APPLIED ECOLOGY

Road development in Asia: Assessing the range-wide risks to tigers

Neil Carter[1]*, Alexander Killion[1], Tara Easter[1], Jodi Brandt[2], Adam Ford[3]

Roads are proliferating worldwide at an unprecedented rate, with potentially severe impacts on wildlife. We calculated the extent and potential impacts of road networks across the 1,160,000-km^2, 13-country range of the globally endangered tiger (*Panthera tigris*)—a conservation umbrella species. We found that roads were pervasive, totaling 134,000 km across tiger conservation landscapes (TCLs), even in tiger priority sites and protected areas. Approximately 43% of the area where tiger breeding occurs and 57% of the area in TCLs fell within the road-effect zone. Consequently, current road networks may be decreasing tiger and prey abundances by more than 20%. Nearly 24,000 km of new roads will be built in TCLs by 2050, stimulated through major investment projects such as China's Belt and Road Initiative. Given that roads will be a pervasive challenge to tiger recovery in the future, we urge decision-makers to make sustainable road development a top priority.

INTRODUCTION

Road networks are expanding worldwide at an unprecedented rate (*1*–*3*). Earth could accumulate another 3 to 4.7 million km of roads by 2050 (*1*). Although roads can facilitate economic development and improve human welfare, they can also have severe effects on wildlife populations by exacerbating habitat fragmentation and human disturbance (*4*–*7*). For example, roads affect wildlife by acting as barriers to movement and reducing gene flow, as well as through direct mortality caused by collisions with vehicles (*8*). Roads also increase access to remote areas, facilitating human settlement growth, natural resource extraction, and hunting and illegal harvest (*9*). Moreover, traffic disturbance from noise, lights, and motion reduces the quality of habitat near roads (*10*).

While roads are now ubiquitous across much of the earth, the construction of new roads will be concentrated in areas with high biodiversity value (*2*, *5*). In Asia alone, road length is expected to double between 2017 and 2020 (*11*). The Asian Development Bank estimated that about \$1.5 trillion per year needs to be invested in new infrastructure projects in the Asia-Pacific region from 2016 to 2030 to meet growth projections (*12*). China's Belt and Road Initiative (BRI), for example, is considered the largest infrastructure project of all time and will entail major risks to biodiversity across Asia, as well as Eurasia and parts of Africa (*13*, *14*). Many of these new roads and highways will likely traverse reserves or other highly biodiverse areas (*14*). Although roads are one of the most important impacts on terrestrial ecosystems, most "road ecology" studies have focused on localized patterns of wildlife mortality or behavior associated with road design as well as investigating the use and effectiveness of impact mitigation measures (*15*). While insightful, these fine-scale interactions are often site specific (*16*) and might fail to estimate the full extent of the impacts from roads on wildlife at broader scales. These broad scale effects are relevant to regional road development policies. Furthermore, we know little about how patterns in road construction will affect biodiversity in the coming decades.

Here, we used a recently developed global roads dataset (*1*) to investigate the extent and potential influence of road networks across the 1,160,000-km^2, 13-country range of the globally endangered tiger (*Panthera tigris*). Despite being a conservation flagship species, few studies assess the impacts of roads on tigers and their recovery [e.g., (*17*, *18*)]. In the Russian Far East, for example, roads reduce tiger survival rates due to collisions with vehicles (*17*). In the Kerinci Seblat region of Sumatra, tigers avoided areas closer to public roads, suggesting that roads act as important barriers to movement (*18*). The emerging impacts of road development on tigers are critical for several reasons. First, much of the tiger's remaining range occurs outside protected areas where policies on road development are less stringent (*4*, *19*). Second, tigers are found mostly in South and Southeast Asia, which will experience accelerating pressure from human development in the coming years (*5*). Third, road construction often catalyzes and exacerbates the three main threats to tigers—prey depletion, habitat degradation, and poaching (*4*). Fourth, tigers are concentrated in source populations across their geographic range, meaning that even a small amount of road construction could disproportionately affect tiger recovery by permanently isolating tiger populations from each other (*20*, *21*).

Protecting tigers is a global conservation priority, exemplified by a landmark international initiative to double global tiger numbers (called "Tx2") from 2010 to 2022 (*22*). The member organizations of this initiative selected 29 priority sites from 76 tiger conservation landscapes [TCLs; blocks of tiger habitat (*23*)] across the tiger's range that were considered crucial for reaching the Tx2 target. In addition to TCLs and the Tx2 priority sites, the International Union for Conservation of Nature (IUCN) synthesized tiger occurrence records in 2014 to produce an updated tiger range map (*19*). Tx2 sites, TCLs, and the IUCN range map help delineate tiger habitats and are important for rallying support for tiger conservation; however, their designation does not come with specific road or land use restrictions. In contrast, protected areas that fall within the tiger range do restrict human development to varying degrees depending on protection status and social-ecological factors (*24*). Spatial assessments of road networks across these various classifications are lacking, which limits tiger conservation planning.

We calculated three metrics—road density, distance to the nearest road, and relative mean species abundance (MSA)—to characterize

[1]School for Environment and Sustainability, University of Michigan, Ann Arbor, MI 48109, USA. [2]Human-Environment Systems, Boise State University, Boise, ID 83712, USA. [3]Department of Biology, University of British Columbia, Kelowna, BC, Canada.
*Corresponding author. Email: nhcarter@umich.edu

how road networks influence tiger habitats. We also used published forecasts of global road expansion to calculate the length of new roads that might exist in tiger habitats for each tiger range country (where projections were available) by 2050. Combined, these metrics provide starting points for range-wide monitoring and impact assessments of road development projects, thereby enabling evaluation of progress toward country-level conservation and sustainable development goals. Our preliminary risk assessment for tigers can inform future research activities and road mitigation or placement strategies at policy-relevant scales, as well as act as a template for similar studies on other road-sensitive species.

RESULTS

Road densities in tiger habitats

Road densities varied widely across tiger range countries (Fig. 1 and table S1). For example, China's mean road density in TCLs (274 m/km^2) was nearly eight times greater than that in Malaysia (35 m/km^2). Road densities were, on average, 34% greater in nonprotected portions (154 m/km^2) of TCLs than the strictly protected areas inside TCLs (115 m/km^2), indicating that road density increased with the relaxation of protection status (tables S2 and S3). This was not the case in Cambodia, Malaysia, and Russia where road densities were actually higher in protected areas than outside them and in India

