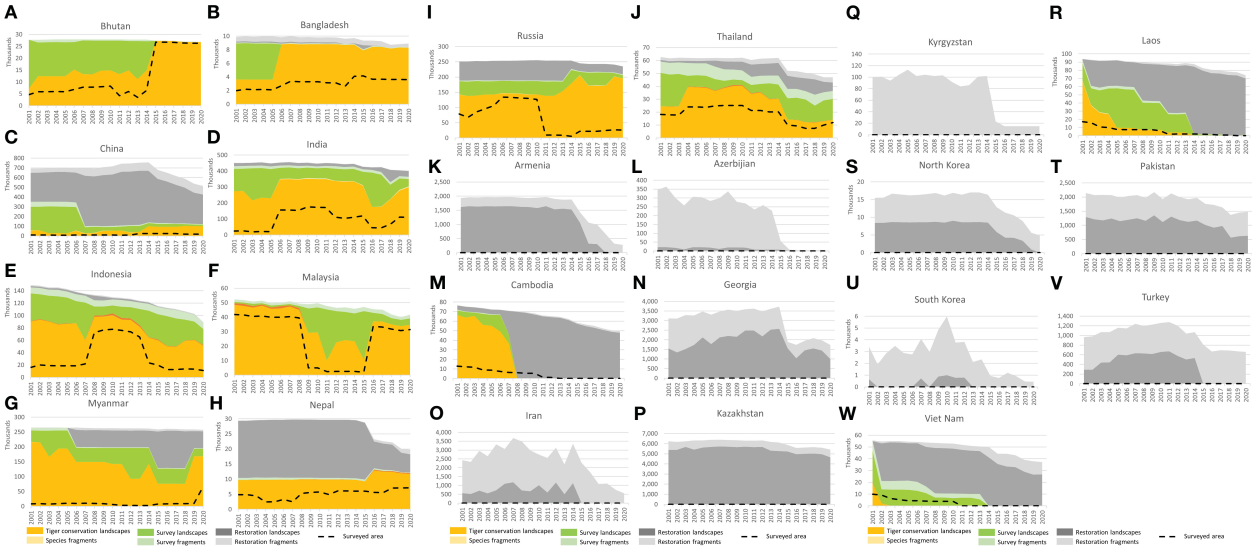

FIGURE 5
National level trends in Tiger Conservation Landscapes, Survey Landscapes, and Restoration Landscapes, fragmented landscapes, and estimated surveyed area from 2001 – 2020. The first 10 figures **(A–J)** show countries, where tigers lived in 2020. The remaining 13 figures **(K–W)** show former 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)

TABLE 2 Continued

				Species Landscapes		Species Fragments		Survey Landscapes		Survey Frag-ments		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

(Continued)

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%	-	-	-	-	-	-	-	-	-	-

(Continued)

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)

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.

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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Influence of resource gradients and habitat edges on density variation in tiger populations in a multi-use landscape

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Spatial heterogeneity in the local densities of terrestrial carnivores is driven by multiple interacting biotic and abiotic factors. Space-use patterns of large carnivores reflect the competing demands of resource selection (e.g., exploitation of habitats with abundant prey) and minimization of risks arising from human interactions. Estimating the relative strength of these drivers is essential to understand spatial variation in densities of large carnivores and there are still key knowledge gaps for many large carnivore populations. To better understand the relative roles of environmental and human drivers of spatial variation in tiger (*Panthera tigris*) densities, we surveyed a 3000 km^2 landscape in North India using camera trap data. Over two years, we photo-captured 92 unique adult tigers. Associating spatial covariates with patterns of detection allowed us to test hypotheses about the relative influence of prey abundance, habitat structure and extent, and proximity to habitat edges on spatial variation in tiger densities across a gradient of anthropogenic disturbance. We documented extensive variation in tiger density within and across management units and protected areas. Spatial variation in prey abundance and proximity to grassland habitats, rather than human use (e.g. extent of human-dominated edge habitat and protection status), explained most of the spatial variation in tiger density in two of the five surveyed sites. The region's largest tiger population occurred in a multi-use forest beyond protected area boundaries, where wild ungulates were abundant. Our results suggest that tigers can occur at high densities in areas with extensive human use, provided sufficiently high prey densities, and tracts of refuge habitats (eg. areas with dense vegetation with low human use). We argue that tiger conservation portfolio can be expanded across multi-use landscapes with a focus on areas that are adaptively managed as "zones of coexistence" and "refuge habitats". Advancing this conservation strategy is contingent on greatly strengthening systems to effectively and equitably redress human–wildlife conflict and leveraging existing policies to strengthen local participation in conservation planning and forest stewardship. Our insights into the environmental drivers of spatial heterogeneity in tiger populations can inform both local management and guide to species recovery in working landscapes.

KEYWORDS

carnivore–prey relationships, conservation zonation, edge habitat, protected areas, spatially explicit capture recapture, tiger–human co-occurrence, working landscapes

Introduction

Worldwide, populations of large-bodied predators have declined and several species are functionally extinct in extensive areas of their native range (Check, 2006; Ripple et al., 2014). Large carnivore declines can have profound direct and indirect impacts on ecosystem structure and function (Dobson et al., 2006; Duffy et al., 2007). Key conservation goals for these species are to first identify, and then sustain, those environmental conditions that promote stable or growing populations. Meeting these goals requires one to identify the ecological and anthropogenic factors that lead to spatial variation in demographic parameters, such as density (*D*) and abundance (*N*) (Boyce and McDonald, 1999; Burton et al., 2011). Our ability to reliably estimate population parameters and link these to environmental drivers in dynamic environments is, in turn, dependent on the design and implementation of robust monitoring programs at appropriate spatial and temporal scales (Nichols and Williams, 2006).

As a consequence of environmental variation, the spatial and temporal distributions of most species are dynamic. Variation in the density of large carnivores, for example, has been attributed to numerous endogenous and exogenous factors (Carbone and Gittleman, 2002; Vanak et al., 2013). Most relevant may be the availability of their principal prey species and the distribution of competitors, which are also temporally and spatially dynamic (Carbone et al., 2011; Harihar et al., 2011; Bhola et al., 2012). Further, the location and extent of habitats required for successful reproduction, and secure from direct human threats, strongly influence the abundance and distribution of many large terrestrial carnivores (Riley and Malecki, 2001; Oriol-Cotterill et al., 2015; Chanchani et al., 2016). For example, in some landscapes large carnivores occur in agricultural areas and other habitats with high levels of human-use (Athreya et al., 2013; Warrier et al., 2020). Carnivore occurrence in human-use areas may reflect a dynamic balance between prey availability and anthropogenic threats (Basille et al., 2009). Physical landscape features, including water bodies, landform and patch connectivity, may also constrain animal movement and strongly influence patterns of space use (Dickson et al., 2005; Harihar and Pandav, 2012). Finally, behavioral factors including territoriality, mating systems and dispersal are key drivers affecting the distribution and abundance of carnivores, and these behaviors are often density-dependent (Smith, 1993; Carter et al., 2015; Chanchani et al., 2018).

Small populations are vulnerable to local extinction, and in South Asia many small tiger populations are embedded in some of the world's most densely populated rural landscapes (The World Bank, 2011; Wikramanayake et al., 2011). To formulate conservation strategies to benefit these populations requires estimation of their local abundances and spatial distributions across the landscape. Subsequently, spatial variation in abundance needs to be linked to underlying causal factors.

