



Spatial population distribution dynamics of big cats and ungulates with seasonal and disturbance changes in temperate natural forest

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ABSTRACT

Wildlife conservation and management in human-dominated landscapes are major concerns for wildlife ecologists and managers. The dynamics of human disturbance, combined with seasonal limitations in the availability of nutritious foods, may restrict wildlife population growth and recovery. However, understanding how large mammal species adjust their population distribution in forest habitats with seasonal changes in food and disturbances requires a deeper and more extensive analysis. In this study, we found that three ungulate species, roe deer (*Capreolus pygargus*), sika deer (*Cervus nippon*), and wild boar (*Sus scrofa*), employ robust, conservative, and flexible distribution strategies, respectively, to adapt to the effects of seasonal changes and human disturbances. Moreover, croplands, villages, and grazing have some negative effects on the distribution of roe deer and sika deer, while wild boar can be highly abundant near human land use. Additionally, roe deer, sika deer, and wild boar are also affected by the abundance of shrub species they consume. During the cold season, the populations of the Amur tiger (*Panthera tigris altaica*) and Amur leopard (*P. pardus orientalis*) were primarily located near roads and dense forests, respectively. In the warm season, the distribution of both big cats was influenced by prey abundance, and Amur tigers also avoided grazing livestock. Nevertheless, the negative effects of human land use on Amur tigers and wild boars increased during the warm season, which was attributed to more frequent human activities during that time. Consequently, it is crucial to implement season-specific habitat management, particularly by regulating human disturbances during the warm season, in order to promote the recovery and expansion of populations of big cats and ungulates.

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1. Introduction

The impact of human disturbance on wildlife has been a longstanding concern in conservation biology (Carney and Sydeman, 1999; Coetzee and Chown, 2016; Cook et al., 2013). As human society rapidly develops, the demand for resources continuously expands, posing a serious threat to wildlife survival (Kadoya et al., 2022; Symes et al., 2018), and resulting in a massive loss of wildlife diversity (Magurran and Dornelas, 2010; Martínez-Ramos et al., 2016). In the current context of escalating biodiversity loss, understanding the distribution patterns and drivers of wildlife abundance is crucial for effective conservation and management activities (Ogutu et al., 2011; Wilson et al., 2017). Existing human disturbance continues to affect wildlife, and there is an urgent need for more in-depth research on how wildlife adjusts its population abundance distribution in human-dominated habitats.

Seasonal changes play a significant role in influencing the population distribution of animals (van Beest and Milner, 2013). This is because the transition between seasons correlates with changes in the availability of food and nutritional resources within the environment (Fryxell and Sinclair, 1988; Pereira et al., 2014). Additionally, the intensity of disturbance from human activity also varies with the season (Farmer et al., 2022). Human activities, such as livestock grazing, planting, and foraging, predominantly occur during the warm season, while they tend to decrease during the cold snowy season. Thus, we expect that wildlife distribution may vary according to human disturbances in combination with more traditional seasonal impacts.

The Amur tiger (*Panthera tigris altaica*) and Amur leopard (*P. pardus orientalis*) are two endangered large carnivores inhabiting forest landscapes (Miquelle et al., 2011; Stein et al., 2020). These felids are highly vulnerable to the impact of human disturbances and were once on the brink of extinction in China due to habitat loss (Miquelle et al., 2010; Yang et al., 1998), which also severely impacted their main ungulate prey (Jiang et al., 2015; Sheng et al., 1992; Tian et al., 2009). Although the harvesting of natural forests has been halted (Jiang et al., 2017), the presence of agricultural towns and human disturbances create a human-dominated forest landscape (Li et al., 2009). This continues to affect the population distribution of these forest-dwelling large mammals (She et al., 2023; Wang et al., 2017; Wang et al., 2018). However, little attention has been paid to the effects of seasonal changes related to the intensity of human activity and the availability of food resources on their population distribution.

In this study, we utilized three years of camera trap data and incorporated multiple habitat factors and human disturbances to evaluate the spatial distribution of Amur tigers, leopards, and ungulate populations in both warm and cold seasons. Specifically, we analyzed seasonal variations in the effects of human land use on the population distribution of each large mammal species. In this