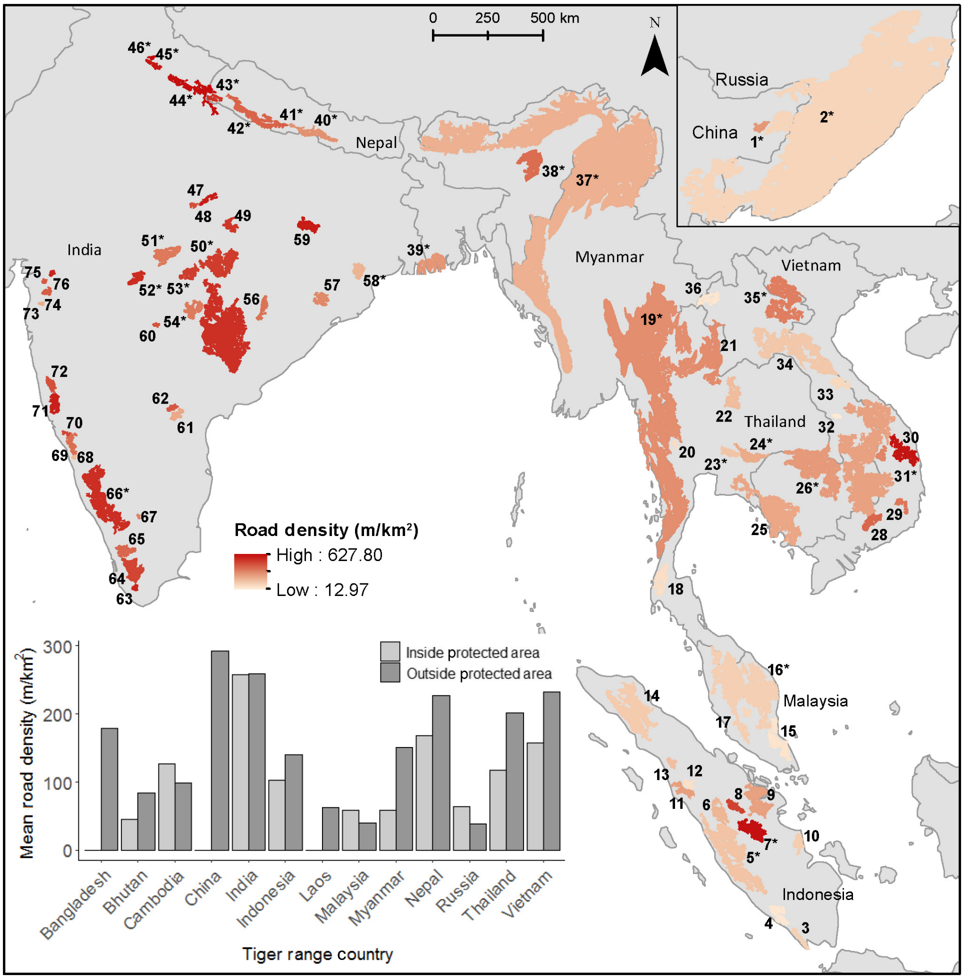

Fig. 1. Map of estimated road densities (m/km^2) for 76 TCLs. The 29 Tx2 priority sites are indicated with an asterisk. Bar graph shows road densities in the protected (IUCN categories Ia, II, and IV) and nonprotected portions of the TCLs for each of the 13 countries in the tiger range. TCLs are as follows: Heilongjiang (1), Russian Far East–China (2), Bukit Barisan Selatan South (3), Bukit Balai Rejang–Selatan (4), Kerinci Seblat (5), Bukit Rimbang Baling (6), Bukit Tigapuluh Landscape (7), Tesso Nilo Landscape (8), Kuala Kampar–Kerumutan (9), Berbak (10), Bukit Barisan South (11), Rimbo Panti–Batang Gadis West (12), Sibologa (13), Gunung Leuser (14), Endau Rompin (15), Taman Negara–Belum (16), Krau (17), Khlong Saeng (18), Tenasserims (19), Salak-Phra (20), Phu Miang–Phu Thong (21), Phu Khieo (22), Khao Yai (23), Thap Lan–Pang Sida (24), Cardamom's (25), Cambodian Northern Plains (26), Southern Annamites (27), Cát Tiên (28), Bi Dup–Nui Ba (29), Kon Ka Kinh (30), Yokdon (31), Xe Bang Nouan (32), Hin Nam Ho (33), Northern Annamites (34), Nam Et Phou Louey (35), Nam Ha (36), Northern Forest Complex–Namdapha–Royal Manas (37), Kaziranga-Garampani (38), Sundarbans (39), Chitwan (40), Bardia South (41), Bardia (42), Suklaphanta (43), Corbett-Sonanadi (44), Rajaji Minor (45), Rajaji Major (46), Panna East (47), Panna West (48), Bandhavgarh-Panpatha (49), Kanha-Phen (50), Pachmarhi-Satpura-Bori (51), Melghat (52), Pench (53), Andhari-Tadoba (54), Indravati (55), Sunabeda-Udanti (56), Satkosia-Gorge (57), Simlipal (58), Palamau (59), Painganga (60), Nagarjunasagar South (61), Nagarjunasagar North (62), Shendurney (63), Periyar-Megamala (64), Anamalai-Parambikulam (65), Western Ghats: Bandipur-Khudrenukh-Bhadra (66), Biligiri Range (67), Western Ghats–Sharavathi Valley (68), Dandeli-Anshi (69), Dandeli North (70), Radhanagari (71), Chandoli (72), Mahabaleshwar Landscape–South (73), Purna (74), Mahabaleshwar Landscape–North (75), and Shoolpaneswar (76).

where densities were about the same (Fig. 1). Note also that Bangladesh, China, and Laos have no strict protected areas in their TCLs. Furthermore, the road densities in the protected areas of TCLs of some countries were higher than those in the nonprotected areas of TCLs in neighboring countries (tables S2 and S3). Mean road densities in the protected areas in Nepal's TCLs (168 m/km^2), for example, were two times greater than the nonprotected portions of TCLs (84 m/km^2) in Bhutan. The difference was almost three times as great between Thailand (117 m/km^2) and Malaysia (40 m/km^2).

Road densities also varied widely within countries (Fig. 1). For example, road densities in Indonesia ranged from the third highest of all TCLs (444 m/km^2, Bukit Tigapuluh Landscape) to the second lowest (17 m/km^2, Bukit Balai Rejang–Selatan; table S4 and fig. S1). Average road density within the 76 TCLs was 184 m/km^2, ranging from a low of 13 m/km^2 in Xe Bang Nouan in Laos to a high of 628 m/km^2 in Rajaji Major in India. Of the 10 TCLs with the highest road densities, 2 are considered global priorities (Corbett-Sonanadi, Bukit Tigapuluh Landscape) and two are regional priorities for tigers (Panna East, Radhanagari). Road densities were also almost 25% greater in Tx2 (209 m/km^2) than non-Tx2 sites (168 m/km^2; table S4), suggesting that roads will be a pervasive challenge to tiger recovery in those priority areas.

Distance to the nearest roads in tiger habitats

More than half of the global supply of tiger habitat is within the road-effect zone (i.e., <5 km from nearest road), likely decreasing prey abundance and increasing levels of human-wildlife conflict and poaching. Distances from the nearest road ranged from 0 to 121 km in TCLs (Russia), with a median of 3.9 km (interquartile range = 8.1 km). However, more than half (57%) of the area in TCLs was less than 5 km from the nearest road—this is notable because this is a distance below which roads negatively affect the abundance of mammals (*25*). Despite having more roads overall, roads were more dispersed in Tx2 sites than in non-Tx2 sites. In Tx2 sites, the median distance to the nearest road was 4.1 km (interquartile range = 8.8 km), compared to 2.9 km (interquartile range = 6.3 km) in non-Tx2 sites (table S5). About 56 and 65% of the areas in Tx2 and non-Tx2 sites, respectively, were less than 5 km from the nearest road (Fig. 2). Moreover, of all distance categories, the shortest distance category (0 to 500 m from the nearest road) was the most common for both Tx2 (14%) and non-Tx2 sites (19%; Fig. 2). Distances from the nearest road were generally longer in protected portions of the TCLs compared to nonprotected portions. In protected portions of TCLs, the nearest road was, on average, 9.5 km away from any given location, whereas this distance was 8.4 km in nonprotected portions. There was a substantial portion (44%) of the protected areas of TCLs that were less than 5 km from the nearest road (Fig. 2), but this was much less than that of nonprotected portions (61%).

Relative MSA in tiger habitats

On the basis of relative MSA values, we predicted that roads in tiger habitat have reduced mammal abundances by ~20% compared to what would be expected if roads did not occur in tiger habitat. This suggests that roads have decreased the abundances of tigers and the species that tigers rely on directly for prey. More than half (54%) of the tiger's entire range mapped by IUCN in 2014 was influenced by roads, as reflected by an MSA < 0.95, and nearly 20% was heavily affected (MSA < 0.5). Moreover, roads influenced 43% of areas where tiger breeding had been detected (a crucial sign of population establishment) between 2009 and 2014. Some sites with known tiger breeding can have extensive road networks (e.g., Fig. 3, bottom), with 14% of the total area of those sites having predicted mammal abundances less than half of those estimated in nondisturbed areas (Fig. 3, top right). Of additional concern is that the predicted average mammal abundance as influenced by roads was lowest in sites where tigers were detected between 2009 and 2014 (MSA = 0.76 ± 0.23) than in any another occurrence category, even compared to sites where tigers were considered to have been recently extirpated (MSA = 0.81 ± 0.22). Almost one-quarter of the area where tigers had been detected between 2009 and 2014 was heavily affected by roads (MSA < 0.5; Fig. 3, top right).

