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CONSERVATION

Tiger recovery amid people and poverty

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Recovery of large yet ecologically important carnivores poses a formidable global challenge. Tiger (*Panthera tigris*) recovery in India, the world's most populated region, offers a distinct opportunity to evaluate the socio-ecological drivers of megafauna recovery. Tiger occupancy increased by 30% (at 2929 square kilometers per year) over the past two decades, leading to the largest global population occupying ~138,200 square kilometers. Tigers persistently occupied human-free, prey-rich protected areas (35,255 square kilometers) but also colonized proximal connected habitats that were shared with ~60 million people. Tiger absence and extinction were characterized by armed conflict, poverty, and extensive land-use changes. Sparing land for tigers enabled land sharing, provided that socioeconomic prosperity and political stability prevailed. India's tiger recovery offers cautious optimism for megafauna recovery, particularly in the Global South.

The Anthropocene is characterized as an epoch of species extinction and species attrition in numbers and range (*1*). Large carnivore populations across the world are most affected, with their recovery posing a formidable challenge to the modern world (*2*). Habitat loss, prey depletion, conflict with humans, and illegal demand for their body parts, combined with low densities and large space requirements for viable population, have driven large carnivores to numbers at which many have lost their functional role and some are on the brink of extinction (*3*, *4*). Losses of large carnivore populations downgrade trophic cascades, affecting ecosystem functioning, disease regulation, and socio-ecological resilience across ecosystems (*5*). Often, conservationists capitalize on the functions and charisma of these large carnivores to garner resources for restoring their populations, which entails restoring their ecosystems, and for allied services (*6*, *7*). Nonetheless, recovery of apex predators remains an exception rather than a rule, with success stories skewed to developed parts of the world (*8*, *9*) and few examples from developing countries (*10*, *11*). Recovery of large carnivores in fragmented habitats amid crowded and poverty-ridden regions of the Global South is a difficult proposition, often enforced through a dogmatic vision of separating people from predators: land sparing (*12*). The alternative—land sharing, between the people and predators (*13*)—is critiqued as unattainable, on the grounds that overlap can only exacerbate conflict (*14*). Land sparing and land sharing are looked on as opposing views; advocates of each point to the other's limitations (*8*). In this work, we demonstrated that both views of land sparing and land sharing were required for recovering tiger populations across India, suggesting that both paradigms play a part in the future of large carnivores.

The tiger acts as a charismatic flagship and an umbrella species for Asian forests but has been extirpated from more than 90% of its historic range over the past century, leaving only about 3600 wild tigers at the onset of this century (*15*). For the first time in modern history, tiger range country leaders and conservation practitioners met at St. Petersburg, Russia, in 2010 to forge the Global Tiger Recovery Program and targeted doubling the tiger population by 2022 (*16*). India achieved this target and now holds ~75% of the global population of tigers amid some of the highest human densities in the world (*16*, *17*). Key to this success are the linked scientific policies backed by governments' commitments and people's participation (*16*). However, it is crucial to evaluate socio-ecological factors that on the ground are related to persistence, recovery, and localized extinction of tigers. This evaluation becomes pertinent considering investments made for land sparing (creation of human-free protected areas through incentivized voluntary relocation of people) and land sharing (streamlining socioeconomic benefits) for tigers in this region with high poverty and the highest human densities (*18*, *19*). Although the success of tiger recovery is symbolized by its population doubling, it is critical to examine whether the population growth resonates with the intended flagship role of the tiger in conserving and increasing biodiverse areas. Hence, we explored the dynamics of tiger occupancy in India to evaluate its recovery from 2006 to 2018; evaluated the socio-ecological characteristics of local extinctions, colonization, and persistence of tigers in India; and examined the spatial association in tiger occurrence with other megafauna species.