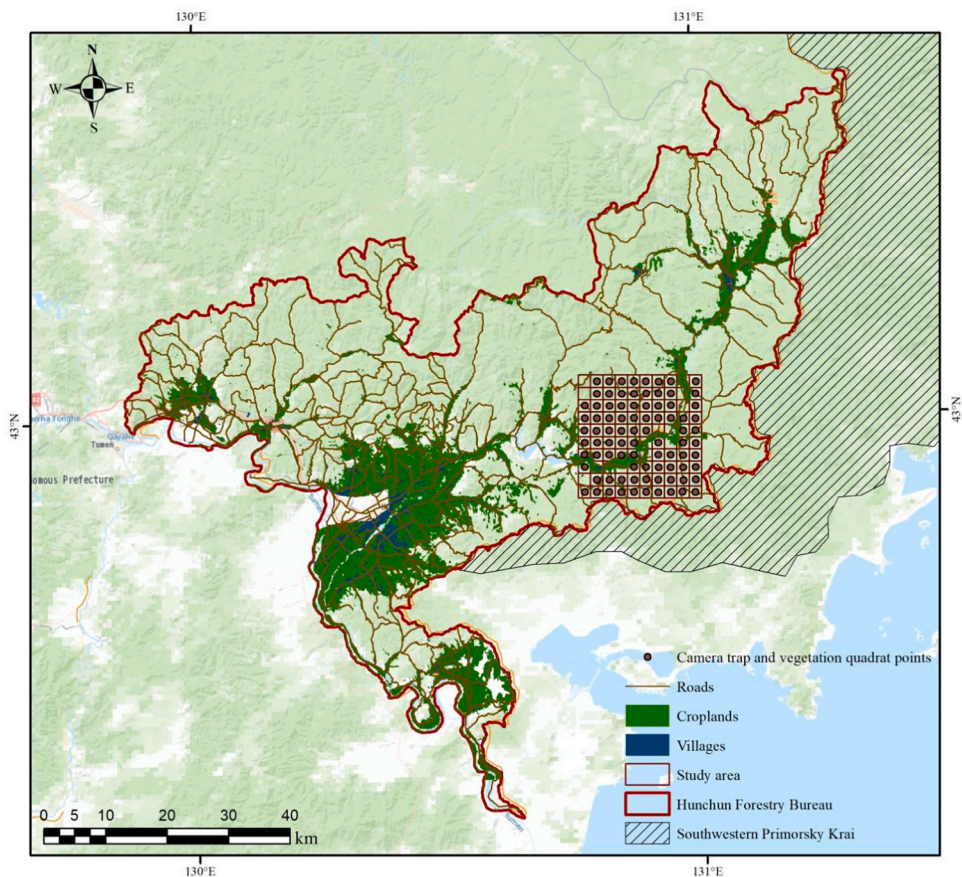


Fig. 1. The distribution of camera traps, vegetation quadrats and human land uses (roads, croplands and villages) in study area.

study, we hypothesized that in human-dominated landscapes: 1) the population distribution of ungulates, i.e., roe deer, sika deer, and wild boar, and the respective driving factors may exhibit seasonal variation, but the extent of these changes varies among species, 2) the factors that affect the population distribution of big cats, i.e., Amur tigers and Amur leopards, change during the warm and cold seasons, and 3) the effects of human land uses on the population abundance distribution of big cats and ungulates are greater in the warm season due to increased intensity of human activity at that time.

2. Methods

2.1. Study area

This study was conducted in the Hunchun Forestry Bureau in Jilin Province, China (Fig. 1), which borders Southwestern Primorsky Krai in Russia to the east and North Korea to the southwest. This area serves as the most vital habitat for Amur tigers and Amur leopards in China (Li et al., 2017; Vitkalova et al., 2018). The area has an average annual temperature of 5.65 °C and an average precipitation of 617.9 mm per year. The landscape is characterized by mountains, with elevations ranging from 5 to 1477 m.

The study site, located in the middle of Hunchun Forestry Bureau, spans an area of 400 km² and is characterized by abundant wildlife and plant resources (Qi and Zhang, 2004). The prominent ungulate prey species in this area include roe deer (*Capreolus pygargus*), wild boar (*Sus scrofa*), and sika deer (*Cervus nippon*). The dominant vegetation types in the region consist of oak forest and deciduous forest, while mixed forest, Korean-pine forest, larch forest, birch forest, and spruce-fir forest are less prevalent. Due to previous agricultural development and logging activities, the study area is characterized by a significant presence of cropland patches and a well-preserved network of forest roads (Fig. 1). Additionally, there are six villages situated alongside the main road (Fig. 1). During the cold, snowy season, human activity is limited and decreased. As temperatures rise seasonally, activities such as cattle grazing, crop cultivation, and the collection of wild vegetables and pine nuts gradually emerge.

2.2. Data collection

The study site design is a 20 × 20 km square divided into a grid system consisting of 100 squares, with each grid measuring 2 × 2 km (Fig. 1). To monitor wildlife, we employed a systematic sampling approach by installing one camera trap at the center of each grid. However, certain areas such as croplands and villages were excluded from camera placement, resulting in a total of 86 designated camera points. Monitoring activities were carried out continuously over a three-year period, from November 2019 to October 2022. Camera maintenance, including the replacement of memory cards and batteries, took place twice a year, specifically in April-May and October-November. We divided the camera dataset into two seasons: warm season (April-October, with an average high temperature of 21 °C and an average low temperature of 10 °C) and cold season (November-March, with an average high temperature of 0 °C and an average low temperature of −10 °C). We recorded the number of independent events that occurred for several target species during each season. In this analysis, we considered all instances of the same species captured within a 30-minute timeframe as the same events (i.e., >30-minute interval for independent captures, O'Brien et al., 2003) and analyzed them accordingly.