Predicted MSA for mammals was 5% higher in Tx2 sites (MSA = 0.82 ± 0.22) than in non-Tx2 sites (MSA = 0.77 ± 0.23). However, two of the lowest MSA estimates were Tx2 sites (table S6 and fig. S1). Road encroachment also substantially affected protected areas in TCLs. Nearly 40% of their area was influenced by roads (MSA < 0.95), and more than 10% was heavily affected (MSA < 0.5).

Future road construction in tiger habitats

We estimated that nearly 24,000 km of new roads will be built in TCLs by year 2050, although this is an underestimate, because data from Myanmar does not exist. The estimated increase in road length and percent change in road length within TCLs varied greatly by country (Fig. 4). The countries with the largest TCL area, and thus potentially the most important foci for the global tiger conservation community, have among the highest expected increases in kilometers of road length and percent change in road length (table S7). For example, India—which has more than 16% of the global TCL area—is expected to add by far the greatest amount of roads in TCLs (14,500 km), which is a 32% increase from current levels. Although Nepal and Bhutan have less total TCL area compared to several other countries, they are expected to add 43% (880 km) and 40% (609 km) more kilometers of roads, respectively, over the next three decades.

DISCUSSION

Our analysis demonstrates that tigers face a ubiquitous and mounting threat from road networks across much of their 13-country range. In terms of road density, TCLs varied considerably by protection status and country. In particular, road densities were higher in nonprotected areas of TCLs compared to protected areas, suggesting that protected areas are limiting growth of road networks in TCLs. These protected areas in TCLs are important, because they support tiger "source" populations that can disperse and repopulate larger landscapes (*26*). However, the relatively high road densities outside protected areas pose a considerable challenge to long-term tiger conservation. Regional road policies may be creating tiger "islands," whereby tiger source populations are becoming increasingly isolated from each other. Tiger dispersal and population expansion into the nonprotected forests connecting those populations are necessary to ensure that the global tiger population has opportunities to grow (*27*). Even protected areas were not immune to road development, with those in the TCLs in India having the greatest density than any other tiger range country. Likewise, road encroachment into areas where tigers have been recently detected (2009–2014) is already pervasive and even greater than places where tiger presence is unknown or unlikely. Tiger habitats have declined by more than 40% since 2006 (*19*), underscoring the importance of maintaining roadless

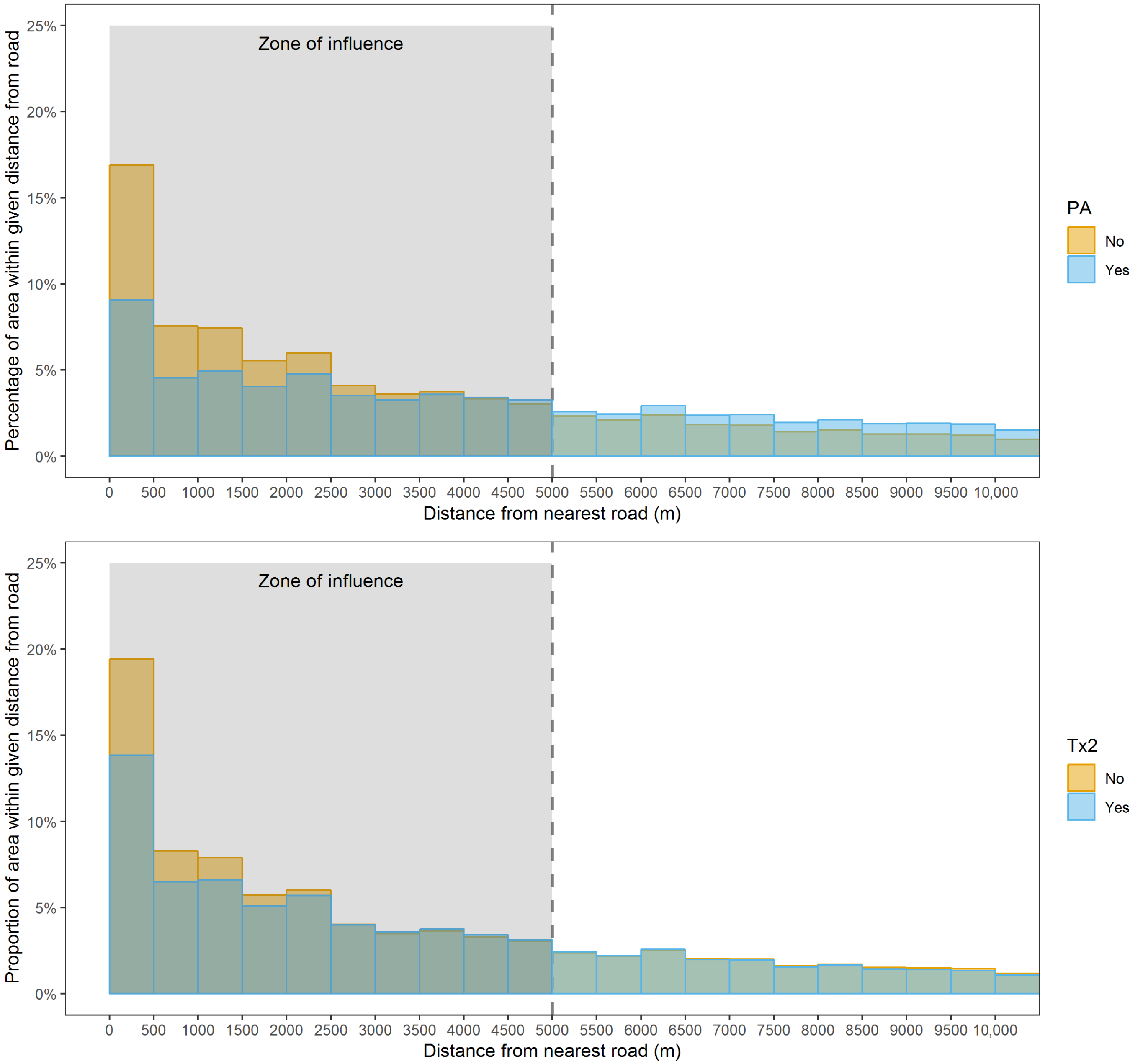

Fig. 2. Distance to the nearest roads in tiger habitats. Distances from the nearest road in protected areas (top) and Tx2 sites (bottom) in TCLs. Distances were calculated using a grid with a resolution of 500 m by 500 m. Distances to the nearest road <5000 m (area highlighted in gray) have been shown to negatively influence the abundances of mammals (*25*). Although the maximum distance from the nearest road was 121,000 m, we constrained the values to 10,000 m for display purposes.

areas and resisting road expansion in places where tigers still exist before it is too late. Doing so can create opportunities for populations of tigers and their prey to make significant recoveries (*28*). Considered an umbrella species (*29*), protecting tigers from road impacts will also promote conservation of many other threatened species and some of the world's greatest biodiversity hot spots.