India has monitored the distribution and abundance of tigers every 4 years since 2006 by surveying all potential tiger habitats (~381,000 km^2) for occurrence of tigers, their co-predators, prey, and habitat quality (*16*). Tiger habitat spanning 20 Indian states was delineated into ecologically meaningful sized grids of 10 by 10 km that have been fixed for sampling since 2006. Each grid cell was surveyed with multiple spatially independent search paths [mean 10 (SE 2), maximum 21] to estimate tiger occupancy and by line transects [mean 4 (SE 1), maximum 14] to estimate prey abundance. This was a large wildlife survey (*20*), conducted by ~44,000 personnel and repeated in 2006, 2010, 2014, and 2018. It covered ~2.5 million km and provided essential data for evaluating the socio-ecological facets of tiger recovery (*21*). We hypothesized that tigers would persist in protected habitats with ample prey, while becoming extinct in areas of increased human and social disturbances, and would colonize socioeconomically moderate multiuse habitats with less intensive human land use and ample prey and in proximity to source populations. We tested these hypotheses using multiseason (quadrennial) occupancy models (MSOM) of tigers for every 100-km^2 cell to account for imperfect detections and to identify socio-ecological correlates. Covariates representing socio-ecological factors that were used for

Table 1. Recovery of tiger-occupied areas in India. Habitat area where tigers were detected (naïve occupancy), areas after correcting for imperfect detections (null model occupancy), and detection corrected occupancy were modeled by using site covariates (best model occupancy). Values in parentheses are 95% confidence intervals.

Year	Naïve occupancy (km^2)	Null model occupancy (km^2)	Best model occupancy (km^2)
2006	66,389	114,562 (109,998 to 119,125)	106,332 (101,777 to 110,886)
2010	64,653	113,103 (107,734 to 118,474)	107,033 (100,938 to 113,128)
2014	77,083	113,673 (108,629 to 118,724)	117,447 (111,236 to 123,659)
2018	91,516	141,539 (136,813 to 146,308)	138,247 (131,953 to 144,541)

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modeling occupancy, extinction, and colonization (*22*) by tigers included prey abundance (encounter rate of wild herbivores), habitat attributes (suitable habitat and land-use proportion), human impacts (forest loss, night-time lights, livestock abundance, and intensity of extractive human use), socioeconomic variables (poverty and armed conflicts), and protection status (protected areas and habitats in their proximity) (table S1). To better understand the relationship of prevailing ecological, sociological, legal, economic, and political conditions that explained dynamic tiger occupancy, we evaluated the MSOM variables using exploratory analysis and nonparametric statistical comparisons.

After correcting for imperfect detections and accounting for the socio-ecological variables, the best among competing models (table S2) estimated tiger occupancy to be increasing at 2929 (±737) km^2 per year [$P < 0.05$, coefficient of determination (R^2) = 0.83] (tables S3 and S4 and fig. S1). The modeled multiseason estimates displayed a consistent improvement