For vegetation survey, we set up a fixed quadrat measuring 30 × 30 m at each camera position to investigate the species and quantity of trees within the quadrat. Additionally, five smaller quadrats measuring 2 × 2 m were placed at the center and four corners of the 30 × 30 m quadrat to investigate the food abundance of shrubs. The investigation of shrubs was conducted simultaneously during the second data recovery of the camera data each year, i.e., October-November. Current-year growth branches of plants were collected in November 2019 and May 2021 to measure the nutrient content of different plant species found in the survey quadrat. Nitrogen, being a crucial nutrient for herbivores, was used to represent the plant nutrition content (Mattson, 1980). The nitrogen content of the plants was analyzed in the laboratory using the Kjeldahl method (Soest, 1963). By surveying the vegetation in each fixed quadrat, we were able to calculate the following parameters: 1) tree density, which was determined by dividing the total number of trees by the area of the quadrat; 2) shrub density, calculated as the number of shrubs in the five small quadrats divided by the total area of the five small quadrats; 3) shrub food abundance, calculated as the number of current-year growth branches for each edible shrub species within the five small quadrats divided by the total area of the five small quadrats; and 4) plant nitrogen supply in cold or warm seasons, which was calculated by the food abundance of each shrub species within the fixed quadrat was multiplied by its respective nitrogen content in cold or warm seasons, and the values were summed to calculate the plant nitrogen supply.

2.3. Statistical analyses

2.3.1. Driving factors of population distribution

Firstly, during each season, we calculated the Relative Abundance Index (RAI) of each species and human disturbance at every camera trap point for analysis of driving factors and population distribution, following the methodology described by O'Brien et al. (O'Brien et al., 2003):

$$RAI_i = \frac{N_i}{Trapday_i} \times 100 \quad (1)$$

Where RAI_i is the relative abundance index of a species at camera trap point i , N_i is the number of individually valid photographs of a species taken at camera trap point i , $Trapday_i$ is the number of shooting days at camera trap point i , multiplied by 100 represents the number of individually valid photos of the target species taken per 100 camera working days.

Table 1

The ungulates population distribution model parameters and environmental variables affecting ungulate population distribution in warm and cold seasons.

Season	Species	Variable	df	LL	AIC	RMSE	R ²
Cold season	Roe deer	Elevation(***) + Villages(***) + Mixed forest(***) + Korean-pine forest(***) + Larch forest(***) + Tree density(*)	8	-192.60	399.56	4.83	0.50
	Wild boar	Villages(***) + River(***) + Oak forest(*) + Food abundance of <i>Quercus</i> (**)	6	-132.41	276.81	2.31	0.52
	Sika deer	Villages(*) + Croplands(**) + River(***) + Mixed forest(***) + Oak(**) + Korean-pine forest(*) + Larch forest(***) + Tree density(*) + Nitrogen supply(***) + Food abundance of <i>Ash</i> (**) + Food abundance of <i>Syringa</i> (**)	13	-184.28	394.56	11.58	0.50
Warm season	Roe deer	Elevation(*) + Slope(*) + Villages(*) + Croplands(*) + Mixed forest(***) + Deciduous forest(***) + Larch forest(***) + NPP(*) + Food abundance of <i>Corylus</i> (*) + Grazing intensity(**)	12	-266.69	557.37	9.21	0.52
	Wild boar	Roads(*) + Oak forest(***) + Spruce-fir forest(***) + Tree density(**) + Food abundance of <i>Honeysuckle</i> (**)	6	-127.27	266.54	1.29	0.50
	Sika deer	Villages(**) + Croplands(***) + River(***) + Oak forest(*) + Mixed forest(***) + Larch forest(***) + Korean-pine forest(*) + Tree density(*) + Nitrogen supply(***) + Food abundance of <i>Quercus</i> (*) + Food abundance of <i>Syringa</i> (*) + NPP(**) + Grazing intensity(*)	15	-234.72	499.44	32.19	0.54

Forest type, river and human land uses represent distance from them; df: Degree of freedom; LL: log-likelihood; AIC: the Akaike information criterion values; RMSE: Root Mean Square Error from 10-fold Cross Validation by 10 repetitions; R²: R-square from 10-fold Cross Validation by 10 repetitions. Significance levels are indicated as: *p ≤ 0.05, **p ≤ 0.01, and ***p ≤ 0.001.

Environmental factors used for population distribution assessment included geographical factors, forest type, and human disturbance (Table S1). There is a significant body of research demonstrating that these factors have crucial effects on animal distribution (Markov et al., 2022; Zhu et al., 2021). Among all the variables, Net Primary Productivity (NPP), Normalized Difference Vegetation Index (NDVI), grazing intensity, and human activity intensity were only included in the population distribution model during the warm season. The reason is that during the cold season, both NDVI and NPP were significantly low, no grazing activity occurred, and human activity was also less and mostly accidental. ArcGIS 10.7 (ESRI, Inc.) was used to process and combine thematic layers. All raster layers were then projected into Universal Transverse Mercator zone 52 N using the WGS84 datum and resampled to a cell size of 30×30 m. For vegetation and human land uses, we utilized the near tool to extract the distance from the monitoring point to the specific forest type or human land uses. For raster data, we use the value-to-point tool for extraction.