Slowing road development in the tiger range is a pressing need. Our findings suggest that the 134,000 km of roads in the tiger's current range may be decreasing abundances of tigers and their prey by more than 20%. Roads can affect tiger abundances via several mechanisms. In India, for example, increasing vehicular traffic is likely increasing direct mortality of tigers and their prey due to vehicle collisions (*30*, *31*). Recent reports indicate that 10 tigers have died from vehicle collisions in India from 2015 to 2017 (*32*), although this number is likely an underestimate due to nondetection or nonreporting. Moreover, a simulation study in Central India found that tiger extinction risk rose steeply (through genetic isolation) when traffic volume increased on roads (*33*). Growth in road networks can also be associated with large-scale habitat degradation and thereby decrease the carrying capacity for tigers in landscapes altered by roads. For example, the Bukit Tigapuluh Landscape, which had one of the highest road densities in our analysis, lost nearly 40 km^2 of forest from 2000 to

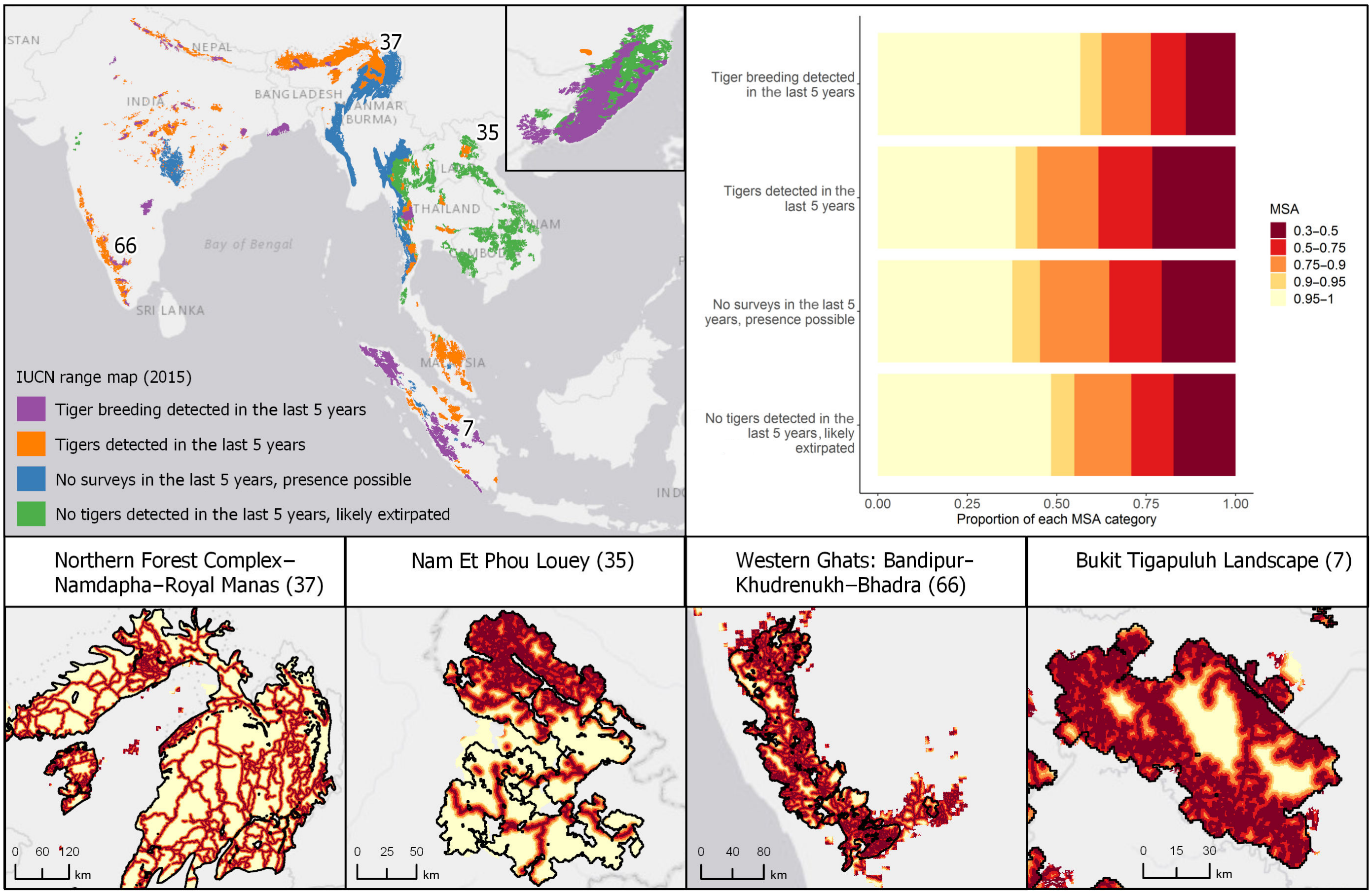

Fig. 3. MSA estimates in tiger habitats. Map (top left) showing the four occurrence categories referenced in the 2014 IUCN tiger range estimates. Top right shows the proportion of each occurrence category with different levels of MSA. The MSA levels were the same as those in (*56*) to aid comparison. MSA ranges from 0 to 1, with lower values indicating a larger reduction in mammal abundance due to nearby roads. MSA levels <0.95 are considered influenced by roads, and levels <0.5 are considered heavily affected. We used MSA as a proxy estimate of road impacts on tigers and their prey. Bottom panels show MSA values (500 m by 500 m, color corresponds to MSA level in the top right panel) for four TCLs spanning the different IUCN occurrence categories. The four TCLs are designated Tx2 priority sites, and their location is indicated by the numbers in the top left panel.

2012 largely due to expansion of palm oil plantations. Adult tigers in that landscape decreased from 36 to 22 over that same time period (*34*). Beyond land transformation, incursion of low-density, low traffic volume logging roads can increase human access to remote forests and exacerbate hunting and poaching pressure on tigers and their prey for years after road construction (*35*, *36*). These "secondary effects" of roads on wildlife, therefore, extend far beyond the road corridor per se (*37*). Evidence of these secondary effects occurred in Russia where tiger prey species were negatively correlated with road density and tiger survivorship and reproduction were higher in roadless areas than areas with primary or secondary roads due largely to road-facilitated poaching (*38*, *39*). In addition, construction of roads or railways in key wildlife corridors can fragment tiger habitats, especially in bottlenecks where tigers have very limited options for movement (*40*). Nepal, for example, is set to build 18,000 km of new roads by 2050 (*1*). Many of these roads are expected to cut through narrow forest tracts in the tiger-occupied lowlands, which could seriously jeopardize the gradual recovery of tigers in the country (*27*).

The rush to build major new roads throughout forested regions of South and Southeast Asia, financed through China's BRI, could have severe impacts on tigers (*41*). As signatories on the Convention on Biological Diversity, all tiger range countries have legally binding responsibilities to create legislation that minimizes harm to threatened species including tigers (*42*). The BRI could be an important partner in that endeavor by adopting biodiversity conservation as one of its core values and learning from and supporting national-level conservation initiatives. That would set the stage for the BRI to plan and implement a network of protected areas and wildlife corridors that help meet, or exceed, the Convention on Biological Diversity's targets for protection and safeguard tigers from the impacts of roads (*13*). The creation of bilateral agreements that include provisions for reducing wildlife poaching and trafficking between China and countries that are part of the BRI would also lessen the impacts of that infrastructure initiative on tigers and other species of conservation concern (*8*). Another policy to minimize road impacts on tigers and other wildlife would be to require Chinese-funded BRI efforts overseas to ascribe to the same strict environmental regulations on road development that now exist within Chinese borders (*14*). Likewise, national bodies and international funding agencies, such as the Asian Development Bank and World Bank, should mandate international oversight and standards on environmental impact assessments (*14*).

