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RESEARCH ARTICLE

Integrating direct anthropogenic disturbances and habitat connectivity to guide the restoration of the Amur tiger population in a newly established national park in China

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Abstract

Context China initiated its national parks in 2016 for safeguarding biodiversity and ecosystem integrity. The newly established Northeast Tiger and Leopard National Park (NTLNP) is essential for saving endangered large cats, but its adequacy for supporting apex predators and their prey remains largely unassessed.

Objectives We evaluated NTLNP's effectiveness in providing habitat and connectivity for the Amur tiger (*Panthera tigris altaica*) and sika deer (*Cervus nippon*). Furthermore, we examined the adequacy of the park's current zoning and quantified direct anthropogenic disturbances in conservation-critical areas to identify management challenges.

Methods We developed a multiscale species distribution model with Bayesian additive regression trees (BART) to simulate habitat distribution for the Amur tiger and sika deer, and employed a circuit theory model to identify potential corridors. Additionally, large-scale monitoring data were used to assess disturbances spatial patterns within core habitat patches and dispersal corridors of tigers.

Results Our results found that tiger and sika deer had highly overlapping habitats (> 50%) concentrated along the China-Russia border. The BART model revealed 4 core tiger habitats (3555.61 km^2) and 28 core sika deer habitats (3468.41 km^2), with 4 tiger corridors and 48 sika deer corridors. The core conservation zones of the park encompassed 81.89% of core tiger habitats and 91.62% of potential tiger corridors, but 58.46% of these habitats and 55.03% of the corridors were affected by ubiquitous presence of humans, free-ranging cattle, and domestic dogs.

Conclusions This work highlighted that while NTLNP's zoning effectively covers tiger habitats and corridors, these areas are heavily impacted by anthropogenic disturbances, posing a significant management challenge. The findings provide important references and tools for designing and managing national parks in China and worldwide.

Keywords Amur tiger · Multiscale modelling · Habitat suitability · Corridor · Zoning designations · Anthropogenic disturbances

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Introduction

Forest loss and habitat fragmentation caused by natural and anthropogenic factors, as well as dwindling prey resources, are major drivers of the decline or extinction of large carnivores globally and the most serious threats to biodiversity conservation (Ripple et al. 2014; Joshi et al. 2016; Fardila et al. 2017). In response, the establishment of protected areas, including national parks, has been recognized as an effective conservation measure (Chowdhury et al. 2022). Since 2010, significant progress has been made in expanding global protected areas, with coverage now reaching approximately 42% of the Earth's terrestrial surface (Li et al. 2024). However, while the expansion of protected areas is a critical step, the quality of these areas has yet to be fully realized. Most analyses of protected area effectiveness emphasize metrics such as total area and representativeness, often overlooking the crucial role of habitat quality in supporting wildlife populations, assuming that the protected areas inherently provide high-quality habitats (Sun et al. 2024). In reality, the heterogeneity of natural landscapes within these areas, coupled with human-induced changes in landscape patterns, may weaken functional connectivity and disrupt habitat use patterns (Watson et al. 2016; Brennan et al. 2022). Therefore, evaluating the conservation effectiveness of these areas for endangered species and addressing challenges in current protected area management are pressing issues that demand urgent attention.

Given these global challenges, China initiated its national parks in 2016 to safeguard biodiversity and the integrity of natural ecosystems. One notable example of such efforts is the Northeast Tiger and Leopard National Park (NTLNP) in China, which was established to protect the critically endangered Amur tiger (*Panthera tigris altaica*) and the sympatric Amur leopard (*P. pardus orientalis*). Approximately a decade ago, the Amur tiger population was estimated at fewer than 600 individuals, fragmented into several isolated populations due to prey depletion, habitat degradation, and poaching (Hebblewhite et al. 2014; Wang et al. 2018). Compared to tiger populations in Russia, Amur tigers in China experienced more severe anthropogenic pressures. Fortunately, since the inception of the NTLNP, habitat protections and disturbance controls have been strengthened, leading to a gradual increase in the small Amur tiger population along the China–Russia border (Wang et al. 2016; Qi et al. 2021). This situation highlights both the potential for successful species recovery and the need for further detailed research on habitat management within protected areas like the NTLNP.

For the Amur tiger, as is the case for many large felids, its geographical distribution, dispersal and habitat selection are largely determined by its selected prey (Petrunenko et al. 2016; Wang et al. 2018). The key to the expansion of the Amur tiger population to inland China lies in the population increase of its main prey, sika deer (*Cervus nippon*), as well as wild boar (*Sus scrofa*) and Siberian roe deer (*Capreolus pygargus*); however, the increase in these ungulates is dependent on the restoration of forest ecosystems (Wang et al. 2016). Over the years, conservation efforts have resulted in elevated population densities and broader distributions of Siberian roe deer and wild boar. However, the population of sika deer, which is considered one of the important prey species for tigers (Sugimoto et al. 2016; Yang et al. 2018), has been severely reduced due to free-ranging cattle grazing (Wang et al. 2018; Feng et al. 2021a, 2021b). Although wild boars are widely distributed in the habitat of the Amur tiger and account for a significant proportion of the tiger's diet (Kerley et al. 2015), tigers typically require at least one medium- to large-sized cervid species in their habitat (Hayward et al. 2012; Miquelle et al. 2018). Given the scarcity of red deer (*Cervus canadensis*) in the Amur tiger's Chinese habitat, sika deer play a crucial role in filling this ecological niche. Tiger occupancy is strongly positively associated with sika deer abundance and vegetation cover (Wang et al. 2018). The current distribution range of tigers along the China–Russia border significantly overlaps with that of sika deer (Wang et al. 2024). The confinement of the sika deer population to borders is a crucial factor limiting the dispersal and establishment of tigers in China. To some extent, recoveries in sika deer numbers also help tigers. Therefore, simultaneously analysing the habitat suitabilities of the Amur tiger and its main prey is highly important for conservation efforts.

Moreover, as a top predator, Amur tigers have large home ranges, low population densities, and high energy requirements; furthermore, they are highly dependent on large, continuous habitat patches (Goodrich et al. 2010). However, due to human disturbances and habitat degradation, suitable habitats for tigers in China are usually small and isolated, hindering them from supporting a large and sustainable tiger population (Wang et al. 2018; 2023). Habitat corridors have proven effective for facilitating the migration and dispersal of large felids between fragmented habitat patches (Thatte et al. 2018; Ashrafzadeh et al. 2020; Makwana et al. 2023). Therefore, identifying and protecting the core habitats and potential corridors in the NTLNP is critical for maintaining tiger population persistence and delineating core conservation zones. In addition, the lack of a clear view of these challenges can lead to insufficient investment in conservation implementation and compromise the effectiveness of the park in delivering the desired conservation outcomes (Wang et al. 2021). Therefore, anthropogenic disturbances within habitat patches and near corridors should also be assessed to understand potential challenges to targeted conservation.

Like many protected areas in China, the NTLNP faces significant challenges in balancing ecological conservation with local livelihoods. Villagers living in and around the NTLNP often depend on natural resources within the park, which can negatively impact wildlife conservation efforts (She et al. 2023). To address these conflicts, mixed zoning designations have been implemented, dividing the NTLNP into core zones with strict prohibitions on human activities and control zones where a wider range of development activities are allowed (Geneletti & van Duren 2008; Xu et al. 2016). Despite these efforts, effective zoning design and rule enforcement remain challenging, as many studies have highlighted difficulties in managing these zones effectively (Xu et al. 2016; Wang et al. 2021). Given these challenges, it is crucial to assess the effectiveness of the NTLNP's zoning scheme, focusing on predicted suitable habitats and dispersal corridors to improve conservation outcomes.