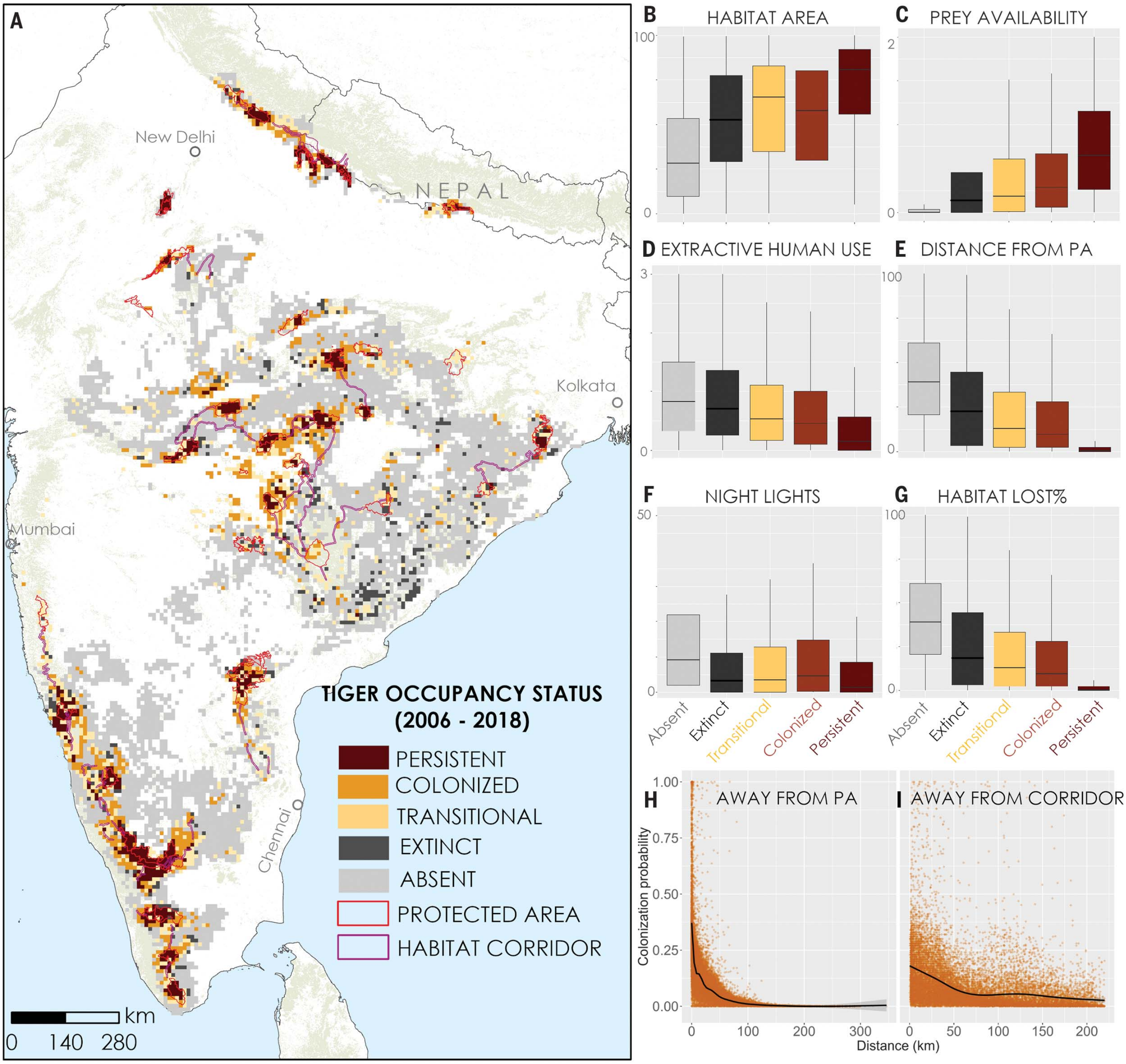

Fig. 1. Spatiotemporal trends in tiger occupancy within India and its socio-ecological covariates. (**A**) Tiger occupancy status from 2006 to 2018. (**B** to **I**) Persistent occupancy was observed within grid cells with (B) large proportion of habitat (square kilometers) and (C) higher prey availability (animals sighted/km). [(B), (C), and (E)] Colonization increased within prey-rich habitats in proximity to tiger-occupied protected areas (kilometers), and (D) tigers were absent or became extinct in areas with greater extractive human use (extraction signs per square kilometer), (F) high urbanization (night-time light radiance index), and (G) proportion of habitat loss (square kilometers). Colonization probability decreased away from (H) protected areas and (I) habitat corridors, highlighting the importance of protected areas and habitat corridors in tiger colonization. Statistical comparisons for (B) to (G) are given in table S5.