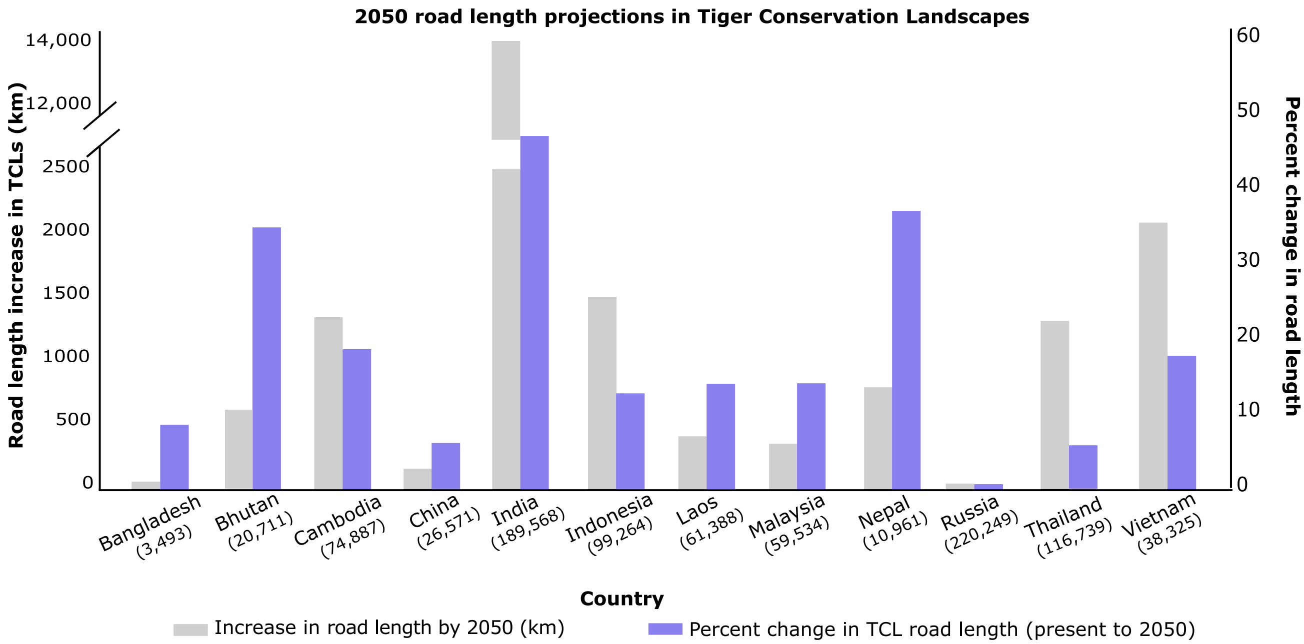

Fig. 4. Projected increase in road length (km) by 2050 in TCLs in tiger range countries. No projection data exist for Myanmar. Country-level projections are from (*1*) and downscaled to TCL based on the current ratio of road length in the entire country to road length in the country's TCLs. The left *y* axis (gray bars) shows absolute increase, and the right *y* axis (purple bars) shows the percentage increase from current road lengths. Values below country names are the total amount of TCL area in country (km^2).

Our results highlight the need to make sustainable road development a top priority. Smart green infrastructure can promote tiger-friendly road projects by avoiding tiger habitats, minimizing and mitigating adverse impacts through design that accounts for consequences on tigers, and compensating for damages to tiger habitats to ensure net positive impacts (*42*). These strategies are part of the "mitigation hierarchy," which provides a template for minimizing environmental harm through policy recommendations at national, sectoral, and project levels. For example, the first filter is to prohibit road development or other infrastructure from priority tiger populations or those areas identified as "no go" zones in national tiger action plans or other legislation. Upgrading existing roads, for example, paving a bulldozed track, should also be avoided in or near tiger priority areas, as those roads increase access to remote forests and might increase the likelihood of vehicle collisions with tigers and their prey (*43*). In places where roads are being planned, strategic environmental assessments can identify methods for reducing cumulative impacts, such as zoning around infrastructure to prevent settlement growth and clearance of forest cover. Crucially, environmental impact assessments should include secondary effects on tigers and meaningfully consult with stakeholders (including local communities where roads will be developed) before project approval (*43*). Biodiversity offsets financed through various mechanisms—e.g., tax and subsidy shifts, protected area transfer funding, and payments of ecosystem services—can also minimize adverse impacts of road projects on tiger habitats (*5*, *42*). However, offsets should not be misused and compromise existing international agreements on the protection of biodiversity (*44*). Although most of the national-level tiger action plans mention the impacts of roads, mainstreaming smart green infrastructure design principles into the plans would provide concrete ways of understanding, monitoring, and mitigating the effects of road development on tigers. More details and recommendations on developing tiger-friendly transportation infrastructure are available in Quintero *et al.* (*42*) and in table S9.

Our metrics provide tools to support sustainable road development. For example, the estimates of road density can be used to classify regions according to their magnitude of road networks. These classifications can then be used to map areas unaffected by roads (i.e., roadless areas), which could be explored as "controls" for future studies. Distance from the nearest roads can be used to geographically define zones of influence within regions to target conservation action. Within the zones of influence, the cell-by-cell estimates of MSA highlights where road impacts on tigers and their prey are potentially (or could be) most pronounced. Combined, these metrics enable rapid risk assessment and can help identify no-go zones for road infrastructure. Identifying no-go zones will be especially useful for those countries where we projected high levels of future road encroachment into tiger habitats, such as in India, Nepal, and Bhutan. Our spatial predictions of risk also allow screening of proposed road developments before decisions on road design, site, and construction preparation have already been made. This is important, as once those decisions have been made, impact assessments are too late to influence road planning (*42*). Our methodology can also provide baseline data to target locations for different conservation strategies, such as alternative road alignments to avoid key tiger habitats, road bundling, closure of vehicular traffic at night, decommissioning existing roads from tiger landscapes with source populations, road signage indicating the presence of tigers, and construction of wildlife crossing structures to maximize connectivity (*45*). Targeted road mitigation measures can, for example, support reintroduction efforts of tigers to places they have recently become functionally extinct, such as in Cambodia and Vietnam (*46*).

Our analysis is only a first step toward understanding and managing road encroachment into tiger habitats. Several avenues of research are needed to improve understanding. For example, how do roads alter tiger movements, hunting success, and mating? How do changes in those fitness-related behaviors translate to population-level effects? What are cost-effective methods for designing wildlife crossings that are most likely to encourage tiger movement over transportation infrastructure and maintain connectivity? Care is also needed to account for local contexts and variation in both space and time. For example, some areas might have relatively high tiger densities despite high road densities (e.g., Corbett National Park, India) because land clearing and road development occurred in the past and tiger numbers have since rebounded. In those cases, tigers may be capable of adapting to road impacts, although the conditions (e.g., low vehicle traffic) that enable tigers to cope with roads need to be better understood. In other cases, recent road development can drive declines in tigers and their prey, regardless of the current road density in the landscape (*47*). Furthermore, road development may create an extinction debt, in which there is a time lag between road construction and declines in tiger populations (*48*), necessitating long-term monitoring of tigers.

To our knowledge, fine-scale spatial data on abundances of tigers and their prey across gradients of road densities do not exist. Therefore, we used MSA as a proxy estimate of road impact on the abundances of tigers and their prey. The mammal datasets used in the meta-analysis were largely of European or North American species and biased toward carnivores and ungulates, comprising 16.3 and 58.1% of the data, respectively (*25*). We consider calculation of the MSA values to be a suitable first step in assessing road impacts on tigers across their range for the following three reasons. First, tiger abundances are tightly linked to ungulate prey abundances (*49*, *50*). Second, tiger occupancy and habitat use have been shown to be negatively affected by roads (*39*, *51*–*53*). Third, previous studies in Southeast Asia, although scarce, show negative relationships between roads and ungulate habitat use (*54*). Collecting more data on road effects on Asian wildlife species is needed to give us more accurate information for a region undergoing rapid change. In addition, our analysis treated all road types as having the same effect on abundances, which is largely appropriate, as most of the roads in the TCLs were considered "tertiary" roads (e.g., roads connecting villages or unpaved rural roads; table S8). However, larger roads, and especially unfenced highways, can act as population sinks for both tigers and their prey due to elevated human-caused mortality. Note that the global roads dataset we used, although the most complete to date, likely does not include every road within TCLs. Our findings, therefore, are conservative estimates of the true scope of the pervasive influence of roads on tigers and their prey.