To address these issues, our study aimed to predict the potential habitats and dispersal corridors for Amur tigers and thus optimize conservation strategies for greater efficacy. We developed a multiscale species distribution model (SDM) to estimate the habitat suitabilities for both Amur tigers and their key prey, sika deer. Species–habitat relationships are scale dependent (Wiens 1989; Levin 1992), and optimizing the scale significantly enhances model predictive power compared with nonoptimized, single-scale models (McGarigal et al. 2016; Bellamy et al. 2020). Previous research has emphasized the importance of multiscale optimization for reliable predictions of carnivore habitats (Vergara et al. 2016; Ashrafzadeh et al. 2020). Additionally, we identified key connectivity corridors and restoration areas likely to enhance habitat connectivity for both tigers and sika deer via circuit theory modelling. We also evaluated anthropogenic disturbances across core habitat patches and corridors and evaluated the effectiveness of the current zoning scheme to provide recommendations for enhancing connectivity between habitat patches. Our findings not only provide valuable guidance for refining conservation policies and enhancing connectivity in the NTLNP but also offer insights that could contribute to the broader improvement and effectiveness of the national park system in China.

Methods

Study area

The Northeast Tiger and Leopard National Park of China is located at the junction of Jilin and Heilongjiang Provinces and borders the Land of Leopards National Park in southwestern Primorye Province, Russia. The park spans 14,926 km^2, with geographic coordinates ranging from 42°31′06″ to 44°14′49″N and 129°5′0″ to 131°18′48″E (Fig. 1). The climate is temperate continental monsoonal, with annual precipitation of 450–750 mm and an average temperature of 5 °C. The NTLNP is rich in natural resources and dominated by forests that cover more than 90% of the area and provide habitat for a variety of wildlife. The main prey species of tigers in the NTLNP are wild boar, sika deer, Siberian roe deer, and domesticated species, such as cows and dogs (Kerley et al. 2015). In addition to the Amur tiger, there are other large carnivores in the park, such as the Amur leopard (*P. pardus orientalis*), Asiatic black bear (*Ursus thibetanus*) and brown bear (*Ursus arctos*) (Jiang et al. 2014). Furthermore, the area has been subjected to cattle grazing, ginseng (*Panax ginseng C. A. Meyer*) planting, frog farming, and edible fern collection for decades (Feng et al. 2021a, b).

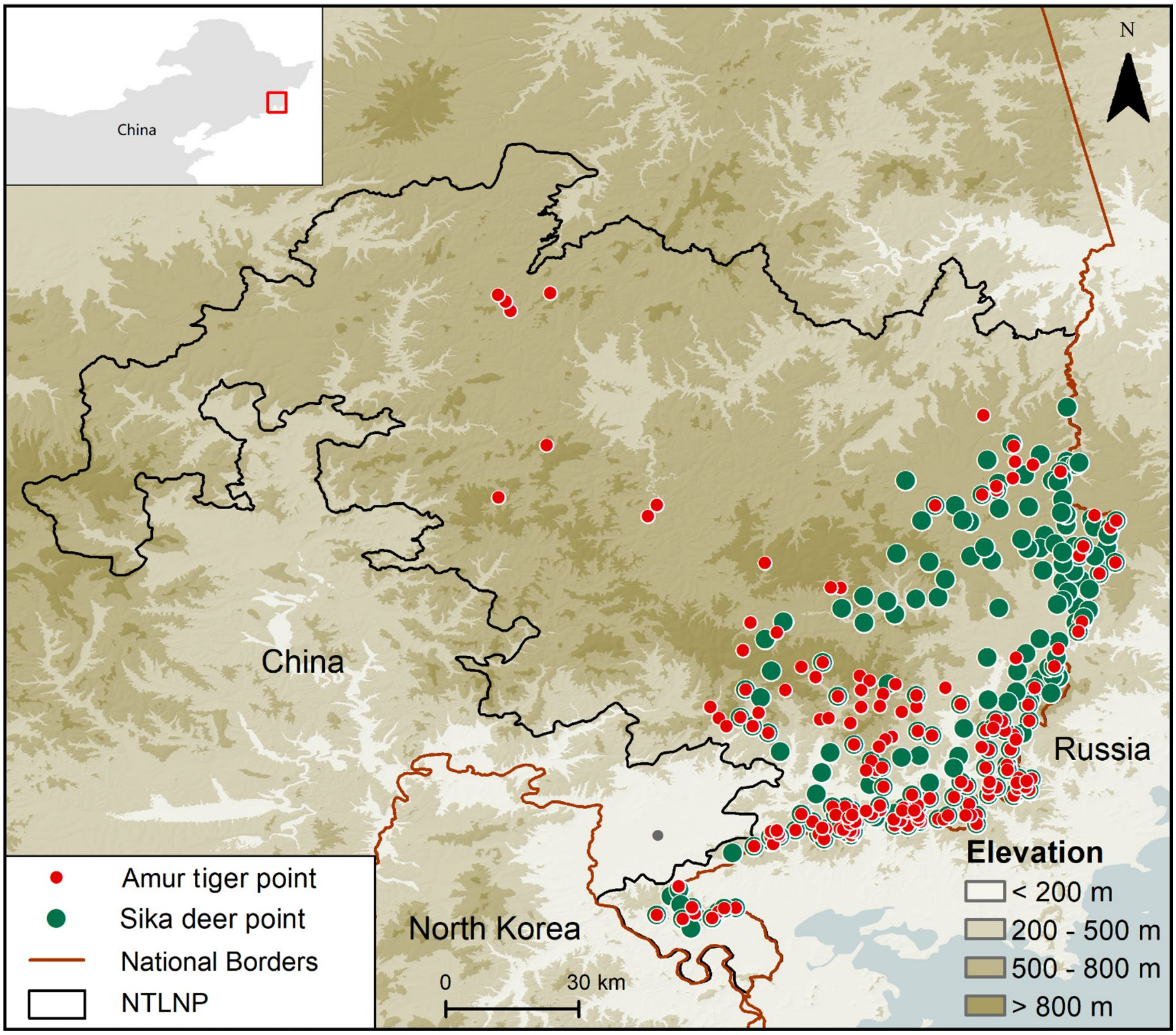

Fig. 1 Overview of the study area and occurrence locations of the Amur tiger (N = 176) and sika deer (N = 204) in the NTLNP (2012–2018)

Occurrence datasets

Our analysis is based on datasets of Amur tiger and sika deer occurrence locations. The tiger dataset comprises 137 occurrence locations determined by 484 camera traps (2012–2018) (Wang et al. 2017; 2018; 2020), 92 occurrence locations determined by tiger scats and footprints (2012–2016) (Dou et al. 2016; Yang et al. 2018), and 35 occurrence locations determined by cattle depredation data, which was provided by the Wildlife Depredation Compensation Office, Forestry Department, Jilin Province (2012–2014) (Wang et al. 2016). To reduce spatial autocorrelation, a buffer analysis was used to filter the occurrence locations to only a single point within 1 km of other points, resulting in 176 occurrence locations for habitat modelling (Fig. 1). The sika deer dataset was derived from 484 camera traps. Finally, 204 occurrence locations were retained for habitat modelling (Fig. 1).