over the naïve occupancy estimates (Table 1) and were statistically similar to independently modeled single-season occupancy estimates (fig. S2), strengthening the reliability of the complex multiseason occupancy models. Tigers consistently occupied 35,255-km^2 areas that were protected or were in proximity to protected areas and had high prey abundance in extensive habitats (Fig. 1 and table S4). Of the total colonized area of 41,767 km^2 in 12 years, tigers colonized 35% of new areas between 2006 and 2010, 20% between 2010 and 2014, and 45% between 2014 and 2018 (fig. S3). Overall, tiger occupancy increased by 30% over the span of the study. Colonization was higher in grid cells that were in proximity to tiger-occupied protected areas, with higher prey abundance, suitable habitats, low human density, and moderately wealthy areas (Figs. 1 and 2 and table S4). Colonization coincided spatially with proximity to protected areas [β coefficient (y) = $0.6075 \times 10^{-0.01}$, $R^2 = 0.58$, $P < 0.1$] (Fig. 1H) and habitat corridors [$y = -0.114\ln(x) + 1.8231$, $R^2 = 0.20$, $P < 0.1$] (Fig. 1I), highlighting their functionality and importance in tiger recovery. Local extinctions (17,992 km^2), spanning over 12 years, were highest (64%) between 2006 and 2010, followed by 17% between 2010 and 2014 and 19% between 2014 and 2018 (fig. S3). Grid cells that experienced tiger extinctions were characterized by isolation from protected areas, increased urbanization and infrastructure development, higher extractive human use, and a higher frequency of armed conflicts (Figs. 1 and 2 and table S4). Areas where tigers became temporarily extinct but subsequently recolonized (transitional) were proximal to either protected areas or habitat corridors. Creation of protected areas and habitat corridors connecting source populations has helped dispersal of the increasing tiger population (*17*), forming metapopulations (*23*) and increasing landscape-level tiger occupancy over the years.

Out of the 1973 grid cells occupied (persistent + colonized + transitional) by tigers, 25% were in the core area of tiger reserves or within national parks [International Union for Conservation of Nature (IUCN) protected area category II], 20% were in tiger reserve buffers or wildlife sanctuaries (IUCN category III), 10% were in tiger habitat corridors, and the remaining 45% were in human multiple-use habitats. However, out of the total consistently tiger-occupied grid cells ($n = 479$), 85% were within tiger reserves, national parks, and wildlife sanctuaries (IUCN categories II and III), 4% were in tiger habitat corridors, and the remaining 11% were in multiple-use mosaics of habitats and agricultural fields outside protected areas. These consistently occupied grid cells housed source populations of tigers, and model sensitivity analyses showed that extinctions in these areas would affect landscape-scale occupancy of tigers (fig. S4). Sensitivity analyses further highlighted the relevance of proximity to protected areas