CONCLUSION

Given the rapid growth of road infrastructure in many areas around the world, broad-scale assessments of road encroachment into the habitats of threatened and endangered species are urgently needed. New data and methods exist to make such assessments possible, opening up new opportunities for research and conservation action. Here, we used recent global roads data to evaluate the pervasiveness of roads throughout the globally endangered tiger's 13-country range and developed the first baseline indices on the threat from existing and future roads in tiger habitats. We found that protected areas, while not always designed specifically for tigers, are relatively effective at limiting road impacts (though exceptions exist), whereas the TCL or Tx2 sites (specifically delineated to guide tiger conservation) are experiencing relatively high road encroachment, suggesting that they need consistent governance structures to effectively limit road development. Furthermore, road encroachment into tiger habitats varied tremendously between and within countries. Our spatially explicit indices can help target conservation interventions to the most affected regions first, although the site-specific social, ecological, and political factors driving road growth must be thoughtfully considered when developing road mitigation strategies. The ubiquity of roads throughout tiger habitats is a highly troubling warning sign for tiger recovery and ecosystems in Asia. We urge decision makers to make sustainable road development—at subnational, national, and transnational scales—a top priority to alleviate its detrimental impacts on wildlife populations.

MATERIALS AND METHODS

Road density

We downloaded the global roads vector data from Globio (*1*). The data were created by harmonizing and integrating nearly 60 geospatial datasets on road infrastructure. To our knowledge, these data thus represent the most comprehensive, consistent, and up-to-date georeferenced information on global roads. Using these data, we calculated current road densities for all 76 TCLs and summarized those estimates by country, protection status [i.e., strictly protected (IUCN categories Ia, II, and IV) versus nonprotected], and Tx2 designation (i.e., Tx2 versus non-Tx2 site). TCL boundaries were downloaded from Global Forest Watch, protected area boundaries from the World Database on Protected Areas (November 2018), and country boundary data from Natural Earth. We included a protected area in the analysis if more than 50% of its area fell within a TCL. We also calculated road densities for the four occurrence categories in the 2014 IUCN tiger range map, including tiger breeding detected in the last 5 years (i.e., 2009–2014); tigers detected (breeding unknown) in the last 5 years; no surveys in the last 5 years, presence possible; and no tigers detected in the last 5 years, likely extirpated.

To calculate road density, road length (m) was calculated for each geographic unit of interest (e.g., TCL). Road length was then divided by total area (km^2) of each geographic unit to calculate road densities (m/km^2). We intersected tiger range countries with TCLs to prevent double counting TCL areas that span multiple countries. All geographic data were projected into the Asia north azimuthal equidistant projection. All analyses were done in R using packages ggplot2, sp, sf, raster, and rgdal, as well as ArcGIS Pro 2.1 (*55*).

Proximity to roads

To calculate proximity to roads, we first created a 10-km buffer around the tiger range to ensure that we captured the effects of any roads that may be just outside the tiger range. We converted the tiger range and the buffered area to a 500-m-resolution raster. We also converted the road vector dataset to a 500-m raster and snapped that raster to the tiger range/buffer raster so that the cells perfectly lined up. Last, we calculated the Euclidean distance (m) from the centroid of every cell within the tiger range/buffer raster to the nearest road cell.

Relative MSAs

A meta-analysis developed by Benítez-López *et al.* (*25*) parameterized mathematical functions that related distance from infrastructure with abundances for mammals and birds. The meta-analysis was based on 49 studies, which included 33 mammal species (*25*). Torres *et al.* (*56*) proposed to use those mathematical functions with maps of proximity to infrastructure to (i) estimate the area of influence of infrastructure and (ii) predict relative MSA values as estimates of the relative impacts of roads on mammals and birds. Those authors applied that approach to Spain (*56*). Here, we extended the application of this approach to South and Southeast Asia and calculated relative MSA values to predict the impact of infrastructure on MSA of mammal species in areas near roads compared to areas far from roads (control areas) for regions relevant to tigers. We calculated the relative MSA for each cell (500 m resolution) by applying a logit transformation

$$\mathrm{MSA}_{(\mathrm{estimated})} = \frac{e^u}{1 + e^u}$$

where $\mathrm{MSA}_{(\mathrm{estimated})}$ is the predicted MSA at the observed distance from the road (see the "Proximity to roads" section). The parameter u is the log-transformed probability of the presence of a species at a certain distance x from the road

$$u = \ln\left(\frac{P_i}{1 - P_i}\right) = \beta_0 + \beta_1 x$$

where β_0 is the intercept for mammals (−0.607) and β_1 is the regression coefficient for the distance, which is 0.00083 m^{-1} for mammals. These coefficients were obtained from (*25*, *56*). The MSA values ranged from 0 (no individuals remaining) to 1 (no effect on species abundance). Last, we calculated statistics of MSA for different geographic units, including TCLs, Tx2 sites, protected areas, and IUCN occurrence categories. The coefficients used were based on mammal abundances relative to both transportation and impervious infrastructure. However, for our purposes, we focused only on roads as a conservative measure of MSA.

Future projections

To estimate the amount of roads that will be added in TCLs by 2050, we first calculated the country-specific ratio of current road length in TCLs and total country road length. Next, we multiplied that ratio by the country-specific estimates of total additional road length (km) for the year 2050, calculated in (*1*). These estimates were calculated by regressing country-specific, current total road length against four country-specific covariates, including land surface area, Organisation for Economic Co-operation and Development membership, population size, and gross domestic product (GDP) per capita (*1*). The authors then applied their regression models to obtain country-level estimates of the total additional road length for the year 2050, based on projections of GDP and population density from the Shared Socioeconomic Pathway scenarios (*57*).