To analyze the habitat factors affecting animal population distribution, we employed the Generalized Linear Model (GLM, (McCullagh and Nelder, 1989) and Generalized Additive Model (GAM, (Panigada et al., 2008). When analyzing the population distribution of ungulates, the GAM appeared to overfit, significantly affecting the reliability of the model. Therefore, the GLM is used for ungulates, with the model distribution family utilizing negative binomial or Poisson distribution. The negative binomial model was implemented using the MASS package in R (Venables and Ripley, 2002). Initially, we conducted a Pearson correlation analysis on the variables. Since the correlation between variables was below 0.7, we retained all variables for model construction (Dormann et al., 2013). For the selection of model variables, the stepwise regression method was adopted to first screen out the model with the minimum Akaike information criterion (AIC). Subsequently, variables with the largest *p*-values were removed one by one until all remaining variables were statistically significant. To compare and evaluate the negative binomial and Poisson models, we utilized the vuong function in the pscl package (Simon, 2020). The model with a smaller AIC and Bayesian Information Criterion (BIC) was chosen. The final model utilizes the train function from the caret package (Kuhn, 2008) for validation. We employed the repeatedcv method for 10 iterations of 10-fold cross-validation (Kuhn, 2008).

For Amur tigers and Amur leopards, we used GLM and GAM to analyze their population distribution. The construction of GAM relied on the mgcv package (Wood, 2017). After completing the correlation analysis of variables and initiating the elimination process, for GAM, insignificant variables were removed one by one based on their significance, starting from the least significant, until all variables became significant. For GLM, the elimination method was the same as that of the ungulate model. After obtaining the optimal GLM and GAM models for the same species, it was found that the AIC of the GAM was smaller than that of the GLM, indicating that the fitting effect of the GAM was better. Therefore, GAM was finally used for the analysis of the big cat models. The validation method used was the same as that applied in the model for ungulates. In the process of establishing models for ungulates and big cats, we incorporated the variables of tree density, shrub density, shrub food abundance, nitrogen supply, human activity intensity, and grazing intensity obtained from our field investigation and camera traps. If these variables remain in the population distribution model, we also need to evaluate the spatial distribution of these variables in the study area when making spatial predictions of population distributions for each animal species. The evaluation model we used for vegetation and human disturbance was GAM and the variables included habitat and human land use factors.

After constructing the models for the big cat and ungulate, we generated predictions for the RAI across the entire study area using the 'predict' function. All analyses were conducted using R version 4.3.0 (R Core Team, 2023).

2.3.2. Seasonal impacts of human land uses on population distribution

To assess the seasonal changes in the impact of human land uses on the population distribution of big cats and ungulates, we calculated the variations in population abundance between the warm and cold seasons. This was done by subtracting the population abundance during the cold season from that during the warm season. Positive values indicate an increase in population abundance from the cold to the warm season, while negative values indicate a decline in population abundance during the warm season. The magnitude of these values represents the degree of the rise or fall in RAI.

Subsequently, we employed GAM to evaluate the relationship between the seasonal change in population abundance and the distance from human land uses. The GAM approach offers flexibility in capturing potential non-linear relationships between variables (Tanskanen et al., 2016), enhancing our understanding of how human land uses impact population distribution for big cats and ungulates in different seasons.

3. Results

3.1. Driving factors and population distribution dynamics of ungulates in cold and warm seasons

The distribution model results for ungulate populations indicate that the three species differ in the factors affecting their respective cold and warm season distribution. Additionally, the three species vary in the degree to which these factors remain consistent between seasons (Table 1; for details see Figure S1-S3). Specifically, 6 habitat factors influenced the distribution of roe deer in the cold season, and 10 factors influenced their distribution in the warm season, with 4 factors (elevation, distance from villages, distance from mixed forest, distance from larch forest) were common to both seasons. As for the distribution of wild boar population, there are 4 factors in the cold season and 5 factors in the warm season, with only 1 factor (distance from oak forest) being common to both seasons. For the distribution of sika deer, there are relatively more habitat factors, with 11 factors in the cold season and 13 factors in the warm season; 10 habitat factors (distance from villages, distance from croplands, distance from river, distance from oak forest, distance from mixed forest, distance from larch forest, distance from Korean-pine forest, tree density, nitrogen supply, food abundance of Syringa) were consistent.