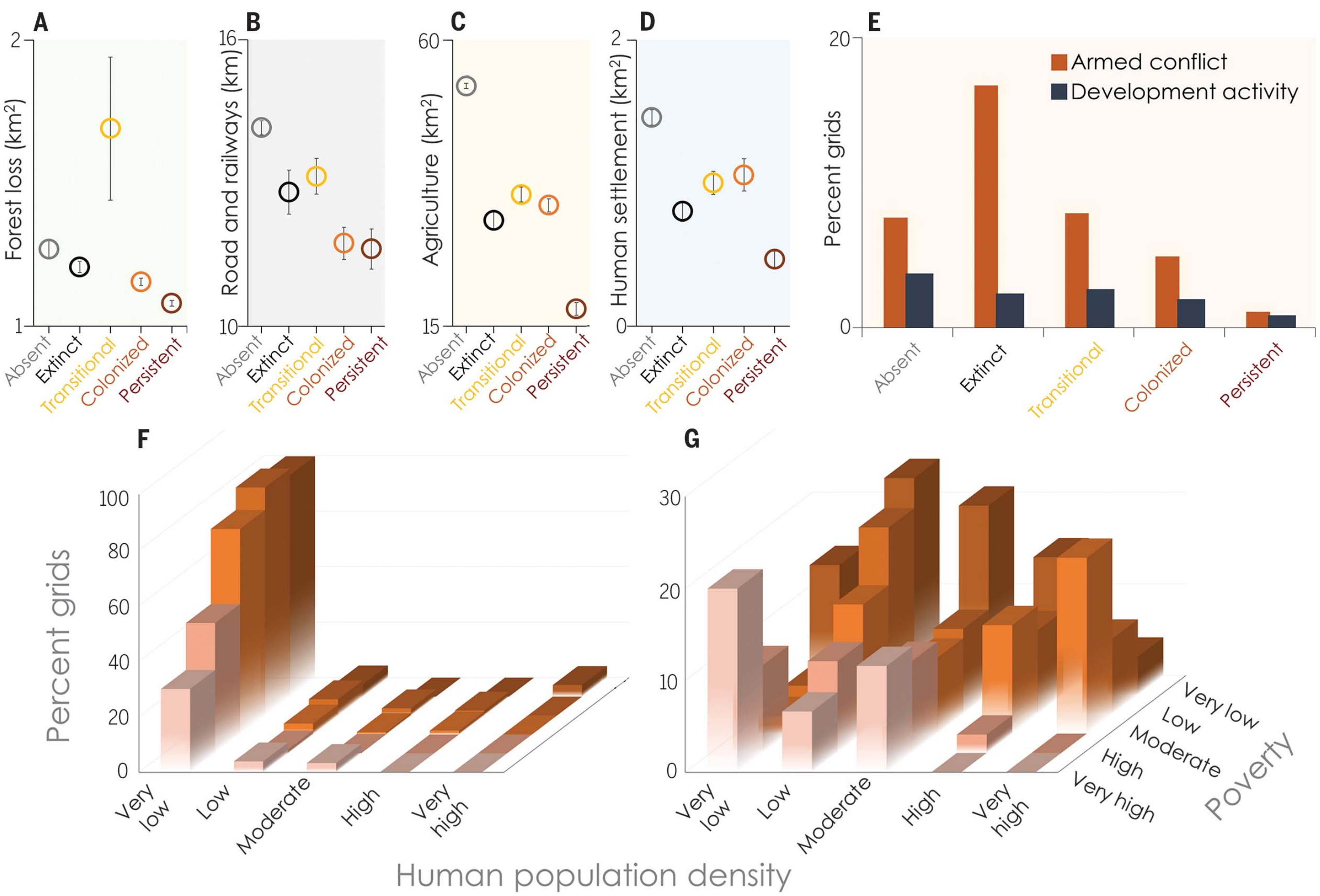

Fig. 2. Socioeconomic covariates of tiger recovery. (**A** to **E**) Threats to tiger-occupied areas are (A) summed average forest loss, (B) length of linear infrastructures per 100 km^2, (C) agricultural areas, (D) human settlement areas, and (E) percent grid cells with armed conflict and developmental activities, across tiger occupancy categories. (**F**) Grid cells with persistent tiger occupancy coincided with least populated and moderate to low rural poverty areas. (**G**) Grid cells colonized by tigers occurred across different human population density and poverty strata, except in areas with high population density and extreme poverty. Statistical comparisons are given in table S5.