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/6/18/eaaz9619/DC1

REFERENCES AND NOTES

1. J. R. Meijer, M. A. J. Huijbregts, K. C. G. J. Schotten, A. M. Schipper, Global patterns of current and future road infrastructure. *Environ. Res. Lett.* **13**, 064006 (2018).
2. W. F. Laurance, G. R. Clements, S. Sloan, C. S. O'Connell, N. D. Mueller, M. Goosem, O. Venter, D. P. Edwards, B. Phalan, A. Balmford, R. Van Der Ree, I. B. Arrea, A global strategy for road building. *Nature* **513**, 229–232 (2014).
3. W. F. Laurance, I. B. Arrea, Roads to riches or ruin? *Science* **358**, 442–444 (2017).
4. W. F. Laurance, M. Goosem, S. G. W. Laurance, Impacts of roads and linear clearings on tropical forests. *Trends Ecol. Evol.* **24**, 659–669 (2009).
5. G. R. Clements, A. J. Lynam, D. Gaveau, W. L. Yap, S. Lhota, M. Goosem, S. Laurance, W. F. Laurance, Where and how are roads endangering mammals in Southeast Asia's forests? *PLOS ONE* **12**, e115376 (2014).
6. P. L. Ibisch, M. T. Hoffmann, S. Kreft, G. Pe'Er, V. Kati, L. Biber-Freudenberger, D. A. DellaSala, M. M. Vale, P. R. Hobson, N. Selva, A global map of roadless areas and their conservation status. *Science* **354**, 1423–1427 (2016).
7. M. Di Marco, S. Ferrier, T. D. Harwood, A. J. Hoskins, J. E. M. Watson, Wilderness areas halve the extinction risk of terrestrial biodiversity. *Nature* **573**, 582–585 (2019).
8. M. S. Farhadinia, A. Maheshwari, M. A. Nawaz, H. Ambarlı, M. A. Gritsina, M. A. Koshkin, T. Rosen, A. Hinsley, D. W. Macdonald, Belt and Road Initiative may create new supplies for illegal wildlife trade in large carnivores. *Nat. Ecol. Evol.* **3**, 1267–1268 (2019).
9. A. P. Clevenger, J. Wierzchowski, B. Chruszcz, K. Gunson, GIS-generated, expert-based models for identifying wildlife habitat linkages and planning mitigation passages. *Conserv. Biol.* **16**, 503–514 (2002).
10. L. Fahrig, T. Rytwinski, Effects of roads on animal abundance: An empirical review and synthesis. *Ecol. Soc.* **14**, 21 (2009).
11. International Forum on Sustainable Infrastructure: Integrating Climate Resilience and Natural Capital into Transport Infrastructure Planning and Design (2017); http://www.gms-eoc.org/events/forum-on-sustainable-infrastructure.
12. ADB, Meeting Asia's infrastructure needs. Asian Development Bank. (2017); https://www.adb.org/publications/asia-infrastructure-needs.
13. A. M. Lechner, F. K. S. Chan, A. Campos-Arceiz, Biodiversity conservation should be a core value of China's Belt and Road Initiative. *Nat. Ecol. Evol.* **2**, 408–409 (2018).
14. A. C. Hughes, Understanding and minimizing environmental impacts of the Belt and Road Initiative. *Conserv. Biol.* **33**, 883–894 (2019).
15. R. Van Der Ree, D. J. Smith, C. Grilo, *Handbook of Road Ecology* (Wiley-Blackwell, 2015).
16. A. P. Clevenger, M. Barrueto, K. E. Gunson, F. M. Caryl, A. T. Ford, Context-dependent effects on spatial variation in deer-vehicle collisions. *Ecosphere* **6**, 1–20 (2015).
17. J. M. Goodrich, L. L. Kerley, E. N. Smirnov, D. G. Miquelle, L. McDonald, H. B. Quigley, M. G. Hornocker, T. McDonald, Survival rates and causes of mortality of Amur tigers on and near the Sikhote-Alin Biosphere Zapovednik. *J. Zool.* **276**, 323–329 (2008).
18. M. Linkie, G. Chapron, D. J. Martyr, J. Holden, N. Leader-Williams, Assessing the viability of tiger subpopulations in a fragmented landscape. *J. Appl. Ecol.* **43**, 576–586 (2006).
19. J. Goodrich, A. Lynam, D. Miquelle, H. Wibisono, K. Kawanishi, A. Pattanavibool, S. Htun, T. Tempa, J. Karki, Y. Jhala, U. Karanth, *Panthera tigris*. The IUCN Red List of Threatened Species e.T15955A50659951. (2015); http://dx.doi.org/10.2305/IUCN.UK.2015-2.RLTS.T15955A50659951.en.
20. P. Chanchani, B. R. Lamichhane, S. Malla, K. K. Maurya, A. Bista, R. Warrier, S. Nair, M. Almeida, R. Ravi, R. Sharma, M. Dhakal, S. P. Yadav, M. Thapa, S. R. Jnawali, N. M. B. Pradhan, N. Subedi, G. J. Thapa, H. Yadav, Y. V. Jhala, Q. Qureshi, J. Vattakaven, J. Borah, "Tigers of the Transboundary Terai Arc Landscape: Status, distribution and movement in the Terai of India and Nepal. National Tiger Conservation Authority, Government of India, and Department of National Park and Wildlife Conservation, Government of Nepal" (2014); http://assets.worldwildlife.org/publications/728/files/original/Final_Tigers_of_the_Transboundary_Terai_Arc_Landscape.pdf.
21. WWF International, Dalberg, The road ahead: Protecting tigers from Asia's infrastructure development boom. (2016); https://www.worldwildlife.org/publications/the-road-ahead-protecting-tigers-from-asia-s-infrastructure-development-boom.
22. World Bank, Global tiger recovery program (2010–2022) (English). Washington, DC: World Bank (2011); http://documents.worldbank.org/curated/en/874191468331048098/Global-tiger-recovery-program-2010-2022.
23. E. Sanderson, J. Forrest, C. Loucks, J. Ginsberg, E. Dinerstein, J. Seidensticker, P. Leimgruber, M. Songer, A. Heydlauff, T. O'Brien, G. Bryja, S. Klenzendorf, E. Wikramanayake, in *Tigers of the World*, R. Tilson, P. J. Nyhus, Eds. (Elsevier, 2010), pp. 143–161.
24. N. E. Clark, E. H. Boakes, P. J. K. McGowan, G. M. Mace, R. A. Fuller, Protected areas in South Asia Have Not Prevented Habitat Loss: A study using historical models of land-use change. *PLOS ONE* **8**, e65298 (2013).
25. A. Benítez-López, R. Alkemade, P. A. Verweij, The impacts of roads and other infrastructure on mammal and bird populations: A meta-analysis. *Biol. Conserv.* **143**, 1307–1316 (2010).
26. J. Walston, J. G. Robinson, E. L. Bennett, U. Breitenmoser, G. A. B. da Fonseca, J. Goodrich, M. Gumal, L. Hunter, A. Johnson, K. U. Karanth, N. Leader-Williams, K. Mackinnon, D. Miquelle, A. Pattanavibool, C. Poole, A. Rabinowitz, J. L. D. Smith, E. J. Stokes, S. N. Stuart, C. Vongkhamheng, H. Wibisono, Bringing the tiger back from the brink-the six percent solution. *PLoS Biol.* **8**, e1000485 (2010).
27. E. Wikramanayake, E. Dinerstein, J. Seidensticker, S. Lumpkin, B. Pandav, M. Shrestha, H. Mishra, J. Ballou, A. J. T. Johnsingh, I. Chestin, S. Sunarto, P. Thinley, K. Thapa, G. Jiang, S. Elagupillay, H. Kafley, N. M. B. Pradhan, K. Jigme, S. Teak, P. Cutter, M. A. Aziz, U. Than,