Predictor variables

Seven a priori variables of four types were used for habitat modelling on the basis of relevant research on tiger (Khosravi et al. 2019; Rather et al. 2020; Carter et al. 2024) and sika deer (Luo et al. 2024); these variables included topography, vegetation, anthropogenic impact and energy landscapes. The topographic variables included elevation, slope, and the topographic position index (TPI). The vegetation variable included canopy height (referred to as canopy). For anthropogenic impacts, we used the distance to settlements and roads. Energy landscapes were determined by spatially explicit projections that map energetic travel costs onto the landscape (Shepard et al. 2013; Carter et al. 2024). Energy landscapes were computed via the R package "enerscape" (Berti et al. 2022), which models the energy cost of movement patterns (Pontzer 2016) via the digital elevation model of NTLNP from the NASADEM dataset at 30 m resolution. We computed energy landscapes for female tigers and sika deer by using average body masses of 150 kg (Miller et al. 2014) and 70 kg (Baskin and Danell 2003), respectively. We focused on females, as they serve as the reproductive unit and are crucial for long-term range expansion (this variable is hereafter referred to as enerscape).

Since species may select environmental factors at different spatial scales, multiscale optimization is an effective method for determining the appropriate scale. (McGarigal et al. 2016). For the Amur tiger, we considered the response at seven different scales and resampled the resolution to 0.5 km for the small scale; 1, 2 and 3 km for the medium scale; and 5, 10 and 20 km for the large scale. The mean values were calculated for each resolution; subsequently, these raster datasets were refined to a standardized resolution of 500 m via bilinear interpolation. These scales correspond to areas ranging from 0.25 to 400 km^2, which cover the average home range of approximately 400 km^2 for females (Hernandez-Blanco et al. 2015). For sika deer, employing the same methodology, we considered the response across four scales: a small scale of 0.5 km and medium scales of 1, 2 and 3 km. These scales correspond to areas ranging from 0.25 to 9 km^2, covering the common home range of sika deer (Dhakal et al. 2023).

Habitat suitability modelling

We used Bayesian additive regression trees (BART) implemented with the R package "embarcadero" (Carlson 2020) to model the distribution of species. BART is a method defined by a prior probability distribution and the likelihood of returning occurrence predictions that quantify the uncertainty around the projections (Carlson 2020). BART has similar or better performance than the majority of more popular machine learning techniques (Thompson et al. 2023). First, we randomly sampled pseudoabsences with the same number of occurrences outside the buffer radius of occurrence in the study area (10 km for tiger and 2 km for sika deer, estimated on the basis of home ranges), avoiding spatial overlap with the presence data (Descombes et al. 2022). Second, we ran a binary BART classification model at each of the spatial scales described above to identify the optimal scale for tiger and sika deer. This scale was determined by evaluating how the ranking of the contribution and importance of variable factors in the model varied across the different scales. Third, we ran the BART model with variable set reduction via an automated variable selection function to identify the main subset of predictors (Chipman et al. 2010). We ran final models separately for each species via default BART model settings (1000 posterior draws with a burn-in of 100 draws) and hyperparameters (power = 2.0, base = 0.95). The automated stepwise reduction algorithm with 10 trees was used to eliminate the variables with the lowest importance and obtain the model with the lowest root mean square error (RMSE).

Model performance was assessed by the area under the receiver operating characteristic curve (AUC), which measures overall discrimination capacity and threshold-dependent metrics and assesses how well the model distinguishes presence from absence. All the analyses were performed in R software version 4.3.3.

Resistance to movement surface

We converted the BART-derived habitat suitability maps into resistance surfaces via multiple transformations (Cao et al. 2020). The higher the habitat suitability index is, the lower the resistance to species migration. The data are rescaled via Eq. (1):

$$hsi\_std = \frac{Max(hsi) - hs}{Max(hsi) - Min(hsi)} \tag{1}$$

where *hsi* is the original habitat suitability index extracted for the study area and where *hsi_std* refers to the standardized habitat suitability index.

The resistance surface was obtained by applying negative exponential transformations (Keeley et al. 2017) via Eq. (2):

$$R = 100 - 99 \times \frac{1 - e^{-C\times(hsi\_std)}}{1 - e^{-c}} \tag{2}$$

where R is the resistance value and parameter c determines the curve shape of the function (here, $c=4$) (Cao et al. 2020; Keeley et al. 2017).

After transformation, the R value ranged from 1 to 100 (the lowest to the highest resistance values), and only areas with low habitat suitability received high resistance values.

Landscape connectivity and corridor network simulation

On the basis of the predictions of the habitat suitability models, we converted the projected probabilities of occurrence for the distributions into a binary outcome (suitable/unsuitable) according to the threshold that maximizes the true skill statistic (TSS) for each species (Liu et al. 2013). We further defined suitable patches ≥ 200 km^2 as core habitats for Amur tigers on the basis of their minimum home range size (Hernandez-Blanco et al. 2015) and those ≥ 10 km^2 for sika deer on the basis of the average home range size of stable populations (Dhakal et al. 2023).

After the core habitats and resistance values were determined, the *Build Network and Linkages* Tool in Linkage Mapper was used to create the ecological corridors between core patches according to the minimum resistance models for tiger and sika deer(Adriaensen et al. 2003). The cost-weighted distance (CWD), Euclidean distance (EuD), and least cost path (LCP) were calculated to quantify the linkages between core patches (Dutta et al. 2016). The higher the ratio of CWD:LCP is, the greater the difficulty in moving between core patches (Li et al. 2020).

To identify key areas to protect and enhance as wildlife corridors, key bottlenecks or pinch points were identified in the resulting corridors via the *Circuitscape* and *Pinchpoint Mapper* tools in Linkage Mapper (Li et al. 2020). Areas with high accumulated current density were identified as key pinch points, which significantly affect the connectivity in the network (McRae et al. 2008; Cao et al. 2020). We also calculated the centrality of core habitat patches via *Centrality Mapper* in Linkage Mapper to identify the importance of individual core habitats and linkages in maintaining connectivity within the landscape (Carroll et al. 2012).

Evaluating the management challenges and protection status

To analyse habitat overlap between the Amur tiger and the sika deer, the total areas of suitable habitats and core habitat patches for both species, including shared spaces, were determined. Additionally, the extent to which the tiger's core habitat patches and the dispersal corridors between them are covered by the core conservation zones of the NTLNP was assessed.

Furthermore, we evaluated the challenges for zoning management of the NTLNP by assessing the spatial distribution of anthropogenic disturbances in the core habitat patches and areas around the dispersal corridors. We calculated the relative abundance index (RAI) for different types of anthropogenic disturbances on the basis of data collected annually from April to November from 484 wildlife monitoring camera traps (2012–2018) and 73 disturbance monitoring camera traps (2017–2023). We then used the *Kernel Density* tool in ArcGIS 10.8.1 with a bandwidth of 3000 m (Wang et al. 2021) to separately evaluate the distributions of the top three most frequent disturbances, livestock, dogs, and humans, as well as their sum. We further classified the disturbed areas in the tiger core habitat patches and the 10 km buffer zone around the corridors (which covers most of the currents around the corridors and is the radius of the tiger's home range) into high- and low-intensity disturbance areas by using the mean density value of each disturbance as the threshold. The challenges of managing human disturbances were assessed by calculating the proportions of habitat areas affected by high- and low-intensity anthropogenic disturbances.