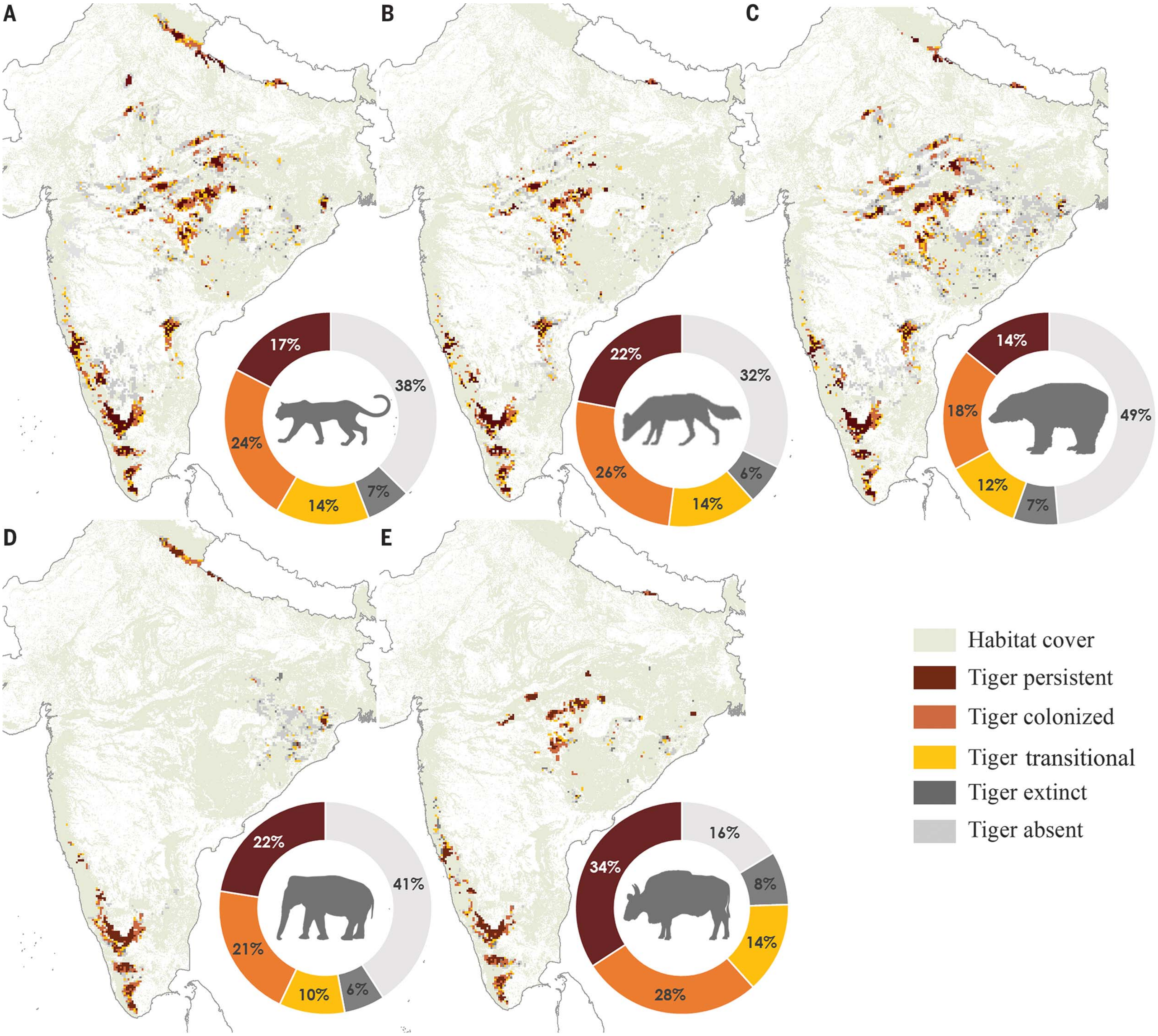

Fig. 3. Distribution of megafauna in tiger habitat of India. (**A** to **E**) Occurrence of (A) leopard (*P. pardus*), (B) dhole (*C. alpinus*), (C) sloth bear (*M. ursinus*), (D) Asian elephant (*E. maximus*), and (E) gaur (*B. gaurus*) overlapped with tiger occurrence by 62, 68, 51, 59, and 84%, respectively.

for increasing tiger occupancy. Like tiger extinction areas, habitats with tiger absence were mostly isolated from protected tiger source populations. These dynamics demonstrate the importance of human-free protected areas (land sparing) (*16*, *24*) for maintaining sources of tigers and their prey. Protection of tiger source populations has permitted their occurrence in multiuse areas (land sharing). Hence, in the case of tigers, land sparing is essential to realize the benefits of land sharing.