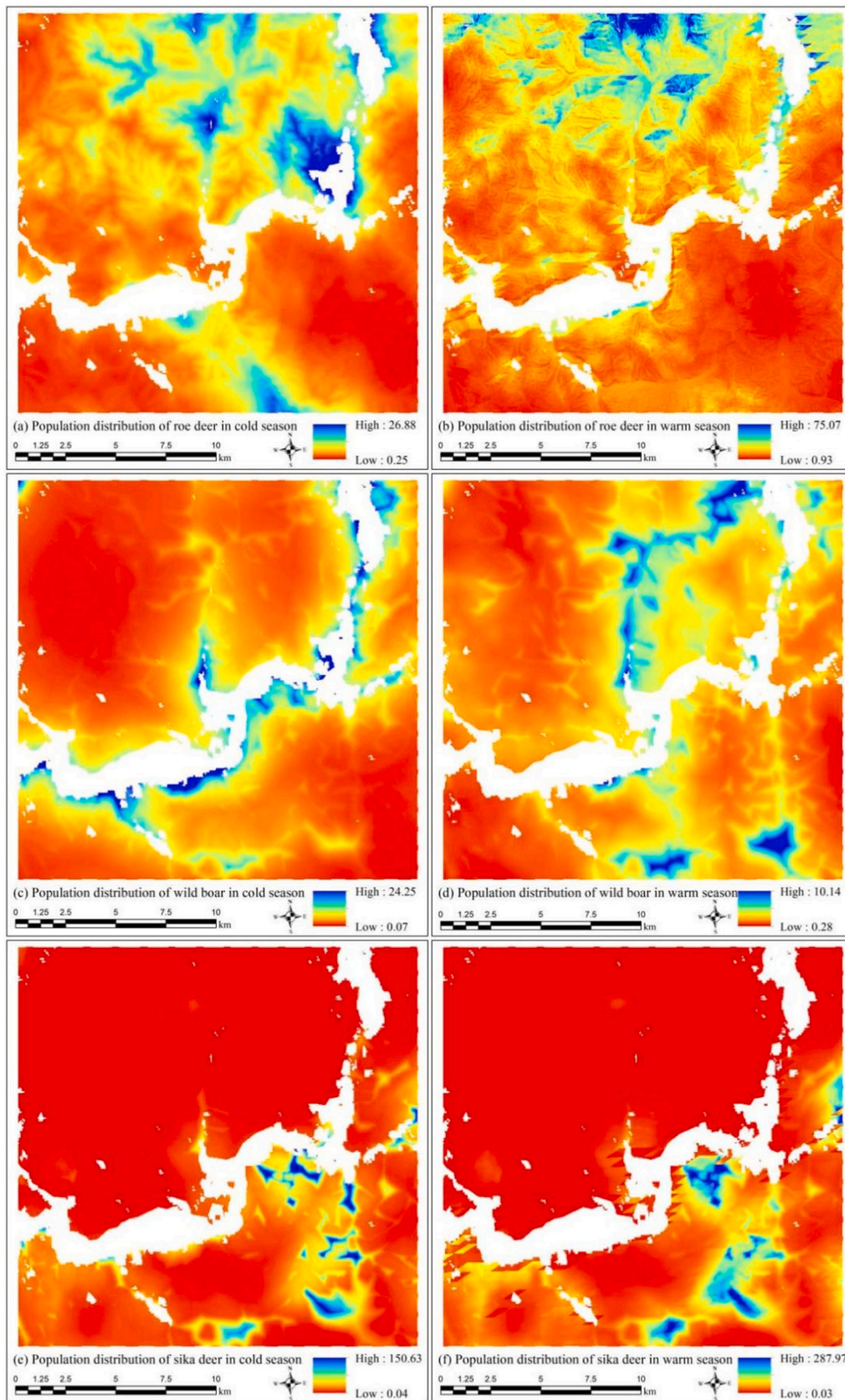


Fig. 2. Population distribution of ungulates in cold and warm seasons, (a) and (b) for roe deer, (c) and (d) for wild boar, (e) and (f) for sika deer.

Table 2

The big cats population distribution model parameters and environmental variables affecting big cats population distribution in warm and cold seasons.

Season	Species	Variable	GCV	Dev. Expl	RMSE	R ²
Cold season	Amur tiger	Aspect(*) + Roads(**)	0.056617	24.3%	0.21	0.25
	Amur leopard	Wild boar(*) + Elevation(*) + Korean-pine forest(*) + Tree density(***)	0.044471	43.5%	0.25	0.29
Warm season	Amur tiger	Wild boar(***) + Roe deer(***) + Slope(*) + Deciduous forest(*) + Birch forest(*) + Roads(*) + Grazing intensity(*) + Human activity intensity(***)	0.037808	62.5%	0.50	0.17
	Amur leopard	Roe deer(**) + Elevation(*) + Larch forest(*)	0.14715	23.1%	0.36	0.23

Forest type, river and human land uses represent distance from them; GCV: Generalised cross-validation; Dev.Expl: Deviance explained; RMSE: Root Mean Square Error from 10-fold Cross Validation by 10 repetitions; R²: R-square from 10-fold Cross Validation by 10 repetitions. Significance levels are indicated as: *p ≤ 0.05, **p ≤ 0.01, and ***p ≤ 0.001.