Results

Scale optimization

The results revealed that the AUC values of the binary BART classification model at each scale were above 0.9, indicating that the model predictions were relatively reliable and could be used for scale selection.

After the contributions of seven environmental variables across seven scales for the Amur tiger and four scales for the sika deer were ranked, the optimal scale for each environmental variable was determined (to retain more details, a finer scale was selected when the scales were of the same order) (Fig. 2, Table S1). As predicted, given the relatively large home ranges of tigers, large-scale habitat use was best for TPI and enerscape. For sika deer, medium-scale habitat use was best for TPI, canopy, settlement and enerscape. The selected optimal scale variables presented correlation coefficients below 0.6, indicating that there was no strong correlation between them (Fig. S1).

Multiscale habitat prediction

The optimal scale variables with the lowest RMSE selected through the automated procedure were ranked in order of importance, and only the slope variable for the Amur tiger was excluded. The BART model showed adequate predictive performance according to the AUC and TSS metrics (for Amur tiger, AUC = 0.973, TSS = 0.872; for sika deer, AUC = 0.914, TSS = 0.683; see Fig. S2 for the model diagnostics). The predicted map indicated that the suitable habitats for sika deer were more fragmented than those for Amur tiger. The largest patch of both species was located mainly in the southeastern region of the NTLNP (Fig. 3).

The RMSE model results identified elevation, settlement, and enerscape as the main factors affecting tiger habitat suitability, with relative importance values of 0.181, 0.169, and 0.168, respectively (Fig. 3b; Table S2). The response curves indicated that tiger habitat suitability was negatively correlated with elevation and positively correlated with distance from settlements. Tigers preferred areas with low elevations (< 400 m) and high distances from settlements (> 10 km) (Fig. S3a). Additionally, suitability was negatively correlated with landscape energy when it was less than 10 kcal but increased as energy exceeded 10 kcal, reaching high suitability after 14 kcal (Fig. S3a). Moreover, tiger habitat suitability was positively correlated with the TPI and canopy height but negatively correlated with the distance from roads (Fig. S3a).

For sika deer, the main factors affecting habitat suitability were canopy, elevation, and TPI, with relative importance values of 0.152, 0.150, and 0.144, respectively (Fig. 3d; Table S2). The response curves revealed that habitat suitability was positively correlated with canopy height and TPI, with a preference for ridge areas with relatively high forest canopies. Suitability was negatively correlated with elevation,

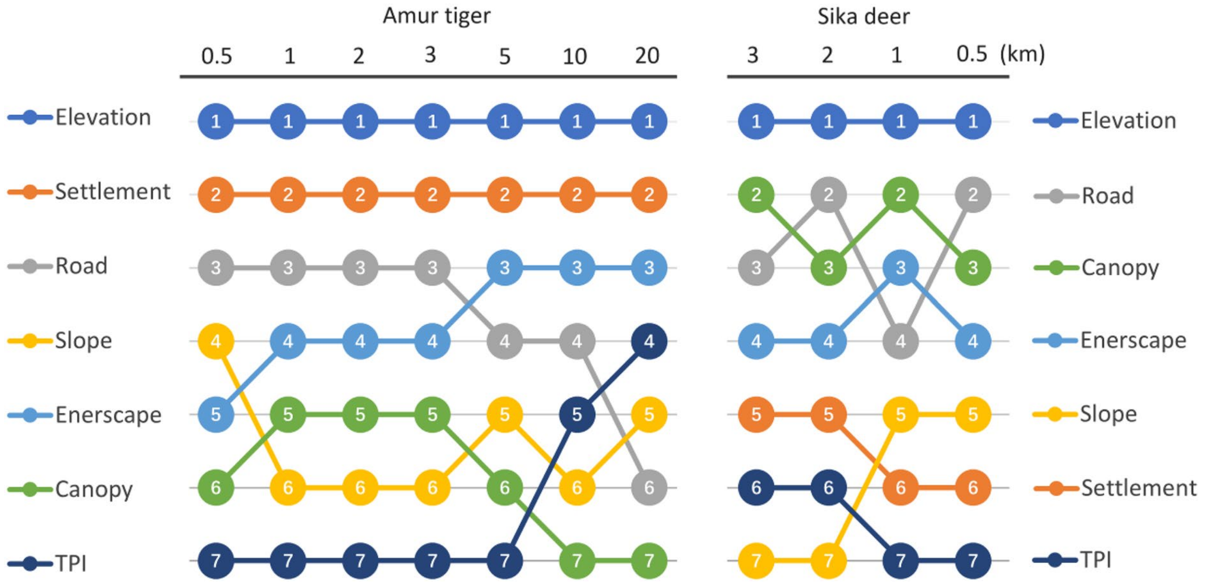

Fig. 2 Ranking of the seven variables according to their percentage contribution to the seven scales of the Amur tiger and the four scales of sika deer