Recent studies have shown that tiger densities vary dramatically at both broad (across landscapes within individual protected areas) and fine (locations within a single Protected Area) spatial scales (Jhala et al., 2015; Duangchantrasiri et al., 2016). The dominant explanatory factor of spatial variation in tiger abundance is variation in prey abundance and availability (Karanth et al., 2004). However, additional environmental and social factors, that are less studied, may significantly interact with prey availability and prove to be important divers of spatial variation in tiger abundance.

In this study, we investigated the influence of four key factors as potential drivers of spatial heterogeneity in tiger density. Our study site was located inNorth India in an area characterized by extensive habitat fragmentation and high human-use, and was centered on forests in Pilibhit District and Kheri District (Dudhwa Tiger Reserve). Initially, we investigated the relationship between tiger and prey density at fine spatial scales to estimate the extent to which local heterogeneity in prey density explained spatial variation in tiger abundance. Relationships between tiger and prey densities have typically been documented at broad spatial scales (e.g., within entire Protected Areas) (Jathanna et al., 2003; Karanth et al., 2004), but less commonly at finer spatial scales (e.g., within a single PA). Previous studies found that finer scale variation in tiger abundance is best explained by variation in habitat quality, prey availability, and management practices (Harihar et al., 2013; Dorozio et al., 2017). To estimate the influence of variation in prey abundance, relative to habitat variation and management regimes, we first estimated the relationship between prey density and fine-scale variation in tiger density.

To evaluate forest structure, including as a result of variation in forest structure and management, we measured variation in canopy cover using remotely sensed data. The primary prey species in our study select forest areas with extensive plant forage in the understory and understory vegetation that provides cover for hunting, feeding and raising young (Dinerstein, 1980; Shrestha, 2004; Sunarto et al., 2012). These environmental factors have rarely been considered when developing conservation strategies for Protected Areas (PAs) and multiple-use forests (MUFs). In India, since the colonial era, large tracts of tiger habitat in have been managed as Reserved Forests (i.e., multiple-use forests), emphasizing commercially valuable timber species. In recent decades, several reserve forests in India have been elevated to PA status, a designation which prioritizes wildlife conservation and prohibits logging. However, many regions of India remain dominated by expansive tracts of homogenous, closed-canopy forests, particularly Sal (*Shorea robusta*). These forests generally have little understory vegetation and support low densities of ungulate prey species (Dinerstein, 1980; Seidensticker et al., 2010; Bhattarai and Kindlmann, 2011). In contrast, in MUFs, selective tree felling creates canopy openings and edges which may increase productivity in the forest understory, including forage plant species consumed by tiger prey species (Alverson et al., 1988; Linkie et al., 2008; Rayan and Mohamad, 2009; Thapa et al., 2023).

Third, tigers achieve their highest densities in habitats that include a mosaic of forests and grasslands. Grasslands often support locally high densities of prey species, including swamp deer (*Rucervus duvaucelii*) and hog deer (*Hyelaphus porcinus*), and provide cover for tigers to rest or raise cubs (Shrestha, 2004; Sunquist, 2010). Therefore, we estimated the relationship between local tiger density and the distribution and extent of grasslands in our study area. Across India, there is extensive variation in grassland management practices. In PAs, grasslands are managed to benefit tiger or prey populations by seasonal burning and cutting to maximize productivity and promote re-growth, practices that create forage for ungulates (Peet et al., 1999b). In contrast, in MUFs, managers often attempt to convert grasslands habitats into timber-supplying woodlands by actively planting woody plant species. There are also differences between PAs and MUFs in human access of grasslands. Grasslands in core habitats of PAs are generally managed solely for wildlife. In contrast, in MUFs, grasslands are available for livestock grazing and for grass harvesting by local communities.

Lastly, we investigated variation in tiger densities as a function of distance to habitat edges. The designation of core (interior) and buffer (edge areas with high human-use zones) in many PAs is a fundamental strategy for tiger conservation in multiple countries across the species range (Panwar, 1982; Nyhus and Tilson, 2004). Such delineations are intended to minimize human–tiger interactions, and serve as "source sites", for breeding tiger populations (Jhala et al., 2021). More recently however, studies have indicated that wild felids may extensively use and breed in habitats beyond PAs, including areas with extensive edge-habitats, especially when these areas provide predator cover and support ungulate prey (Lewis et al., 2015; Chanchani et al., 2016; Kafley et al., 2016). These findings also raise questions about how tiger populations can be sustained in multi-use forests, beyond existing Tiger Reserves the which requires the creation of strictly inviolate zones as essential for tiger conservation (eg. Jhala et al., 2021) multi – use landscapes. To shed light on these contrasting strategies, we investigated whether tiger densities were lower at habitat edges, and assessed how edge-use was influenced by vegetation cover, prey availability and human-use.

We carried out camera trap surveys to estimate variation in tiger density as a function of prey abundance, habitat type, and human-use in several PAs and MUFs in the Central Terai Landscape (CTL) in North India. We estimated these relationships at two spatial scales. At the broad spatial scale (management unit, for example national park or Reserved Forest), we hypothesized that tiger abundance would be greater in PAs, especially when connected to other PAs in the CTL. At finer spatial scales, defined by a mesh of points, each representing an area of (0.34 km^2), we tested four hypotheses: 1) spatial gradients in prey density would best explain fine-scale spatial variation in tiger density; 2) open-canopy forests would support higher tiger densities than closed-canopy forests; 3) tiger density would decline as distance to large grasslands increased; and 4) tiger density estimates would not differ between PAs and MUFs, and between forest interior and edge areas.

Materials and methods

Study area

The CTL (Figure 1) spans 5400 km^2 abutting the lower Himalayan Ranges in the states of Uttarakhand and Uttar Pradesh in India and southwest Nepal. The CTL is recognized as a globally important eco-region and supports numerous endemic and endangered plant and animal species (Olson and Dinerstein, 1998), including tigers, hog deer (*Axis porcinus*), swamp deer (*Rucervus duvaucelii*), rhinoceros (*Rhinoceros unicornis*), and elephants (*Elephas maximus*). Key vegetation communities are deciduous forests dominated by *Sal* and grasslands characterized by *Saccharum spontaneum*, *Themeda arundinacea, Narenga porphyrocoma, Imperata cylindrica* and associated species (Dinerstein, 1980; Johnsingh et al., 2004). The regions grasslands and associated wetlands, important habitats for large mammals, have been greatly reduced in extent by agricultural expansion from historic to more recent times (Peet et al., 1999a, Peet et al., 1999b; Johnsingh et al., 2004). Today, the CTL is one of the most densely populated regions across the tiger's range with human population density of about 600 persons/km^2 and population growth rates of about 30% (in the 2001–2011 decade). Aside from the region's forests, the only areas that have escaped extensive land use change lie in immediate proximity of the Sharda and Ghaghra Rivers that experience extensive annual floods during the monsoons.