In the study area, the primary distribution area of roe deer was located in the northern part (Figs. 2a-2b). The average RAI for roe deer was 3.84 ± 2.84 (mean \pm SD) during the cold season and increased to 11.91 ± 8.49 (mean \pm SD) during the warm season. Wild boars primarily inhabit near croplands during the cold season, while they are mainly found in forest areas far from villages and croplands during the warm season (Figs. 2c-2d). The average RAI for wild boar was 1.63 ± 1.57 (mean \pm SD) during the cold season, with a slight increase to 1.74 ± 1.06 (mean \pm SD) during the warm season. For sika deer, their primary distribution areas were in the southern part of the study area during both seasons (Figs. 2e-2f). The average RAI for sika deer was 6.18 ± 10.66 (mean \pm SD) during the cold season and significantly increased to 15.32 ± 26.87 (mean \pm SD) during the warm season.

3.2. Driving factors and population distribution dynamics of big cats in cold and warm seasons

The population distribution of Amur leopards and Amur tigers is influenced by a limited number of factors. During the cold season, the population abundance of Amur leopards is higher in areas that are far from Korean-pine forest, have a medium elevation (400–500 m), high tree density, and a high RAI for wild boar, with tree density exerting the largest influence. In the warm season, the Amur leopard population was more distributed in areas with high altitude, medium RAI of roe deer, and near larch forest, and these three factors all had strong effects (Table 2; Figure S4). As for Amur tigers, they tend to have a higher population abundance in sunny slopes and areas near roads during the cold season, with both factors exerting a strong impact. However, Amur tiger populations were more distributed in areas characterized by low slopes, medium RAI of roe deer, high RAI of wild boar, proximity to deciduous forests, far from birch forests and roads, low grazing intensity, and high human activity intensity, during the warm season. The human activity intensity, grazing intensity, RAI of roe deer and RAI of wild boar exerting a stronger influence for population abundance of Amur tiger in warm season (Table 2; Figure S5).

During the cold season, Amur leopards were distributed across the majority of the study area, while in the warm season, their

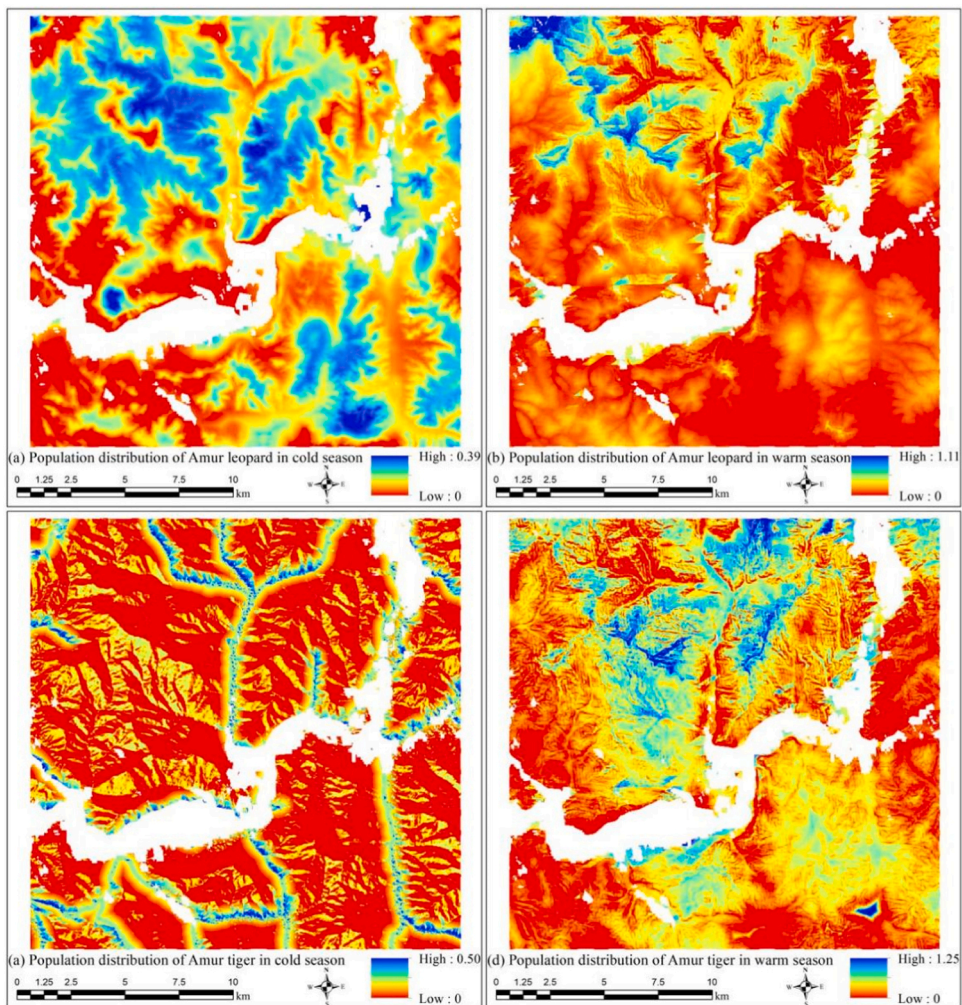


Fig. 3. Population distribution of big cats in cold and warm seasons, (a) and (b) for Amur leopard, (c) and (d) for Amur tiger.

distribution primarily shifted to the northern part (Figs. 3a-3b). The average RAI for Amur leopards was 0.11 ± 0.08 (mean \pm SD) during the cold season, and it increased to 0.15 ± 0.17 (mean \pm SD) during the warm season. Amur tigers were primarily distributed near roads during the cold season, but their distribution expanded to cover most of the study area during the warm season (Figs. 3c-3d). The average RAI for Amur tigers was 0.08 ± 0.10 (mean \pm SD) in the cold season and increased to 0.16 ± 0.13 (mean \pm SD) in the warm season.