Habitats that were devoid of tigers (157,527 km^2) were predominantly spread across the states of Chhattisgarh, Odisha, and Jharkhand. Recovery of tigers in protected areas of this region (Guru Ghasidas, Palamau, Udanti-Sitanadi, Similipal, Satkosia, and Indravati), possibly through reintroduction or supplementation, and strengthening habitat connectivity between subsequent source populations can effectively repopulate tigers in another ~10,000 km^2. However, these areas are among the poorest districts in India (Fig. 2), with high incidences of bushmeat consumption, often with the use of traps and snares that are usually indiscriminate in killing prey and predators (*16*). Biodiversity recovery in these poorer districts entails investments in socioeconomic upliftment of communities, much more so than in other areas. Such a strategy requires multisectoral synergies between governmental agencies, civil societies, and scientific institutions to ensure inclusive benefit sharing with local communities. Implementation as is done in many tiger reserves, by sharing a substantial proportion of revenues from tiger reserves with the communities in proximity (*16*), may initiate a win-win strategy for people and tiger recovery.

The frequency of armed conflicts in a grid cell significantly increased tiger extinction probability (table S4). Sociopolitical stability and wildlife conservation go hand in hand; examples abound from across the world where political instability leads to drastic wildlife declines, especially of endangered species in trade

(*25*). Militants exploit wildlife products for arms, turning lawless regions into poaching havens (*26*). Within India, Manas National Park lost its greater one-horned rhinoceros (*Rhinoceros unicornis*) during the politico-ethnic conflict (*27*); Nepal's rhinoceros population was decimated during the period of civil unrest (*28*). Therefore, it is not surprising to see tigers and their prey either absent or extirpated from regions with armed conflict (Fig. 2E). In total, 47% of grid cells that experienced tiger extinctions were in districts affected by the Naxal armed conflict (fig. S5). Tiger reserves affected by the Naxal conflict were in the states of Chhattisgarh (Indravati, Achanakmar, and Udanti-Sitanadi) and Jharkhand (Palamau). Tiger reserves where armed conflict has been recently controlled displayed recovery (Nagarjunsagar-Srisailam, Amrabad, and Similipal). Several tiger habitats in the states of Odisha, Chhattisgarh, Jharkhand, Telangana, Andhra Pradesh, and eastern parts of Maharashtra have been experiencing armed insurgencies (fig. S5), and it is in these habitats that tiger occupancy was low and extinction probability high (Fig. 2 and fig. S5). These are areas where, with greater political stability, we might expect tiger recovery.

Contrary to conventional expectation of spatial separation in humans and large carnivores, human density—although low in persistently occupied areas compared with absent areas—was not a major deterrent to tiger colonization and recovery (Fig. 2, D and G, and fig. S6). The areas that were newly colonized by tigers had an average density of 250 (±8) humans/km^2. Tigers occurred and colonized habitats interspersed with agricultural and human settlements (Fig. 2 and fig. S7). Habitats outside of tiger reserve cores and national parks are used by communities for their livelihoods (*17*). This land sharing with tigers varied across India, likely because of different sociocultural tolerances by people. Community tolerance to large carnivores in their backyards is mostly driven by economics (*29*), social settings (*30*), and cultural factors (*31*), in which India is richly diverse. Tigers shared space with people at high densities in some areas (such as Madhya Pradesh, Maharashtra, Uttarakhand, and Karnataka), whereas they became extinct or were absent from areas with a legacy of extensive bushmeat consumption or commercial poaching, even when human density was relatively low (such as in Odisha, Chhattisgarh, Jharkhand, Northeastern states of India, and most of Southeast Asia) (*28*–*30*). Thus, it is not simply the density of humans but rather their attitudes and lifestyles that determine stewardship for tiger recovery.