Our study area included three PAs and three MUFs within the CTL (Figure 1; Table 1). The PAs, including Dudhwa National Park and Kishanpur and Katerniaghat Wildlife Sanctuaries, were established between 1972 and 1977 and are collectively known as the Dudhwa Tiger Reserve. Management actions in Tiger Reserves like Dudhwa prioritize the conservation of habitats for tigers and

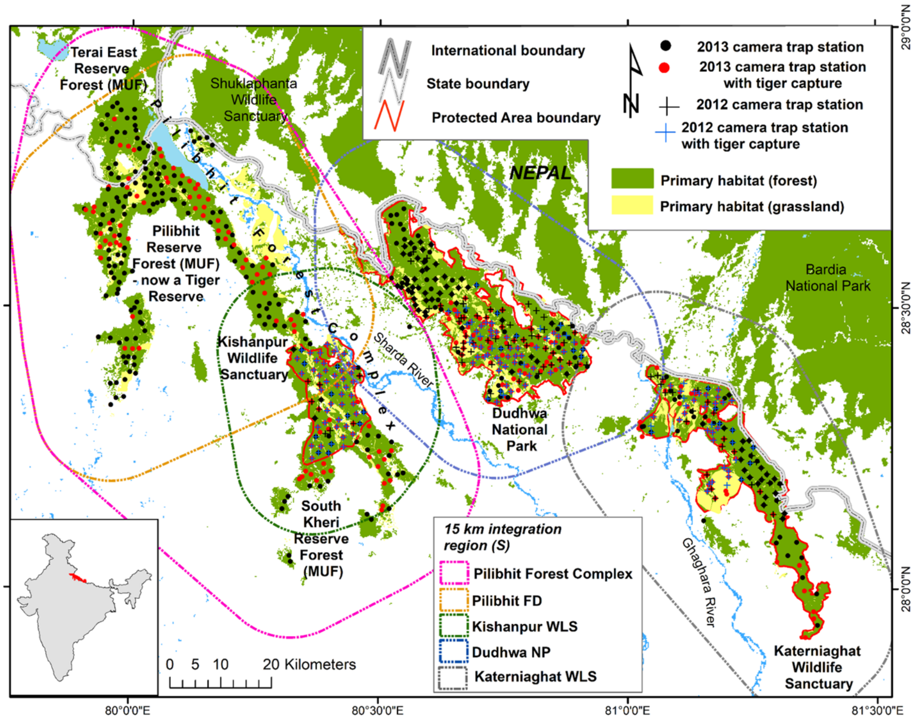

FIGURE 1
Map of the Central Terai Landscape depicting locations of camera traps, with and without tiger captures, in 2012 and 2013. The region of integration associated with each site's density estimate are depicted as polygons. The region of integration was delineated using a grid of evenly spaced points each representing an area of 0.336 km^2. Points that intersected "habitat" were all assigned covariate values, whereas points in non-habitat areas were masked-out from the analysis.

other wildlife. In contrast, MUFs in the CTL were managed for timber production, via selective felling, for approximately 150 years. In addition, these MUFs are extensively used by local communities to extract fuel-wood, fodder and other resources (Strahorn, 2009).

The three MUFs, collectively called the Pilibhit Forest Complex, (PCF; 1400 km^2 in extent) lie within the largest area of contiguous primary forest and grassland habitat in the CTL. The largest MUF within the PFC,was re-designated as Pilibhit Tiger Reserve in 2014, based on the results of our study. Within the CTL, Dudhwa National Park has limited connectivity to other tiger habitats, while the other PAs and MUFs are connected, via conservation corridors, with tiger habitats in Nepal (Figure 1; Chanchani et al., 2016).

Field sampling

We sampled tiger populations using camera traps from November 2011 to June 2012 and November 2012 to June 2013. Each sampled area (PA or MUF) was referred to as a "site" (Table 1, Figure 1). Each site was sampled for ≤ 60 days to meet the assumption of demographic closure required by the closed-population, capture–recapture analyses we conducted (Karanth and Nichols, 2002; Royle et al., 2009; Table 1).

Each sampling station consisted of a pair of cameras (Cuddeback Attack, Cuddeback INC. WI, USA) housed in metal security cases and secured to a post or tree 2–5 m from the edges of trails or unpaved roads, about 50–60 cm above the ground. Camera trap stations within the survey grid were spaced 1–2 km apart. To maximize the probability of capture, camera stations were installed in carefully selected locations, for example, at wildlife trail intersections and along drainages. Camera trap data were downloaded every 5–7 days.

We had too few cameras to survey a site in its entirety using a single survey block (camera traps deployed across a site simultaneously). Therefore, we employed an incomplete trap layout design (Karanth and Nichols, 2002; O'Brien and Kinnaird, 2011), and sampled large study sites using 2–3 survey blocks. Each block of camera trap stations was active for 15–30 days, after which cameras were moved to an adjacent block (Table 1). In Katerniaghat WLS, we sampled approximately 30% more area in 2013, than in 2012. In DNP, a similar area was sampled in 2012 and 2013 (Figure 1).

Identifying individual tigers

Photographs of adult tigers (post-dispersal, ≥ 2 years of age) were visually analyzed by three independent observers to identify unique individuals. In addition, we used pattern recognition software (Extract Compare; Hiby et al., 2009) to corroborate identities of all usable images in the dataset (a library of tiger images is available online; Chanchani et al., 2014a; Appendix S1). Detection history matrices recorded tiger capture histories,

TABLE 1 Details of camera trap sampling for tigers in the Central Terai Landscape (2012 and 2013).

Site	Protection designation	Area (km2)	Sampling period	Trap nights	Trap stations	Sampling blocks	Mean inter-trap spacing (km)	Tiger Density, SE and CI**
2012								
Dudhwa NP	PA	700	Feb–Apr 2012	2626	159	3	1.78	2.05 (0.56); 1.21–3.48
Katerniaghat WLS	PA	443	Apr–Jun2012	2190	82	2	1.37	1.55 (1.26); 0.39–6.24
Kishanpur WLS	PA	206	Dec–Feb 2012	2648	63	1	1.63	5.45 (1.29); 3.45–8.61
2012 subtotals		*1349*		*7464*	*304*	*6*		
2013								
Dudhwa NP	PA	700	Feb–April 2013	4861	202	2	1.42	1.93 (0.92); 0.8–4.7
Katerniaghat WLS	PA	443	Nov–Jan 2013	3663	111	2	1.52	2.87 (0.72); 1.78–4.65
Pilibhit Complex								3.4 (0.51); 2.54–4.56
Kishanpur WLS	PA	206	Apr–Jun 2013	2655	67	1	1.53	4.97 (1.27); 3.04–8.12
Pilibhit FD	MUF*	712	Apr–Jun 2013	2814	171	3	1.96	3.28 (0.71); 2.16–4.98
South Kheri& Surai (PFD)$^{++}$	MUF*	452	Apr & Jun 2013	1201	74	2	2.63	
2013 subtotals		*2513*		*15194*	*625*	*10*	*9.06*	
TOTAL				22658	929	16	9.06	

**Estimates for all sites are model averaged, with the exception of DNP'13 for which the estimates are from a single well supported model D(prey), w=0.85^{++}. We did not separately estimate density for South Kheri and Surai Forest Divisions because of sparse data in these sites. These capture events were however included in the models for PFC. The five sites for which data were analyzed separately are: Dudhwa National Park, Kishanpur wildlife Sanctuary, Katerniaghat Wildlife sanctuary, Pilibhit Forest Division and Pilibhit Forest Complex. Trap nights computed by summing trap functionality of stations (i.e. pairs of camera traps) over the sampling period.

referenced by individuals, trap station (location) and sampling occasion (24-hr period, within the sequence of days over which cameras were active).

Overview of SECR analysis

By estimating the locations of individual activity centers based on animal movement within the trap array, spatially explicit capture recapture (SECR) models provide model-based estimates of density (D) (Borchers and Efford, 2008; Royle et al., 2013; Efford et al., 2015).