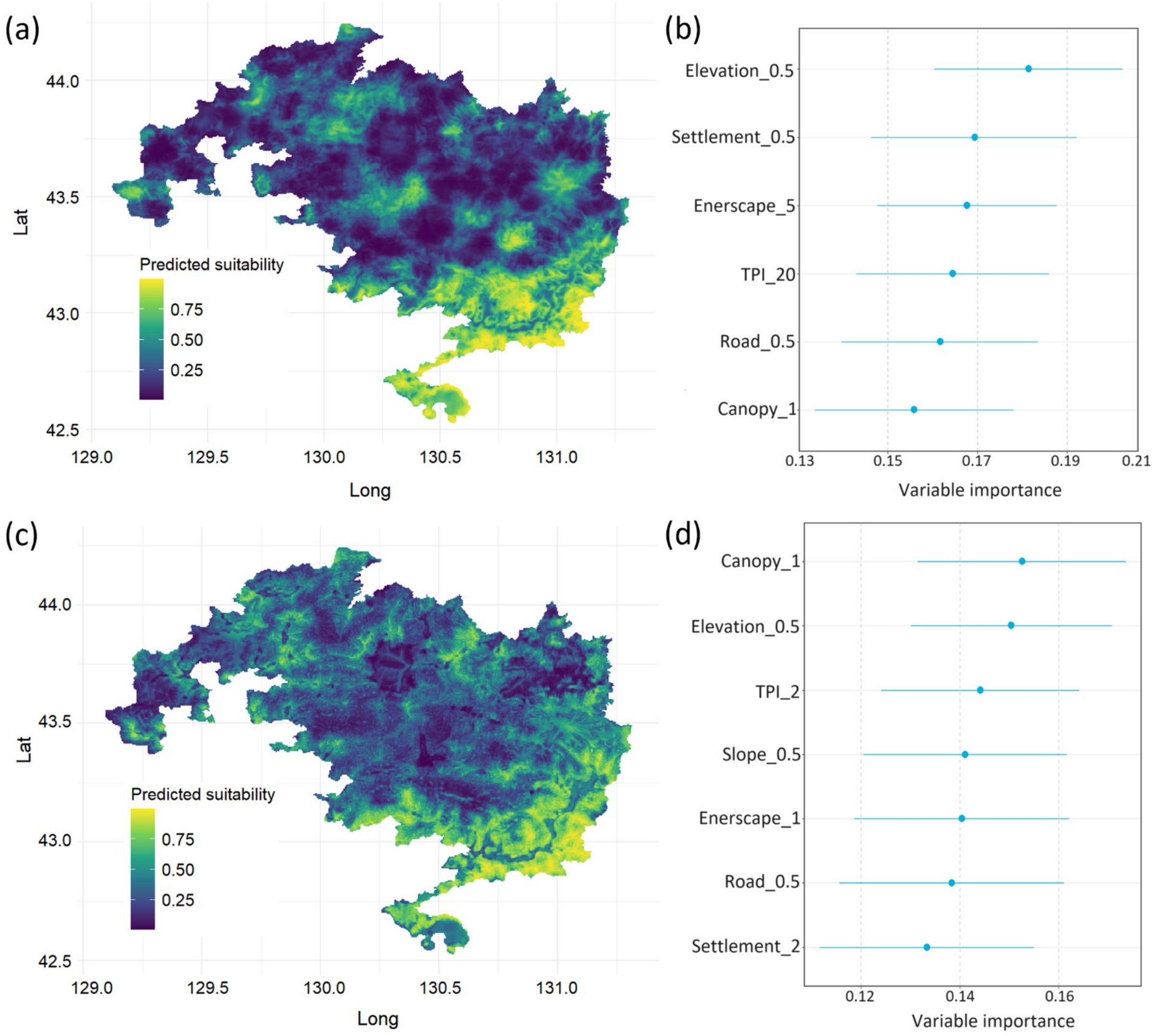

Fig. 3 Model-predicted habitat suitability and importance of environmental variables for the Amur tiger (**a**, **b**) and sika deer (**c**, **d**)

with lower suitability at higher elevations (> 700 m) (Fig. S3b). In addition, overall, sika deer habitat suitability was greater in areas with lower slopes and landscape energy and was negatively correlated with distance from roads. The distance from settlements exhibited a unimodal pattern, with a preference for areas 5–10 km from settlements (Fig. S3b).

Estimates of habitat

On the basis of the thresholds of predicted suitability that maximize the TSSs for the binary outcomes (suitable/unsuitable), which were 0.434 for tigers and 0.519 for sika deer, we estimated 4647.12, 3809.87 and 2579.19 km^2 for the tiger habitat, sika deer habitat, and their shared potential habitat, respectively (Fig. 4a, Table 1). Furthermore, four core habitat patches for tigers were identified, totalling 3555.61 km^2 and covering 23.8% of the NTLNP (Fig. 4b, Table S3); 28 core habitat patches for sika deer were identified, totalling 3468.41 km^2 and covering 23.2% of the NTLNP (Fig. 4b, Table S4). The shared core habitat area for both species was 2012.76 km^2 (Table 1), comprising 55.6% and 67.7% of the tiger and sika deer core habitats, respectively, and 13.48% of the NTLNP. This area was located primarily in the

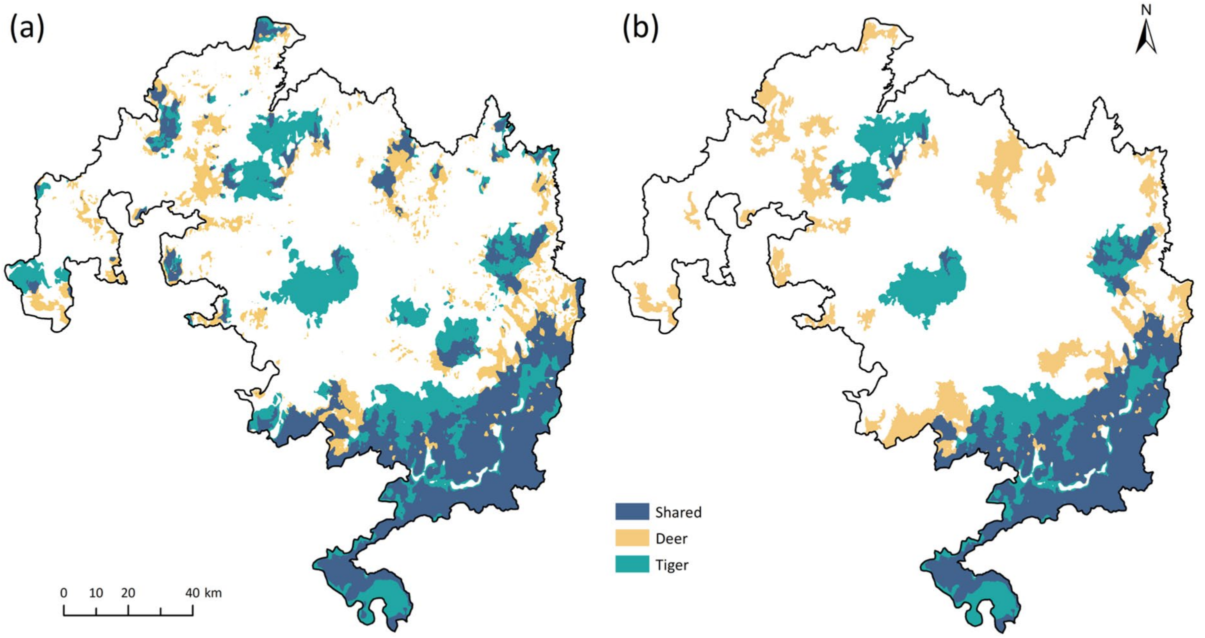

Fig. 4 Thresholded habitat predictions. All habitats (**a**) and core habitat patches (**b**) for the Amur tiger and sika deer

Table 1 Estimates of potential and core habitats (in km^2) for the two species and their shared habitats

Species	Potential habitat	Core habitat
Tiger	4647.12	3555.61
Deer	3809.87	3468.41
Shared	2579.19	2012.76

southeastern part of the park, near the China-Russia border (Fig. 4b).

Core habitat connectivity

The landscape analysis identified 4 LCPs among the 4 core habitat patches for the Amur tiger, with an average length of 29.14 km (range: 7.46–57.14 km; Table S5). L1 and L3 had the highest CWD:LCP ratio and CWD:EucD ratio, indicating the highest movement costs (Fig. 5a; Table S5). The cumulative current density map revealed numerous pinch points in potential corridors, including L2 and L4, which could be pivotal corridors for tiger dispersal (Fig. 5a). Additionally, patch C3 had the highest centrality and played a crucial role in connecting other patches (Fig. 5a; Table S3).

For sika deer, the model identified 48 LCPs among the 28 core habitat patches, with an average length of 16.02 km (range: 0.2–45.67 km; Table S6). L1–L11, L13 and L14 presented the highest CWD:LCP ratios and CWD:EucD ratios, indicating that they presented the highest cost of movement (Fig. 5b; Table S6). The cumulative current density map also highlighted numerous pinch points, with key corridors for sika deer dispersal, including L2, L4, L5, L19, L29, L38, and L40 (Fig. 5b). Additionally, patches C1, C3, and C17 had greater centrality and were key to connecting to other patches (Fig. 5b; Table S4).

Efficacy of zoning designation

The core conservation zones occupied half of the NTLNP and were well designed to encompass the core habitat patches of the Amur tiger. The core habitat patches within the core conservation zones accounted for 81.89% (2911.86 km^2) of the total core habitats (Fig. 6). The core habitat C4 was the best covered habitat, with 94.77% of its area protected by the core zones. The largest core habitat, C1, covered 85.10% of the total area. Habitats C2 and C3 were covered at rates of 73.34% and 56.41%, respectively.