A large proportion of tiger-occupied habitats (45%) was shared with ~60 million people in India (fig. S6C). This co-occurrence with people coincides with relatively economically prosperous areas, many of which harness substantial financial benefits from tiger-related tourism as well as proactive government-sponsored schemes for compensating the loss caused by conflict (*16*). The rates of tiger colonization were lowest in areas of high rural poverty rate, as derived from indicators of health, education, and standard of living (fig. S6B and fig. S7) (*32*). Often, marginalized communities rely heavily on extractive use of forest resources and bushmeat for their livelihood (*33*, *34*), which is becoming unsustainable with growing human populations and declining biodiversity (*35*). Economic prosperity achieved through alternative and nonconsumptive use of ecosystems and biodiversity allows tigers and associated ecosystems to recover. However, economic prosperity usually leads to intensive land-use change, which had a negative impact on tiger occurrence (table S4). Tiger recovery is thus constrained at opposite ends of the socioeconomic spectrum, by intensive urbanization and poverty (fig. S8). Hence, adopting an inclusive and sustainable rural prosperity in place of an intensive land-use change–driven economy can be conducive for tiger recovery, aligning with India's modern environmentalism and sustainability (*36*, *37*). Investments for inclusive and equitable eco-development projects within shared landscapes would enable tiger recovery. Protected areas can also bring possibilities not only to protect biodiversity but also to alleviate poverty and secure ecosystem services by sharing benefits with local communities in the proximity (*24*, *38*).

A cornerstone to the success of tiger recovery in India would be the realization of its originally envisaged flagship role for garnering resources for biodiversity conservation. The mere presence of an apex predator usually heralds the existence of a complex ecosystem, composed of vegetation, prey, and often a functional mesocarnivore community (*7*). Naturally, tiger-occupied areas were found to be a subset of the distribution of major tiger prey such as spotted deer (*Axis axis*), sambar deer (*Rusa unicolor*), swamp deer (*Rucervus duvaucelii*) and gaur (*Bos gaurus*) (fig. S9), which had the largest contribution in explaining tiger occupancy (table S4). Moreover, the sampled region is also a subset of the historical range for many megafauna species in the region. Within the tiger's distribution range, tiger-occupied habitats spatially coincided with the distribution of co-occurring megaherbivores: Asian elephant (*Elephas maximus*; 59%) and gaur (84%) (Fig. 3). Other large carnivores such as leopard (*Panthera pardus*), dhole (*Cuon alpinus*), and sloth bear (*Melursus ursinus*) also coincided with 62, 68, and 51% tiger-occupied areas, respectively (Fig. 3). Furthermore, ecosystems protected for tiger recovery reinforced biotic resistance to biological invasions as well as contributed to carbon sequestration, benefiting the global climate (*39*, *40*). This accentuates the umbrella role of tigers in extending cobenefits to biodiversity and biosphere.

Irrespective of political parties, the government of India has shown deep-seated pride in conserving the tiger, its national animal (*16*). Conservation investments by governments—enabled through dedicated legislation in land sparing, prohibiting forest land diversions, and ensuring benefit-sharing with local communities—have largely enabled tiger recovery. These legislative instruments not only ensure tiger recovery but also can yield equitable cobenefits (*41*). Our study suggests that downgrading such existing instruments (*42*) would have far-reaching ramifications on tiger recovery and biodiversity conservation.

Carnivore-human co-occurrence is possible because of effective land-use plans and policies in vast landscapes of North America and Europe (*8*, *43*). India, despite having the world's highest human population density and only 18% of the global tiger habitat, harbors >75% of the global tiger population (~3600 tigers) (*17*). Although this sets a perfect narrative of wildlife-human co-occurrence, it is unattainable in the absence of human-free legally protected areas, embedded in socioeconomically prosperous and politically peaceful multiuse areas. The human attitude toward biodiversity, particularly large carnivores such as the tiger, is based on cultural acceptance as well as economic benefits; the latter requires meticulous governance, and the former requires conscious nurturing. The success of tiger recovery in India offers important lessons for tiger-range countries as well as other regions for conserving large carnivores while benefiting biodiversity and communities simultaneously. It rekindles hope for a biodiverse Anthropocene.

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SUPPLEMENTARY MATERIALS

science.org/doi/10.1126/science.adk4827
Materials and Methods
Figs. S1 to S9
Tables S1 to S6
References (*44–48*)
MDAR Reproducibility Checklist

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Correction (20 February 2025): The Funding section in the Acknowledgments has been updated to include two funding sources for author N.A.M.