In SECR, the probability model for detection histories includes parameters for the distribution of activity centers (both within and beyond the trap area), and for detection probability (assumed to be<1 and decline with increasing distance from an animal's activity center to a trap). We estimated detection probability as a function of two parameters – a spatial scale parameter (σ) and a baseline detection probability (g_0; the probability of detection assuming that a camera trap location is coincident with an individual's activity center) (Efford et al., 2009). Because individuals within a population may have vastly different space use (e.g., males have larger home ranges than females), g_0 and σ may co-vary. In such cases, estimates were obtained by replacing the conventional detection parameterization g_0 and σ by an alternate "compensatory heterogeneity" parameterization $a_{0,}$ σ (Efford and Mowat, 2014). Compensatory heterogeneity implies a negative covariance between $g_0$and σ among individuals of one or both sexes. This occurs when the differences in detection probability of a given animal at specific locations are directly proportional to the amount of time it spends at different locations within its home range (Efford and Mowat, 2014). The distribution of animal activity centers in SECR models can be described as a homogenous or inhomogeneous Poisson point-process. Homogeneity implies that the expected value of density is uniform across the state-space over which activity centers are distributed (a pre-defined part of the model), whereas an inhomogeneous point process implies that density varies across space, as a function of environmental covariates (Efford and Fewster, 2013).

TABLE 2 Candidate covariates available in model-fitting to explain spatial heterogeneity in tiger density.

Covariate	Hypothesized relationship with tiger density	Covariate preparation	Data source
Prey density (Prey)	Strongly positive (Carbone and Gittleman, 2002; Karanth et al., 2004).	Combined estimates of prey density for 7 species derived for each point in the integration region using distance sampling and GAMs (Appendix S1).	Line transect sampling in the CTL conducted concurrently with tiger monitoring.
Percent tree cover (TreeCov)	Negative. Dense dipterocarp forests in the Terai are associated with low tiger and prey densities (Shrestha, 2004; Bhattarai and Kindlmann, 2011) but some studies have argued that densely forested areas provide optimal habitats for tigers (Kanagaraj et al., 2011).	Derived from remotely sensed data (MODIS global imagery, 250 m resolution).	Land Processes Distributed Active Archive Centre, USGS. Accessed on December 12, 2014.
Distance (m) to large grasslands (Grass)	Negative. Grasslands provide cover and are also the preferred habitats of species such as hog deer and swamp deer (Smith et al., 1998).	All grasslands within the CTL were hand digitized from satellite imagery. Grasslands > 1 km^2 in area were retained for analysis.	Google Earth imagery from November 2013 at 1 cm: 0.0076 km resolution.
Distance (km) to primary habitat (forest and grassland edges). (Edge)	Negative. Although ecological literature has argued that edges may be associated with reduced presence/abundance of carnivores because of high human disturbance (Bhattarai and Kindlmann, 2013), Chanchani et al. (2016) found no support for this relationship in their occupancy analyses in the CTL. Edges may be used extensively by tigers because when such areas are associated with riparian/grassland habitats, and because crop-raiding prey may abound along habitat edges.	Hand digitized database of forest and grassland boundaries.	Google Earth imagery from November 2013 at 1 cm: 0.0076 km resolution.

Modeling detection parameters and sex-specific capture heterogeneity

We used SECR models (maximum likelihood parameterization implemented in the R package *secr*, version 2.9.5; Efford, 2015) to test hypotheses about spatial heterogeneity in tiger density (Table 2). We assumed that the distribution of tiger activity centers followed a Poisson point process (Efford and Fewster, 2013). Following Royle et al. (2009), we delineated a grid (580 × 580m) over which individual tiger activity centers could be distributed. This state space included the tigers' primary habitats, forest and grassland areas. Each square gird cell (0.34 km^2) represented a potential activity center. The region *S* (integration region) over which activity centers could be distributed was defined collectively by a habitat mask comprising of the camera trap array, a 15 km buffer around the trapping array that included forests, grasslands and other features identified as "habitat".Tiger density was estimated separately for each site (Table 1) using a two-step procedure in a multi-model hypothesis testing framework (Burnham and Anderson, 2002; Doherty et al., 2010). First, we assessed relative support for models with alternate parameterizations of g_0 and σ, or a_0 and σ with and without sex-specific heterogeneity. Because male home range sizes are generally larger than those of females (Smith, 1993; Sollmann et al., 2011), we allowed detection parameters to vary by sex using a two-class hybrid mixture model (Efford, 2014). The hybrid mixture model includes a mixing proportion parameter '*pmix*', which enables class-specific modeling of detection parameters and sex ratio estimation. Further, we fit three additional models: common detection parameters for all individuals $[g_0(.),\ \sigma(.)]$ and sex-specific heterogeneity with respect to g_0 or σ (models $[g_0(sex),\ \sigma(.)]$ and $[g_0(.),\ \sigma(sex)]$. Finally, we evaluated support for the compensatory heterogeneity parameterization (a_0, σ) by building one additional model $[a_0(.),\ \sigma(sex)]$. For all five alternative detection function parameterizations, we retained a "global" structure for density, allowing it to vary as a function of four covariates: distance to large (>1km^2) grasslands ('*grass*'), percentage of tree canopy cover ('*treecov*'), prey density ('*prey*'), and distance to nearest forest edge ['*edge*'; model: *D*(*grass*+*treecov*+*prey*+*edge*)]. Relative support for models was assessed using Akaike Information Criteria (AICc) adjusted for small sample sizes (Burnham and Anderson, 2002). The best supported model (lowest AICc score) from each model set was selected and carried forward into the second analysis step.

Evaluating hypotheses about spatial variation in tiger density

We retained the best supported covariate structure for the detection parameters, in subsequent models. For each of our data sets (Table 1), we fit 15 models that represented our *a priori* hypotheses about the relative effect of prey density, habitat (vegetation cover) and proximity to edges on fine scale spatial variations in tiger density (Appendix S3: Table S1). We compiled values for five covariates (prey density, distance from grasslands, percent tree cover, distance to forest edges and distance to the international border) for each point (potential tiger activity centers), representing a 580 × 580 m (0.34 km^2) area over the integration region (Table 2).

Hypotheses tested

Hypothesis 1

Spatial variation in prey density is the strongest predictor of heterogeneity in tiger density. We derived spatially explicit prey density estimates from variable-distance line transect data (Buckland et al., 2001). Sparse detections of several ungulate species (e.g., swamp deer) precluded species-specific modeling of parameters. As a result, we combined detection records for seven ungulate species – chital, wild pigs, nilgai, hog deer, swamp deer, barking deer and sambar – and estimated the cumulative detection probability and density for all seven species using program Distance (Buckland et al., 2001) (Appendix S1). Subsequently, we estimated spatial heterogeneity in ungulate density, as a function of environmental covariates, using generalized additive models to generate density surfaces (Miller et al., 2013). These spatially explicit estimates of prey density served as a covariate in the tiger SECR models (Appendix S1).

Hypothesis 2

Areas with dense tree canopy cover (e.g., *Sal* forests) would have lower tiger and prey densities, a result of minimal understory plant productivity. Tree canopy was estimated from a remotely sensed global tree canopy cover database (Table 2).

Hypothesis 3

Tiger densities would decrease as a function of increasing distance from grasslands. Distance to large grasslands was estimated by digitizing all tall and short grasslands >1km^2 from remotely-sensed imagery.

Hypothesis 4

Tiger density will be lower along the international border with Nepal, a region with very high human-use and high poaching pressure (Wikramanayake et al., 2010; Chanchani et al., 2014b). To test this hypothesis, we estimated two covariates – distance from each potential tiger activity center to the nearest habitat edge (PA or MUF boundary), and distance to India's international border with Nepal (Table 2).

We established camera trap grids over larger areas of PAs and MUFs in the CTL than in previous surveys conducted under the India Government's official tiger monitoring program (Jhala et al., 2011). To ensure that our estimates were comparable to those from previous surveys, and to disentangle sampling effects on estimates of density from previous studies, we sub-sampled data from 2013 to replicate survey effort (coverage) from previous camera-trap surveys (Harihar et al., 2017). This adjustment also allowed us to assess whether density estimates from small trapping grids can be extrapolated to predict density across large contiguous habitat tracts (Appendix S4).