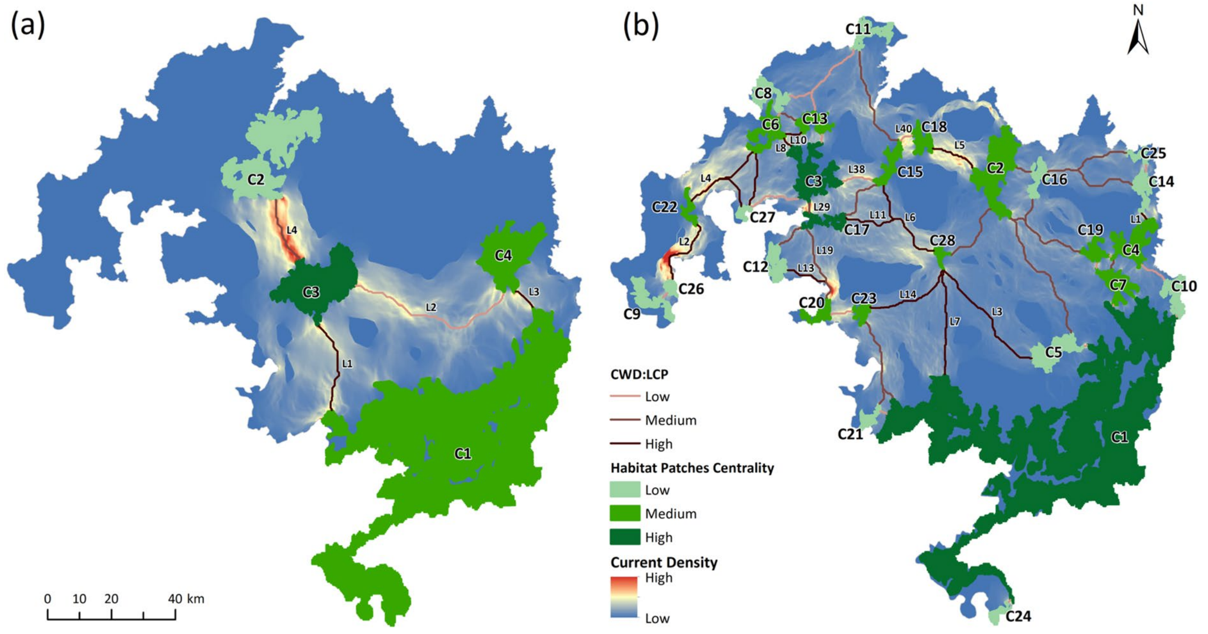

Fig. 5 Habitat connectivity between core habitats and pinch points identified across potential corridors for Amur tiger (**a**) and sika deer (**b**). The habitat patch centrality level and quality of corridors (CWD: LCP) were divided on the basis of the Jenks natural breaks classification method. The black numbers indicate the IDs of the core habitats and potential corridors

The core zones of the NTLNP also provided substantial coverage of potential corridors, with 91.62% of the length of the LCPs within the zones (Fig. 6). Three of the four potential corridors were fully covered; only L4, which showed dispersal pinch points distributed in and around the uncovered section, was not entirely included. To ensure the connection between core habitats C3 and C2, extending the core conservation zones eastwards in this area is necessary (Fig. 6).

Management challenges of disturbances

Anthropogenic disturbances are widespread in the NTLNP. The three most frequent anthropogenic disturbances, livestock, dogs and humans, have different distributions. The habitat area affected by livestock disturbance accounts for approximately 34.67% of the core habitat patches and 27.15% of the potential corridor areas in the NTLNP. Core habitat C3 and path L1 were the most severely disturbed by livestock, with 43.54% and 46.87% of the area disturbed, respectively, and habitat C3 was subjected predominantly to high-intensity disturbances (Fig. 7a). The habitat area affected by dog-driven disturbance accounts for approximately 45.25% of the core habitat patches and 38.19% of the potential corridor areas. Additionally, over 60% of path L1 was affected by dog disturbances, with almost equal amounts of low- and high-intensity disturbances (Fig. 7b). Among the three types of disturbance, human disturbance was the most severe, with 52.81% and 54.41% of the core habitat and corridor areas disturbed, respectively. In core habitat C4, more than 90% of the area was disturbed, as was nearly 70% of path L1, of which high-intensity disturbance dominated (Fig. 7c). Overall, a total of 58.46% of core habitats and 55.03% of corridor areas were affected by anthropogenic disturbances. C4 and L1 were more severely disturbed, with 92.28% and 69.54% of the area disturbed, respectively (Fig. 7d).

Discussion

Scale-dependent habitat selection

We harnessed large-scale Amur tiger and sika deer occurrence data to uncover the ecological requirements of both species and provide baseline information to inform potential future restoration of the tiger

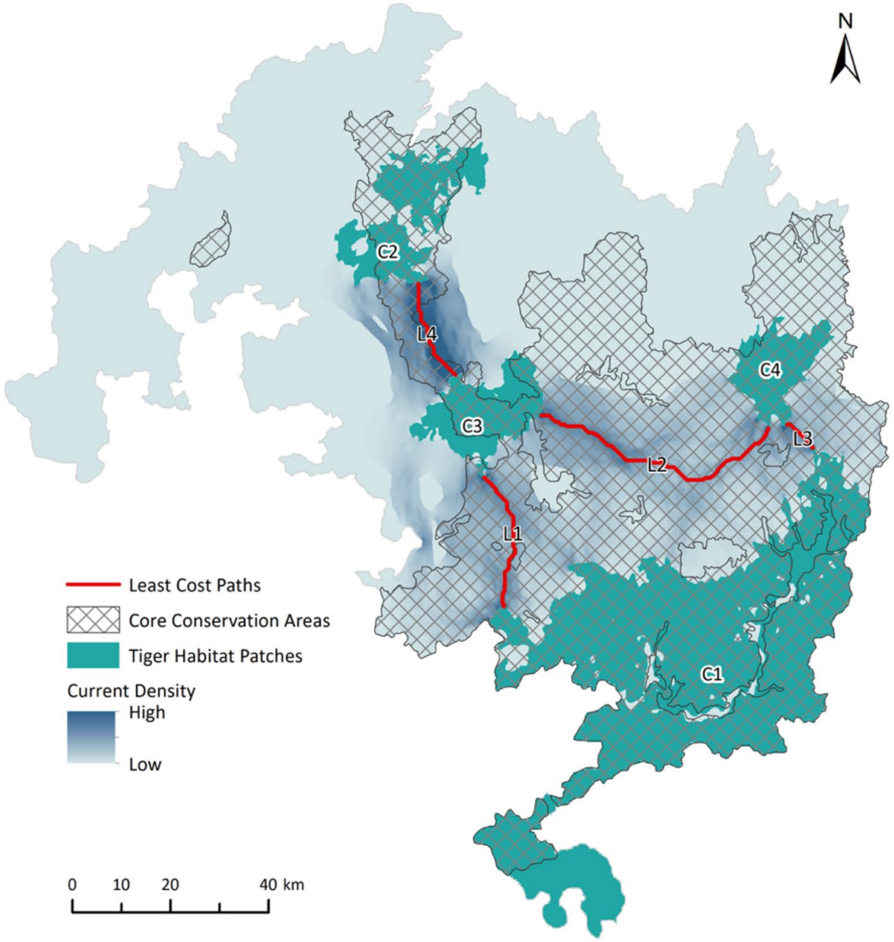

Fig. 6 Distribution of core habitats and potential corridors of the Amur tiger and core conservation zones in the NTLNP