A landscape-based conservation strategy to double the wild tiger population. *Conserv. Lett.* **4**, 219–227 (2011).
28. A. Harihar, P. Chanchani, J. Borah, R. J. Crouthers, Y. Darman, T. N. E. Gray, S. Mohamad, B. M. Rawson, M. D. Rayan, J. L. Roberts, R. Steinmetz, S. Sunarto, F. A. Widodo, M. Anwar, S. R. Bhatta, J. P. P. Chakravarthi, Y. Chang, G. Congdon, C. Dave, S. Dey, B. Durairaj, P. Fomenko, H. Guleria, M. Gupta, G. Gurung, B. Ittira, J. Jena, A. Kostyria, K. Kumar, V. Kumar, P. Lhendup, P. Liu, S. Malla, K. Maurya, V. Moktan, N. D. N. Van, K. Parakkasi, R. Phoonjampa, W. Phumanee, A. K. Singh, C. Stengel, S. A. Subba, K. Thapa, T. C. Thomas, C. Wong, M. Baltzer, D. Ghose, S. Worah, J. Vattakaven, Recovery planning towards doubling wild tiger Panthera tigris numbers: Detailing 18 recovery sites from across the range. *PLOS ONE* **13**, e0207114 (2018).
29. M. Barua, Mobilizing metaphors: The popular use of keystone, flagship and umbrella species concepts. *Biodivers. Conserv.* **20**, 1427–1440 (2011).
30. S. Gubbi, H. C. Poornesha, in *Handbook of Road Ecology*, R. Van Der Ree, D. J. Smith, C. Grilo, Eds. (Wiley-Blackwell, 2015), pp. 317–321.
31. S. Gubbi, H. C. Poornesha, M. D. Madhusudan, Impact of vehicular traffic on the use of highway edges by large mammals in a South Indian wildlife reserve. *Curr. Sci.* **102**, 1047–1051 (2012).
32. S. Kunju, Wildlife road kills on the rise in India, shows official data (2017); https://focusingonwildlife.com/news/wildlife-road-kills-on-the-rise-in-india-shows-official-data/.
33. P. Thatte, A. Joshi, S. Vaidyanathan, E. Landguth, U. Ramakrishnan, Maintaining tiger connectivity and minimizing extinction into the next century: Insights from landscape genetics and spatially-explicit simulations. *Biol. Conserv.* **218**, 181–191 (2018).
34. M. S. Luskin, W. R. Albert, M. W. Tobler, Sumatran tiger survival threatened by deforestation despite increasing densities in parks. *Nat. Commun.* **8**, 1783 (2017).
35. A. Benítez-López, R. Alkemade, A. M. Schipper, D. J. Ingram, P. A. Verweij, J. A. J. Eikelboom, M. A. J. Huijbregts, The impact of hunting on tropical mammal and bird populations. *Science* **356**, 180–183 (2017).
36. W. F. Laurance, Tropical logging and human invasions. *Conserv. Biol.* **15**, 4–5 (2001).
37. A. W. Coffin, From roadkill to road ecology: A review of the ecological effects of roads. *J. Transp. Geogr.* **15**, 396–406 (2007).
38. L. L. Kerley, J. M. Goodrich, D. G. Miquelle, E. N. Smirnov, H. B. Quigley, M. G. Hornocker, Effects of roads and human disturbance on Amur tigers. *Conserv. Biol.* **16**, 97–108 (2002).
39. M. Hebblewhite, D. G. Miquelle, H. Robinson, D. G. Pikunov, Y. M. Dunishenko, V. V. Aramilev, I. G. Nikolaev, G. P. Salkina, I. V. Seryodkin, V. V. Gaponov, M. N. Litvinov, A. V. Kostyria, P. V. Fomenko, A. A. Murzin, Including biotic interactions with ungulate prey and humans improves habitat conservation modeling for endangered Amur tigers in the Russian Far East. *Biol. Conserv.* **178**, 50–64 (2014).
40. A. R. Joshi, E. Dinerstein, E. Wikramanayake, M. L. Anderson, D. Olson, B. S. Jones, J. Seidensticker, S. Lumpkin, M. C. Hansen, N. C. Sizer, C. L. Davis, S. Palminteri, N. R. Hahn, Tracking changes and preventing loss in critical tiger habitat. *Sci. Adv.* **2**, e1501675 (2016).
41. F. Ascensão, L. Fahrig, A. P. Clevenger, R. T. Corlett, J. A. G. Jaeger, W. F. Laurance, H. M. Pereira, Environmental challenges for the Belt and Road Initiative. *Nat. Sustain.* **1**, 206–209 (2018).
42. J. D. Quintero, R. Roca, A. Morgan, A. Mathur, X. Shi, Smart green infrastructure in tiger range countries: A multilevel approach (Washington, DC, 2010); https://openknowledge.worldbank.org/handle/10986/27751.
43. W. F. Laurance, A. Peletier-Jellema, B. Geenen, H. Koster, P. Verweij, P. Van Dijck, T. E. Lovejoy, J. Schleicher, M. Van Kuijk, Reducing the global environmental impacts of rapid infrastructure expansion. *Curr. Biol.* **25**, R249–R262 (2015).
44. M. Maron, A. Gordon, B. G. Mackey, H. P. Possingham, J. E. M. Watson, Stop misuse of biodiversity offsets. *Nature* **523**, 401–403 (2015).
45. J. Jaeger, L. Fahrig, K. Ewald, in *Proceedings of the 2005 International Conference on Ecology and Transportation*, C. Irwin, P. Garrett, K. McDermott, Eds. (Center for Transportation and the Environment, 2005), pp. 151–163.
46. T. N. E. Gray, R. Crouthers, K. Ramesh, J. Vattakaven, J. Borah, M. K. S. Pasha, T. Lim, C. Phan, R. Singh, B. Long, S. Chapman, O. Keo, M. Baltzer, A framework for assessing readiness for tiger *Panthera* tigris reintroduction: A case study from eastern Cambodia. *Biodivers. Conserv.* **26**, 2383–2399 (2017).
47. M. D. Barnes, I. D. Craigie, L. B. Harrison, J. Geldmann, B. Collen, S. Whitmee, A. Balmford, N. D. Burgess, T. Brooks, M. Hockings, S. Woodley, Wildlife population trends in protected areas predicted by national socio-economic metrics and body size. *Nat. Commun.* **7**, 12747 (2016).
48. D. Tilman, R. M. May, C. L. Lehman, M. A. Nowak, Habitat Destruction and the Extinction Debt. *Nature* **371**, 65–66 (1994).
49. K. U. Karanth, J. D. Nichols, N. S. Kumar, W. A. Link, J. E. Hines, Tigers and their prey: Predicting carnivore densities from prey abundance. *Proc. Natl. Acad. Sci. U.S.A.* **101**, 4854–4858 (2004).
50. C. S. Miller, M. Hebblewhite, Y. K. Petrunenko, I. V. Seryodkin, J. M. Goodrich, D. G. Miquelle, Amur tiger (*Panthera tigris altaica*) energetic requirements: Implications for conserving wild tigers. *Biol. Conserv.* **170**, 120–129 (2014).
51. M. Linkie, I. A. Haidir, A. Nugroho, Y. Dinata, Conserving tigers Panthera tigris in selectively logged Sumatran forests. *Biol. Conserv.* **141**, 2410–2415 (2008).
52. T. Wang, J. Andrew Royle, J. L. D. Smith, L. Zou, X. Lü, T. Li, H. Yang, Z. Li, R. Feng, Y. Bian, L. Feng, J. Ge, Living on the edge: Opportunities for Amur tiger recovery in China. *Biol. Conserv.* **217**, 269–279 (2018).
53. G. Jiang, H. Sun, J. Lang, L. Yang, C. Li, A. Lyet, B. Long, D. G. Miquelle, C. Zhang, S. Aramilev, J. Ma, M. Zhang, Effects of environmental and anthropogenic drivers on Amur tiger distribution in northeastern China. *Ecol. Res.* **29**, 801–813 (2014).
54. A. J. Lynam, N. Tantipisanuh, W. Chutipong, D. Ngoprasert, M. C. Baker, P. Cutter, G. Gale, S. Kitamura, R. Steinmetz, R. Sukmasuang, S. Thunhikorn, Comparative sensitivity to environmental variation and human disturbance of Asian tapirs (*Tapirus indicus*) and other wild ungulates in Thailand. *Integr. Zool.* **7**, 389–399 (2012).
55. R Core Team, R: A Language and Environment for Statistical Computing (2019); https://www.r-project.org/.
56. A. Torres, J. A. G. Jaeger, J. C. Alonso, Assessing large-scale wildlife responses to human infrastructure development. *Proc. Natl. Acad. Sci. U.S.A.* **113**, 8472–8477 (2016).
57. K. Riahi, D. P. van Vuuren, E. Kriegler, J. Edmonds, B. C. O'Neill, S. Fujimori, N. Bauer, K. Calvin, R. Dellink, O. Fricko, W. Lutz, A. Popp, J. C. Cuaresma, S. KC, M. Leimbach, L. Jiang, T. Kram, S. Rao, J. Emmerling, K. Ebi, T. Hasegawa, P. Havlik, F. Humpenöder, L. A. Da Silva, S. Smith, E. Stehfest, V. Bosetti, J. Eom, D. Gernaat, T. Masui, J. Rogelj, J. Strefler, L. Drouet, V. Krey, G. Luderer, M. Harmsen, K. Takahashi, L. Baumstark, J. C. Doelman, M. Kainuma, Z. Klimont, G. Marangoni, H. Lotze-Campen, M. Obersteiner, A. Tabeau, M. Tavoni, The Shared Socioeconomic Pathways and their energy, land use, and greenhouse gas emissions implications: An overview. *Glob. Environ. Chang.* **42**, 153–168 (2017).

Acknowledgments

Funding: This work was supported by the NSF Idaho EPSCoR Program IIA-1301792. A.F. was funded, in part, by the Canada Research Chairs program. **Author contributions:** N.C., A.K., T.E., J.B., and A.F. developed the research idea and study design. N.C., A.K., and T.E. conducted all analyses. N.C., A.K., T.E., J.B., and A.F. drafted the manuscript. **Competing interests:** The authors declare that they have no competing interests. **Data and materials availability:** All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials. Additional data related to this paper may be requested from the authors. The geospatial data that support the findings of this study are available in figshare with the identifier 10.6084/m9.figshare.11632935.

Submitted 24 October 2019
Accepted 7 February 2020
Published 29 April 2020
10.1126/sciadv.aaz9619

Citation: N. Carter, A. Killion, T. Easter, J. Brandt, A. Ford, Road development in Asia: Assessing the range-wide risks to tigers. *Sci. Adv.* **6**, eaaz9619 (2020).