Prior to implementing the SECR analysis, we tested for correlations among the five covariates. The distance to international border covariate was subsequently excluded from analysis because it was strongly correlated with prey density (R=0.78). Pair-wise correlations were < 0.5 for all other covariates. We assessed relative support for models using AIC based on model weights (*w*), adjusted for small sample sizes.

Estimating tiger abundance

We estimated tiger abundance (*N)* as the number of activity centers within the boundaries of PAs and MUFs (Efford and Fewster, 2013). In addition to density estimates, we *N* within the specific boundaries of an administrative region, such as an individual PA (Efford and Fewster, 2013). The boundaries of these regions were a subset of the integration region (*S*) for each site (Figure 1). We compiled and compared model-averaged estimates of *N* for all 15 models, and for all eight model sets (Figure 2; Appendix S3: Supplementary Table S1).

Results

We sampled tiger habitats using 929 camera trap stations (304 locations in 2012 and 625 locations in 2013). Camera traps were cumulatively active for a period of 22,658 trap nights. The mean inter-trap distance was 1,36 m (Table 1). Over the study duration, cameras recorded1352 independent captures of 92 distinct adult tigers (45 males, 44 females) and two individuals of indeterminate sex (Table 3). Across the two years, the average number of recaptures/individual was 12.49 for adult male tigers (SD=15.70) and 9.33 for female tigers (SD=8.94; Table 3).

Heterogeneity in detection parameters

Model selection results from the first analysis step varied between sites and across years (Appendix S2: Supplementary Table S1). Sex-specific heterogeneity in the spatial scale parameter $\sigma(sex)$ was supported in six of the eight model sets. In two of the six model sets, inclusion of the "compensatory heterogeneity" detection parameter [$a_0(.)$, $\sigma(sex)$] had greater support than the conventional baseline encounter parameter [$g_0(.)$, $\sigma(sex)$]. In addition, there was evidence of sex-specific heterogeneity for both g_0 and $\sigma[g_0(sex)$, $\sigma(sex)]$ in only one of the eight model sets. Lastly, the constant model [$g_0(.)$, $\sigma(.)$] was well supported (> 50% AIC weight) in only one of the eight model sets (Appendix S2: Supplementary Tables S1–S3).

Site-level estimates of tiger density and detection parameters

Overall, tiger densities were higher in sites with higher prey densities, independent of management designation and degree of human disturbance. Site- and year-specific estimates of tiger density (individuals/100 km^2) were highest for Kishanpur Wildlife

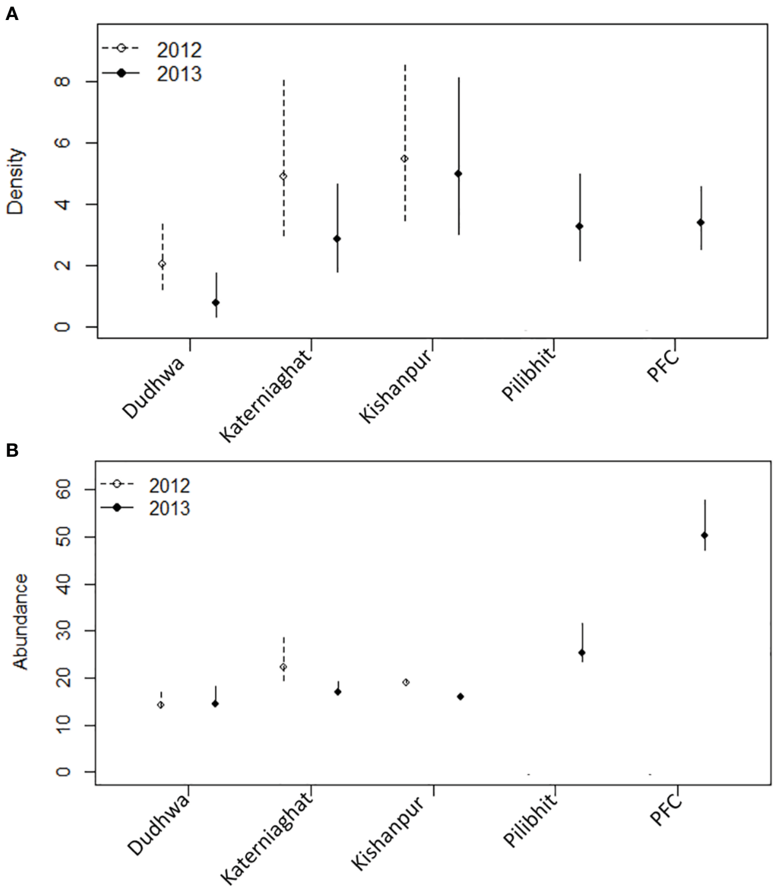

FIGURE 2
(A) Estimates of tiger density (individuals/100 km^2), **(B)** abundance, and associated 95% confidence intervals for the CTL (note scale differences on the y-axes). Separate estimates are provided for the five sites sampled in 2013 and three sites in 2012. All estimates are from the best supported model for each site/year. The D(.) model was the best supported model, with the exception of Katerniaghat in 2012 D(Grass) and DNP in 2013 D (Prey), for which estimates are for the median covariate value. PFC is the Pilibhit Forest Complex which included Pilibhit Forest Division, Kishanpur Wildlife Sanctuary and South Kheri Forest Division.

Sanctuary KWLS $\hat{D}_{2012}$ = 5.45 (SE=1.29), KWLS $\hat{D}_{2013}$ = 4.97 (SE=1.27). Tiger density was the lowest for Dudhwa National Park, [DNP $\hat{D}_{2012}$ = 2.05 (SE = 0.56) $\hat{D}_{2013}$ = 1.88 (SE = 0.52)]. The other PAs and MUFs had intermediate tiger densities: Katerniaghat Wildlife Sanctuary [KGWLS $\hat{D}_{2012}$ = 4.76 (SE=1.14), KGWLS $\hat{D}_{2013}$ = 2.78 (SE=0.72)]; Pilibhit Reserved Forest [PRF $\hat{D}_{2013}$ = 3.028 (SE=0.71)]; and Pilibhit Forest Complex [PFC $\hat{D}_{2013}$ = 3.4 (SE=0.51)] (Figure 2; Appendix S3: Table S1). In the three sites surveyed in 2012 and 2013, estimates were marginally higher in 2012 than in 2013, but less precise (Figure 3; Appendix S3: Table S1). Corresponding estimates of prey density (combined for all ungulates) were 29.81 (SE=5.69) animals/km^2 in KWLS, 13.64 (5.28) in DNP, 4.4 (1.55) and 22.4 (8.10) in KGWLS (in forests and grasslands respectively) and 40.05 (SE=0.23) in PFD (Bista, 2011; Chanchani et al., 2014a).

Model-averaged estimates of σ were approximately two times higher for male (range: 2.08–6.931 km) than for female tigers (range: 1847–2962 m; n= 6 site/year combinations; Appendix S3: Table S4). Estimates of σ were largest for both males and females in Katerniaghat Wildlife Sanctuary, a site with even sex ratios and lower tiger density. In contrast, the lowest estimates of σ were recorded in Pilibhit Forest Division and Kishanpur Wildlife Sanctuary, where sex ratios were female-biased, and tigers occurred at relatively higher densities. Both σ and g_0/a_0 estimates and their CIs were similar across all 15 models assessed in the eight model sets (Appendix S3: Supplementary Table S4). Estimates of σ were consistently higher in 2013, than in 2012, especially in Dudhwa National Park and Katerniaghat Wildlife Sanctuary where survey effort was greater in 2013 (Table 1).