population in the NTLNP. Our results indicated a high overlap in the potential geospatial distribution of tiger and sika deer (Fig. 4); furthermore, the ecological drivers of tiger occurrence are largely the same as those driving sika deer occurrence (Fig. 3). This situation highlights strong niche identity, as observed in other predator−prey contexts (Farhadinia et al. 2015; Shahsavarzadeh et al. 2023), indicating that the settlement of tigers cannot be separated from the high abundance of large ungulate wildlife populations (Karanth et al. 2004; Miquelle et al. 2010). Our study demonstrated that both Amur tiger and sika deer habitat suitability are affected by variables at different spatial scales. The Amur tiger responded to most of the habitat variables at broader scales. This finding is in general agreement with the findings of other carnivore species studies at multiple scales (Khosravi et al. 2019; Rather et al. 2020), thus highlighting the importance of considering ecological scales in studies of species distributions (McGarigal et al. 2016; Macdonald et al. 2019).

The relationships between tiger suitability and the settlement distance variable at the small scale reflects the tendency of tigers to avoid anthropogenic pressure in disturbed and human-dominated landscapes (Rather et al. 2020). However, owing to their broader plasticity and adaptability (Kaji et al. 2022), sika deer were found at edges, though they avoid human disturbances at a broader spatial scale. Furthermore, compared to sika deer, TPI and energy landscapes related to energy expenditure influenced the distribution of tigers at larger scales (Fig. 3). This may be because tigers need to utilize their energy efficiently within their large home ranges and need to rely on specific terrain features to improve hunting and movement efficiency (Goodrich et al. 2010). This finding confirms the findings of previous studies showing that large carnivores respond to habitat variables at

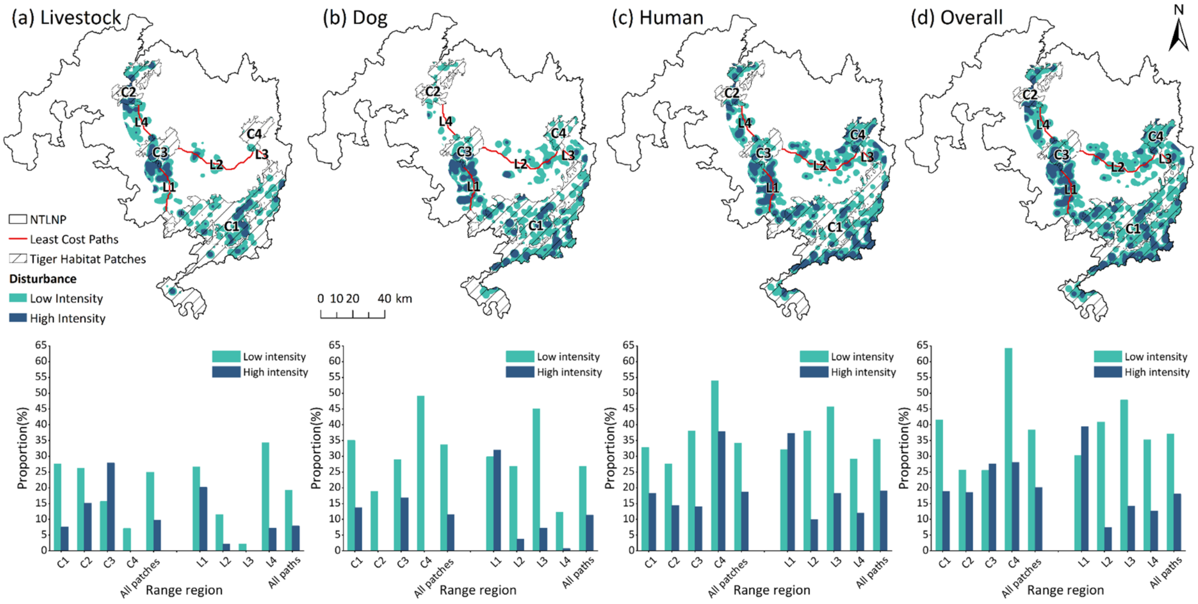

Fig. 7 Spatial distributions of areas affected by different levels of **a** livestock disturbance, **b** dog disturbance, **c** human disturbance and **d** overall anthropogenic disturbance across core habitats and potential corridor areas of the Amur tiger

broader spatial scales (Khosravi et al. 2019; Rather et al. 2020).

Notably, at the medium scale, canopy height was the most important factor affecting the potential distribution of sika deer. Sika deer occurrence was positively correlated with canopy height. Canopy height is a key indicator of forest ecosystem health and function; thus, this finding suggests that sika deer require forests that are contiguous, ecologically stable, and have rich canopies at broader spatial scales. In the past two decades, multiple natural forest protection projects have been carried out in important wildlife distribution areas in Jilin and Heilongjiang Provinces to reduce wood production, protect public welfare forests, and cultivate forest resources. Consequently, these measures have contributed to the recovery of sika deer, which are the main prey in the region (Kerley et al. 2015). Their careful management will offer a promising foundation for reviving tigers in the NTLNP.

Core habitats and connectivity

We confirmed the tiger records in all four predicted core habitats; these patches were subjected to long-term camera-trapping monitoring to capture the demographic dynamics of the tigers (Wang et al. 2018). For example, in patch C2, we observed the settlement of a breeding female tiger, indicating that the tiger population is expanding into the interior of the NTLNP. The persistence of large carnivores in small habitat patches relies highly on the immigration of individuals from large patches to surrounding small patches, which serve as sources and sinks, respectively (Lamb et al. 2020; Bertassello et al. 2021). Among these patches, C1 acts as the source, whereas patch C3, located at the critical junction connecting patches C1 and C2, has the highest centrality and serves as the sink, indicating its possible role as a stepping stone for tigers. Our results from the connectivity analysis identified potential paths for tiger movement between different habitat patches; moreover, all of these paths were within 1000 km of the dispersal distance of tigers (Carroll & Miquelle 2006). However, the actual usage of these paths by tigers is still poorly understood, especially for those with evident pinch points. Therefore, we recommend that future tiger conservation in the NTLNP focus on the dispersal and migration of individuals between patches. For example, incorporating telemetry studies with satellite collars to track specific tigers will greatly enhance our understanding of functional connectivity and the effectiveness of predicted corridors.

The model revealed that suitable habitats for sika deer are predominantly located in the mountainous areas southeast of the park and are relatively limited and fragmented. Multiple LCPs connect these fragmented habitats, but most paths are quite long, especially those linking large patches and their surrounding satellite patches with interior patches. Currently, sika deer activity has been observed only in large patches and surrounding areas; thus, it is unclear whether sika deer can utilize potential dispersal paths to disperse further into the park interior. Several narrow patches in the central region serve as stepping stones for sika deer dispersing towards the northwest of the park. Enhancing the suitability and size of patches C2, C16, C23, and C28 to maintain stable sika deer populations remains a significant challenge. In particular, the location of the C28 patch is also a stepping stone for the Amur tiger. Maintaining a stable prey population in this area is crucial for the successful dispersal of Amur tigers.