3.3. Changes in the effect of human land uses on population distribution in different seasons

The effects of human land use on the seasonal variation of population distribution of several species are somewhat different. When it comes to roe deer and sika deer, their population distribution did not change strongly in response to human land uses in different seasons (Table S3). However, the population distribution of wild boar exhibited great changes in response to villages (Deviance explained = 41.9%) and croplands (Deviance explained = 32.3%) between the cold season and the warm season (Table S3). Compared with the cold season, wild boars tended to stay far away from villages and kept a distance of 1500 m from croplands in the warm season (Fig. 4). For Amur leopards and Amur tigers, only roads had a greater impact on the distribution of the Amur tiger population during the warm season (Deviance explained = 29.7%, Table S3). In the warm season, Amur tigers are more likely to avoid roads (Fig. 4).

4. Discussion

4.1. Seasonal changes in population distribution and adaptation strategies of ungulates

The human-dominated landscape has become a persistent problem due to the development of human society (Li et al., 2009). Such landscapes experience high-intensity disturbances that can significantly impact the survival of animals (Ciuti et al., 2012; Krishna et al., 2016). Hence, it is crucial to explore the adaptation strategies of animals in human-dominated landscapes (Balouch et al., 2022; Kniowski and Gehrt, 2014; Nawrocki et al., 2019). This study examines the population distribution and driving factors among three prominent ungulate species (roe deer, wild boar, and sika deer) and reveals that each species adopts unique adaptive strategies in

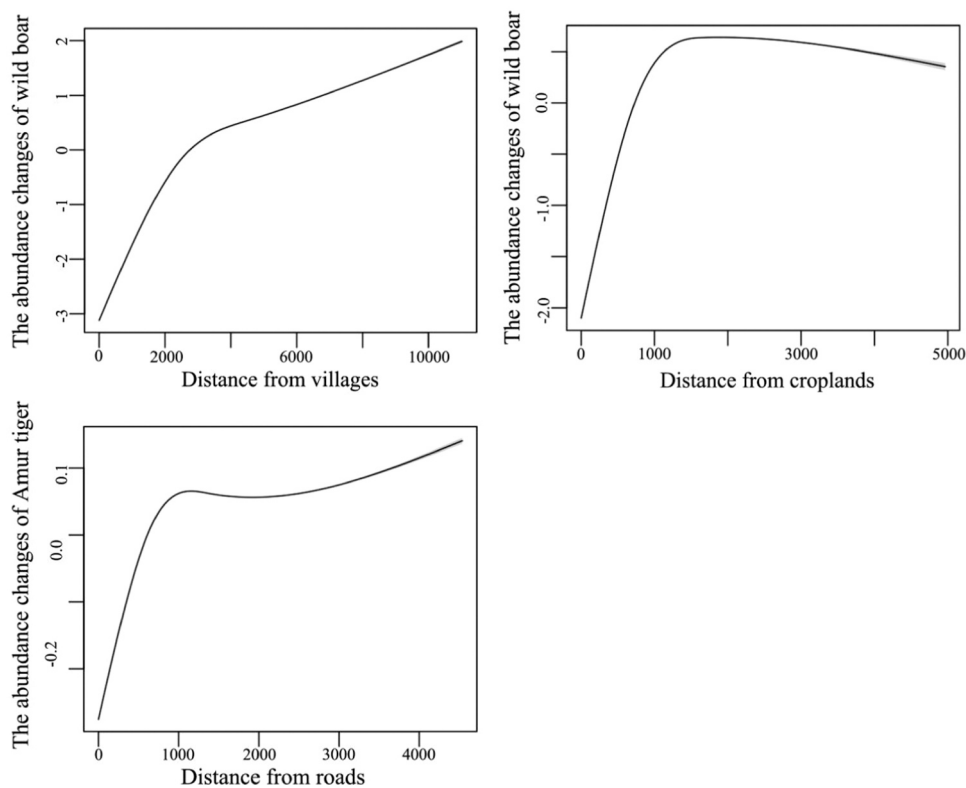


Fig. 4. Seasonal changes in the effects of human disturbance on the abundance of big cat and wild boar populations. The rising curve means that the influence of human land use is greater in warm season (as the distance from human land use increases, the magnitude of animal abundance growth in the warm season relative to the cold season increases), the horizontal curve means that the human land use effects on animals will not change in different season (the magnitude of animal abundance growth in the warm season relative to the cold season does not vary with changes in distance from human land use), and the downward curve means that the influence of human land use is greater in cold season (in areas closer to human land use, the magnitude of the warm season animal abundance growth is greater than that of the cold season). Distances are measured in meters.

response to seasonal changes in human-dominated landscapes.