Fine-scale variation in tiger density

Similar to broad-scale patterns in tiger density, variation in prey abundance explained the greatest amount of the fine-scale variation in tiger density (Table 4). Hypothesis 1, was strongly supported in Dudhwa National Park (2013), where the model (*D*(*Prey*)) had 85% overall support (Appendix S3: Supplementary Table S1). In Dudhwa, there was a steep gradient in prey density: high in the south and low in the north (Figure 3; Appendix S6). In four of the seven additional model sets, [*D*(*Prey*)] contained >10% of the model support. The distance to grassland (hypothesis 2) model [*D*(*Grass*)]

TABLE 3 Summary of photo captures of tigers from camera trap sampling in the CTL (2012 and 2013).

Site* and year	M_{t+1}	Individuals with recaptures	Count of tiger captures	Female			Male			Sex unknown		
				Count	Sum	Recaptures (average)	Count	Sum	Recaptures (average)	Count	Sum	Recaptures (average)
Dudhwa NP 2012	14	12	131	5	42	8.4	9	84	9.33			
Katerniaghat WLS 2012	18	15	88	7	35	5	11	53	4.82			
Kishanpur WLS' 12	19	16	264	11	119	10.8	8	143	17.17			
Dudhwa NP 2013	14	13	274	7	92	13.1	7	182	26			
Katerniaghat 2013	17	16	265	10	106	10.6	7	101	14.43			
Kishanpur 2013	16	15	256	9	151	16.8	7	145	18.13			
Pilibhit Reserved Forest '13	23	17	94	11	43	3.91	10	49	4.9	2	2	1
Pilibhit Forest Complex '13	45	38	393	25	213	8.52	18	175	9.72	2	5	2.5

had support (w=0.48) only in the model sets pertaining to Katerniaghat Wildlife Sanctuary (2012). In Katerniaghat WLS, grassland habitats occur only in its eastern and southern reaches, with the remaining areas dominated by dense, even-age deciduous forests. In other sites where grasslands were distributed more uniformly, the distance to grassland covariate received less support.

Hypothesis 2 – vegetation, and hypothesis 3 – edges (*TreeCov* and *Edge*) had less support than models with no covariates [null model, $D(.)$] in seven of eight model sets. Overall, in six of the eight model sets, the null model had the most support. AICc weight for the [$D(.)$] model varied between 0.8 in Kishanpur Wildlife Sanctuary (2013) and 0.23 in Pilibhit Complex (2013) (Appendix S3: Supplementary Table S1). In several sites, models with one or more covariates had similar support to the null model. Because the addition of one or more covariates did not result in improved model fit, these models were considered uninformative (Arnold, 2010).

Estimates of tiger abundance

The largest tiger population in the CTL was recorded in the PFC ($\hat{N}_{2013}$ = 50.54, SE=2.63), which at the time of our study was composed on >80% MUF (Figure 1). Within the PFC, the largest tiger population was recorded in Pilibhit Forest Division, a MUF ($\hat{N}_{2013}$ = 25.22; SE= 1.71). The 200 km^2 Kishanpur Wildlife Sanctuary – which is the sole PA within PFC,supported a large tiger population ($\hat{N}_{2012}$ = 19.21; SE=1.54) and ($\hat{N}_{2013}$ = 16.0; SE = 0.02).

Dudhwa National Park supported a relatively small population of tigers ($\hat{N}_{2012}$ = 14.25, SE = 0.51; $\hat{N}_{2013}$ = 14.16, SE = 0.41). Dudhwa is similar in size to Pilibhit Forest Division, but only connected to other tiger habitats in India through corridors spanning agricultural land. Large areas of Dudhwa National Park support low prey densities (Figure 5; Appendix S6). In Katerniaghat Wildlife Sanctuary, the estimated number of tigers was $\hat{N}_{2012}$ = 19.21 (SE = 1.54) and $\hat{N}_{2013}$ = 17.11 (SE =0.33) in 2012 and 2013, respectively. Katerniaghat is 40% smaller than Dudhwa National Park and the two PAs have similar prey densities.

Estimated sex ratios for adult tigers were female-biased in Kishanpur WLS, but male-biased or equal in Dudhwa NP and Katerniaghat WLS (Table 3). Significantly, sex ratios varied over the two years of study. Even though density estimates were similar across years, at several sites (e.g. Katerniaghat WLS, Dudhwa NP), there was a high turnover (~30%) of adult tigers between successive surveys (for age and sex-specific details of tiger captures, see Appendix S5: Figure S1). The point estimates for the 15 models within each of the eight model sets (site × year) were consistent, with similar precision (Figure 2; Appendix S3: Table S1).

Discussion

Tiger densities varied considerably across sites, both within PAs and MUFs. In our study area, the only management unit that supported a population with > 25 adult females was the Pilibhit Forest Complex. This result was surprising given that ~ 85% of this areas was managed as MUF with selective logging operations and

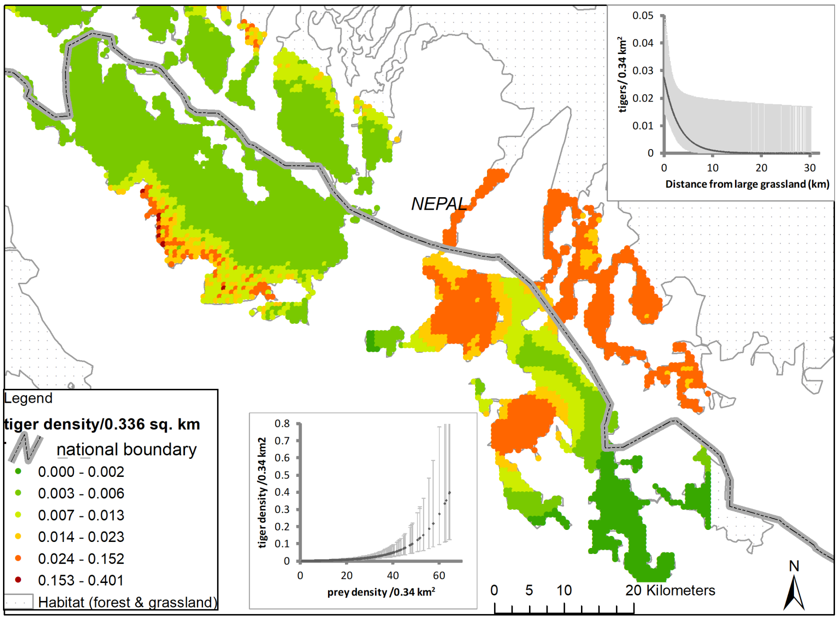

FIGURE 3
Density surface output for Dudhwa National Park and Katerniaghat Wildlife Sanctuaries. Inhomogeneous point process models D ~ (prey) in DNP 2013 and D ~ (distance to grasslands) in Katerniaghat 2012. Each point on the map represents a habitat area of 0.34 km2 within the integration regions of Dudhwa and Katerniaghat, respectively. Cool shades (blues and greens represent areas with higher tiger densities, warm shades (yellows and reds) represent areas of low density. Covariate relationships with tiger density for the two sites, and associated 95% confidence intervals have also been plotted.

TABLE 4 Relative support for the 15 alternate models that were run for each site. AICc weights are reported, and darker shades represent greater support.