Studies have shown that maintaining a minimum effective population of 15–20 adult female Amur tigers requires a minimum of 6000–8000 km^2 of suitable habitat with high connectivity (Hernandez-Blanco et al. 2015). The core habitat predicted in the NTLNP and Land of Leopard National Park in Russia totals approximately 6000 km^2 (Wang et al. 2023), which is sufficient to host the minimum population of Amur tigers. These results underscore the importance of transboundary conservation. However, the tiger-suitable habitat patches are fragmented in the NTLNP. The keys to conservation lie in ensuring the quality of suitable habitats, minimizing disturbances in habitats, enhancing landscape connectivity, and forming highly connected suitable habitats.

Zoning effectiveness and management challenges

Notably, although the core protected areas in the NTLNP zoning designation cover most important Amur tiger habitat patches and paths, protective actions outside the core protected areas may be needed to complement conservation efforts. We found that the core protected areas inadequately cover patches C2, C3, and path L4. Monitoring data indicate that the C2 region is a hotspot for red deer, an important supplementary and alternative prey species to sika deer for tiger population recovery. In addition, patch C3 is important as a stepping stone for the spread of the tiger and sika deer populations, as it has large areas of mixed coniferous and mixed deciduous forests, which are preferred by tigers However, L4, as the only corridor connecting patches C2 and C3, has evident pinch points. These areas require increased protection to enhance habitat connectivity within the park and support the long-term survival of tigers. Accommodating these priority areas is critical for tiger population recovery and dispersal when optimizing core protected areas. However, it is essential to acknowledge the presence of villages around these areas. Therefore, long-term park development planning must carefully consider the costs of land acquisition and the dependence of local communities on natural resources to balance potential benefits and costs.

Anthropogenic disturbances in the identified suitable habitat patches and paths are widespread. The disturbance caused by livestock is severe in patches C2, C3, and paths L1 and L4, as cattle grazing, a mainstay of local industry, has been increasing over the past 30 years (Wang et al. 2016). The pressure caused by free-ranging cattle on sympatric wild herbivores such as sika deer is particularly acute (Feng et al. 2021a, b; Roberts et al. 2021). Grazing can have a cascading effect throughout the food chain by altering the abundance of prey on which the Amur tiger depends (Schieltz and Rubenstein 2016). This effect limits the further development of the tiger population (J. Feng et al. 2021a, b; Feng et al. 2021a, b). Currently, grazing is a major driver of global biodiversity loss (Selinske et al. 2020; Wang et al. 2024). In particular, excessive cattle grazing disturbs wild cervids by depleting understorey vegetation (Wang et al. 2017; Li et al. 2022), and a decline in key ungulate prey species density threatens the survival of large carnivores (Sandom et al. 2018). Therefore, rational management of cattle grazing in the NTLNP is urgently needed. Grazing is a significant local industry, and transitioning the industry will take time. Thus, before complete grazing cessation, we recommend implementing a gradual reduction plan for grazing in key wildlife dispersal areas such as paths L1, L4, and patch C3; establishing compensation standards for cessation; and strengthening supervision and enforcement to maximize the chances of survival for the Amur tigers and their prey.

In addition, dogs have extensively infiltrated the corridors and source patch C1. Dogs can act as bridges for virus transmission through indirect contact with wildlife or predation. For example, canine distemper virus (CDV) has caused a significant decline in carnivore populations such as Serengeti lions (*P. leo*) (Weckworth et al. 2020), Ethiopian wolves (*Canis simensis*) (Gordon et al. 2015) and tigers in Sikhote-Alin (Gilbert et al. 2015; Miquelle et al. 2015). Dogs play an important role in virus transmission. The consequences of CDV spread to the Amur tiger population could be devastating (Wang et al. 2023). To reduce the risk of disease transmission from dogs to wildlife, we suggest that the local governments implement policies aimed at gradually controlling dogs, if not completely prohibiting all dogs in the core range of the tigers.

Human activities are ubiquitous and abundant across core habitats and connectivity corridors. Patch C4, located in Heilongjiang Province, is the most severely affected patch. The presence of numerous settlements, extensive arable land, and construction areas within Heilongjiang Province significantly limits the utilization of patch C4 by tigers and hinders their dispersal into the interior of the park through path L3. Overall, anthropogenic disturbances in tiger-suitable habitats are concerning, particularly in critical dispersal areas such as path L1 and patch C4, which are severely affected. Future work should focus on optimizing management policies and enhancing active patrol management and monitoring to reduce the dependence of local livelihoods on natural resources. Given the ecological impacts of activities such as grazing, ginseng cultivation, and Chinese brown frog (*Rana chensinensis*) farming, stricter regulation and targeted management are needed to mitigate habitat degradation in key tiger areas. At the same time, payment for ecosystem services (PES) represents a viable approach to reconciling conservation and local development. By providing incentives for reduced resource use or habitat protection, PES can help ease human pressures on tiger habitats while supporting community livelihoods (Tuanmu et al. 2016; Wang et al. 2021). Integrating such incentive-based measures into future policy frameworks, alongside improved enforcement and land-use planning, may offer a more balanced and effective pathway toward long-term conservation goals.

These findings are particularly relevant in the context of China's ongoing efforts to expand and optimize its national park system. By 2021, China officially established five national parks, including NTLNP, with a total protected area of 230,000 km^2. Additionally, 44 national park candidate areas have been identified, covering nearly 900,000 km^2. China aims to complete the spatial layout of its national park system by 2035. Despite significant progress in biodiversity conservation, challenges remain in assessing habitat quality for endangered species and managing anthropogenic disturbances. Our study offers critical insights and practical guidance for the design and management of national parks and protected areas in China and globally, aiming to enhance biodiversity conservation efforts.

Conclusions

In this study, the multiscale BART model results reveal the differences in habitat selection scales between the Amur tiger and its primary prey, sika deer. However, the findings also indicate a high overlap in the potential geospatial distribution of the two species. The identified core habitats align with the high occurrence probabilities observed in the field, and the potentially suitable predicted habitats correspond to points of tiger inland dispersal, indicating the reliability of the model predictions. This study demonstrates that multiscale modelling provides an effective means for optimizing conservation management planning. By applying the circuit theory model, we identified four potential dispersal corridors, considering length and width, that align with the movement patterns of tigers. These corridors provide a reference for conservation efforts in the areas most likely to be utilized by tigers. Additionally, by evaluating the effectiveness of park zoning designations and human disturbances in tiger habitat patches and dispersal corridors, we found that the zoning designations of the NTLNP perform well in covering critical tiger habitats and corridors. However, we discovered that the identified habitats and corridors, even those within core conservation zones, are widely subject to anthropogenic disturbances and associated fear and disease threats. This situation highlights significant challenges for future park management. We recommend that future zoning plans consider the inclusion of regions crucial for habitat connectivity, as well as potential habitats within the core conservation zones of the NTLNP; furthermore, regulatory efforts should be strengthened.

Author contributions TW, DW and YS: conceived the ideas and designed the study. DW and YS: were involved in the development of the model. DW: contributed to writing the original draft and visualization. JLDS and JG: advised on the analyses. All authors contributed critically to the drafts and gave final approval for publication.

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Data availability The data that support the findings of this study are available in the supplementary material of this article.

Declarations

Conflict of interest The authors declare that none of the authors have competing financial or non-financial interests.

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