No.	Model	N par	DNP 2012	DNP 2013	KGWLS2012	KGWLS 2013	KWLS2012	KWLS 2013	PILI 2013	PFC 2013
1	D (Grass)	6	0.05	0	0.48	0.08	0.05	0.06	0.06	0.13
2	D (TreeCov)	6	0.25	0.03	0.02	0.1	0.36	0.07	0.08	0.06
3	D (TreeCov + Grass)	7	0.01	0	0.17	0.01	0.03	0	0.02	0.03
4	D (Prey)	6	0.25	0.85	0.02	0.11	0.05	0.05	0.27	0.11
5	D (Prey + Grass)	7	0	0.03	0.09	0.01	0	0	0.04	0.06
6	D (Prey + TreeCov)	7	0.01	0.07	0	0.01	0.04	0	0.06	0.03
7	D (Prey+ TreeCov + Grass)	8	0	0	0.01	0	0	0	0.01	0.01
8	D (Edge)	6	0.02	0	0.02	0.15	0.05	0.06	0.06	0.12
9	D (Grass + Edge)	7	0	0	0.05	0.02	0	0	0.01	0.1
10	D (Edge + TreeCov)	7	0.01	0	0	0.01	0.03	0	0.01	0.03
11	D (Edge +* Grass)	8	0	0	0	0	0	0	0	0.02
12	D (Edge + TreeCov + Grass)	8	0	0	0.01	0	0	0	0	0.02
13	D (Edge1 + Prey	7	0	0.02	0	0.01	0	0	0.03	0.04
14	D (Global)	9	0	0	0	0	0	0	0	0
15	D (.)	5	0.4	0	0.13	0.49	0.38	0.76	0.35	0.23

high levels of day-time human-use. In contrast, the region's two largest PAs, with an emphasis on wildlife management for several decades, supported fewer tigers at lower densities.

It is increasingly being recognized that large carnivores may extensively use areas beyond PA boundaries, including edge habitats and agricultural lands even if they face elevated mortality risks in such areas (e.g. leopards in South Africa, Balme et al., 2010). In India, several MUFs and PAs outside of the CTL, and with high human-use, support tiger populations with densities similar to nearby PAs (e.g., Ramnagar, 24-Parghanas (Sunderbans), Wayanad and Sathyamangalam (based on estimates from Qureshi et al., 2023). Globally, several other large carnivore species also co-occur with humans beyond PA boundaries. These include black bears (Evans et al., 2017), jaguars (Boron et al., 2016), snow leopards (Sharma et al., 2015), grizzly bears and wolves (Chapron et al., 2014), lions (Banerjee et al., 2013; Venkataraman, et al., 2020), Eurasian lynx (Basille et al., 2009) and leopards (Athreya et al., 2013; Kshettry et al., 2020) (Figure 4).

In our study, the presence of the largest tiger population in our study area in an MUF rather than in a PA is explained, at least in part, by the distribution and abundance of wild herbivores (tiger prey species) in the landscape. Previous research estimated the density of ungulate prey to be almost four-fold higher in Pilibhit (40.5 animals/km^2), than in Dudhwa (13.6), whereas Kishanpur (29.81) and Katerniaghat (forests 4.41, grasslands 22.40) had intermediate prey densities (Chanchani et al., 2014a; Figure 5). The relationship between prey and tiger densities is well established and prey recovery programs are central to tiger conservation efforts across the species range (Karanth et al., 2004; Harihar et al., 2014). We note that at the fine spatial scale (580 m × 580 m secr mesh), the prey covariate was only supported in Dudhwa, where spatial heterogeneity in tiger densities strongly mirrored steep gradients in wild ungulate densities (Appendix S6). In contrast, prey and tiger densities were not as strongly spatially structured in other areas like Pilibhit Forest Division. Further, the absence of a consistent relationship between these variables across years is possibly a consequence of variation in survey effort between 2012 and 2013 in some sites (Appendix S4).

Similarly, proximity to grasslands did not consistently explain spatial variation in tiger densities. While terai grasslands have been associated with high herbivore densities (e.g. Wegge and Storaas, 2009), large tracts of tall grasslands in the study areas only supported low densities of wild herbivores, and were consequently associated with lower tiger densities than expected. The exceptions were grasslands where both short and tall grasses were found, including some areas with extensive livestock grazing.

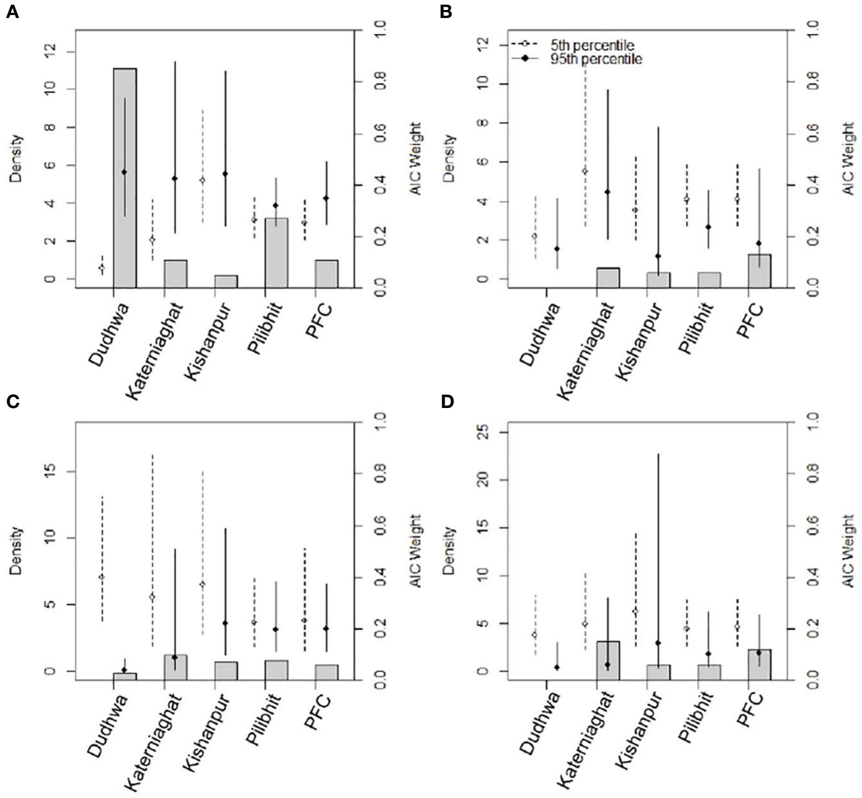

FIGURE 4
Estimates of tiger density and AIC support for five sites in the CTL (2013 data) from models representing our four key hypotheses **(A)** prey density; **(B)** distance to large grasslands; **(C)** percent tree cover and; **(D)** distance to habitat edges. Hollow circles and dotted error bars represent tiger densities and 95% confidence intervals associated with minimum covariate values (5th percentile), whereas solid circles and error bars are estimate of density and associated 95% confidence intervals near the upper boundary of covariate values (95th percentile). Gray bars (secondary y-axis) depict AIC weights associated with the models.

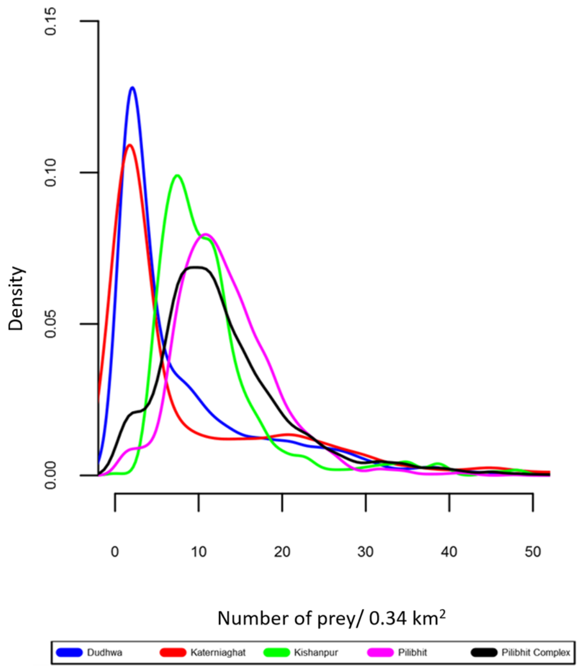

FIGURE 5
Density plot for distribution of prey density in the CTL's five study sites. This depicts the distribution of prey densities. The peaks indicate the most common density value within a site, and the horizontal spread of the plots indicates the degree of spatial heterogeneity in estimated prey densities (wider plots indicate greater heterogeneity).

A likely explanation for low herbivore densities in tall grasslands is that palatable grasses for wild ungulates sharply declines within about three months of prescribed winter burning both in PAs and MUFs (Rastogi et al., 2022).

We did not find a statistically significant relationship between tiger densities and proximity to edges, with tiger density hotspots both occurring forest edges and within the forest-interior (Appendix S6). Edge-habitats, proximate to the agricultural matrix and human settlements, with extensive tiger use were also associated with high densities of wild prey, and usually had tracts of grasslands or forests with dense understory which tigers exploited as cover. Use of forest edge habitats may also be because tigers in this landscape extensively use the surrounding agricultural matrix (Warrier et al., 2020).

Effecting tiger recovery and enabling human tiger coexistence in multi-use landscapes

While large carnivores have persisted in some multi-use landscapes, previous research from the terai and elsewhere indicates tiger occupancy and density can be severely depressed in areas with extensive human use (MadhuSudan, 2004; Harihar et al., 2009). Our research raises important questions about factors and "mechanisms of coexistence" that may be critical in determining whether or not, and in what densities tigers occur in human dominated landscapes. We posit two working hypotheses in the context of our study.

First, vegetation attributes that affect the distribution and density of wild herbivores may be an indirect but primary determinant of carnivore density variation, relative to the influence of human presence. In our study area, large parts of the core zone of Dudhwa National Park, with very limited human presence supported markedly lower tiger densities than areas with much higher human "disturbance" – i.e. the PA's edges or Pilibhit Forest Division in which wild herbivore densities were several orders of magnitude higher (Appendices S1, S6). The most likely explanation for this variation in prey densities is understory composition and palatability, as Dudhwa's sal (*Shorea robusta*) dominated interior and shrubby understory supports lower ungulate densities relative to PA and understory of the Pilibhit Forest Complex.

Second, tiger densities in areas with high human use, may also critically depend on presence, extent and distribution of refuge habitats (Valeix et al., 2012; Chanchani et al., 2016; Grilo et al., 2019; Oeser et al., 2022). These are habitat tracts that are secluded, relative to surrounding areas which have higher human presence, where tigers can shelter away from people, hide and feed on kills, raise cubs, and survive, even if people are in close proximity, allowing tigers to behaviorally trade-off risk and resources, including through temporal adjustments of activity (Carter et al., 2012; Oriol-Cotterill et al., 2015). In multi-use landscapes, habitat refuges may exist in the form of tracts of marshy grasslands, steep and densely vegetated terrain, dense and thorny understorey, or even sugarcane thickets. Given adequate numbers of prey, the extent and distribution of such habitat refuges in an area may well be a critical factor that sets a ceiling on how many tigers the area can support.

Breeding tiger populations are unlikely to persist in areas where human presence is so pervasive that even such refuges are routinely intruded or degraded by excessive resource use or extraction. Likewise, tiger populations are unlikely to survive in areas where protection is deficient, and there are is high hunting pressures on tigers or their prey species (Dinerstein et al., 2007). In such contexts, it will be important to tease apart potential effects of hunting from other anthropogenic pressures (eg. livestock grazing, non-timber forest produce harvesting, and silviculture operations).

In summary, we argue that multi use landscapes that support tigers, or are envisioned as tiger-recovery areas represent "zones of coexistence". Empirically identifying refuge habitats in such zones will be a critical strategy to effect recovery and enable tiger-persistence, provided such efforts are supported by local forest users. De facto refuge habitats within multi-use landscapes can help increase tiger survival rates (Carroll and Miquelle, 2006). Decision making regarding their identification and management should include local village institutions (e.g. Velázquez et al., 2009), and be informed by the resource access and land tenure rights of communities, levels of conflict, and levels of local acceptance of dangerous wildlife, like tigers and support for their conservation. Ultimately such areas may only support stable or growing tiger populations if comprehensive conflict management systems are in place, and if the tangible and hidden costs of conflict are adequately redressed (Karanth and Gopal, 2005; Goodrich, 2010).

Supporting information

Supporting information includes the following: Appendix S1 – Preparation of prey density covariate; Appendix S2 – Result summary from global models to ascertain supported detection covariates; Appendix S3 – Site and year specific estimates of density, abundance and detection parameters; Appendix S4 – Effect of reducing trap area on estimates of density and detection parameters (subset analysis); Appendix S5 – Details of tiger capture dynamics and inter-annual turn-over in sampled populations; Appendix S6 – Approximate home ranges of tigers photo captured on camera traps during the 2 years sampling period relative to the density of ungulate prey species.

Data availability statement

The datasets presented in this article are not readily available because Tigers are an imperilled species and large spatial datasets can be shared with due approval from concerned authorities. Requests to access the datasets should be directed to pranav.chanchani@gmail.com.

Ethics statement

Ethical review and approval was not required for the study on animals in accordance with the local legislation and institutional requirements. Non invasive sampling methods were deployed. Animals did not need to be captured or handled

Author contributions

PC: Designed study, conducted fieldwork, analyzed data, wrote and edited manuscript BN: Provided supervision for study design & analysis, edited manuscript AB & RW: conducted fieldwork, curated data, supported data analysis and edited manuscript SN & RS: conducted fieldwork, curated data and reviewed manuscript MG: facilitated fieldwork and edited and reviewed manuscript BG: supported data analysis and edited manuscript. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The 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/fevo.2024.1209309/full#supplementary-material

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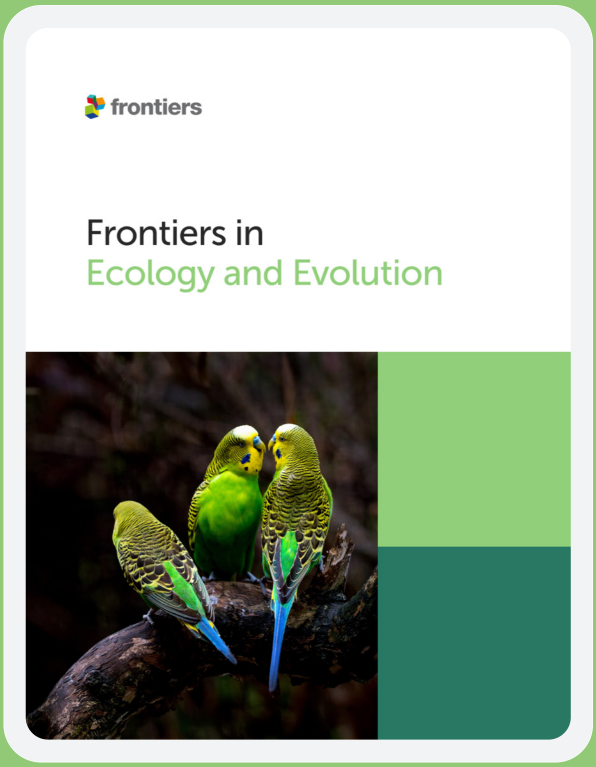

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