The distribution of roe deer populations is influenced by various factors during both the cold and warm seasons (Figure S1). Our results align with previous research indicating that roe deer populations tend to be more prevalent in regions with low tree density and low elevation during the cold season, and in deciduous forests with high elevation and low slope during the warm season (Qin, 2011; Zhou et al., 2010). Conversely, roe deer are less commonly found in coniferous forests throughout both seasons (Qin, 2011; Zhou et al., 2010). The population distribution of roe deer also varies between the cold and warm seasons, but its primary range has been in the northern part of the study area. This distribution pattern may be attributed to the roe deer's tendency to move within its home range (Gaudry et al., 2015), indicating that the population distribution of roe deer remains relatively stable and is less affected by seasonal changes. Human land use practices often have a negative impact on the distribution of roe deer (Qin et al., 2008; Zhou et al., 2010), and our findings confirm this. However, our analysis indicates that grazing has a greater impact on roe deer populations compared to villages and croplands (Figure S1). This might be due to direct competition for food between livestock and roe deer (Feng et al., 2021; Li et al., 2017; Soofi et al., 2018). As a result, roe deer tend to avoid areas with a high abundance of livestock.

The habitat factors that influence the population distribution of sika deer in both the cold and warm seasons are almost identical (Figure S2). The distribution range of sika deer remains largely consistent in both seasons, with changes only observed in population abundance. However, studies conducted in Japan have reported significant variations in the habitat use and distribution of sika deer between the cold and warm seasons (Laneng et al., 2023; Sakuragi et al., 2003), indicating that specific factors restrict the sika deer population distribution in the study area. Two reasons may explain the relatively fixed distribution of sika deer. Firstly, our analysis results show that sika deer tend to stay far away from villages and croplands in both seasons. Other studies have also shown that sika deer are highly sensitive to human land use (Seki and Hayama, 2021). Since there are more croplands and villages in the middle of our study area (Fig. 1), the northward spread of sika deer is limited. Secondly, research results indicate that grazing has a stronger impact on sika deer population distribution than human land uses. When livestock occupy too much forest land, sika deer may even actively migrate (Feng et al., 2021). Therefore, grazing in Hunchun during the warm season may also be an important factor limiting the distribution of sika deer. These reasons may lead to a more conservative distribution strategy for sika deer.

The wild boar is known for its adaptability and wide distribution among ungulate species (Markov et al., 2022). In this study, wild boars exhibited more flexible strategies to cope with seasonal variations in human-dominated landscapes, demonstrating greater adaptability compared to the two deer species. The results found that wild boars displayed significant variations in the habitat factors influencing the population in changing seasons (Figure S3), causing substantial shifts in the population distribution. Remarkably, this finding contrasts with the observed habitat selection pattern of European wild boar populations (Morelle and Lejeune, 2015; Thurfjell et al., 2009). Another finding that contradicts common sense is that wild boars tend to avoid oak forests in both warm and cold seasons. Normally, oak forests produce acorns that provide additional food for wild boar, so they should be more abundant in such forests (Orłowska and Nasiadka, 2022). However, in the Hunchun area, many oak forests were used for cattle grazing, which has seriously altered the understorey vegetation (Li et al., 2017). This has resulted in a reduction of edible plants for wild boar. Therefore, it can be reasoned that wild boar would stay away from the oak forest. Wild boars were the only ungulates in the study area that were not affected by human disturbance. They were found to have a higher distribution near various human land use areas during both the cold and warm seasons. During the cold season, wild boars tend to stay close to villages because the large areas of clustered croplands surrounding them (Fig. 1) provide a plentiful food source (Anderson et al., 2012; Zhao et al., 2019). This may also explain why the abundance of wild boar in the research area did not decrease significantly in harsh winter survival conditions, unlike the populations of roe deer and sika deer. During the warm season, wild boars prefer areas near roads, which tend to offer an abundance of shrubs (Buckley et al., 2003; Kuang et al., 2010) that provide edible branches for the wild boar.

According to population distribution models, three species of ungulate are influenced by the abundance of specific shrub species. The shrub species that affect the distribution of wild boar change between seasons. The flexible shrub preference is one of the reasons for the change in the distribution of wild boars during cold and warm seasons (Ballari et al., 2015). Additionally, each ungulate species prefers different types of plants, which promotes their coexistence in the same area and reduces resource competition among them (Liu and Huang, 2023). Nitrogen supply only affects the distribution of sika deer, showing a negative correlation in both cold and warm seasons. This could be because shrubs are dense in areas with high nitrogen supply, and sika deer require more open spaces (Latham et al., 2015; Uzal et al., 2013), so they tend to distribute in areas with low nitrogen supply.

4.2. Seasonal changes in population distribution and influencing factors of big cats

Numerous studies have shown that human disturbances and prey abundance significantly impact the distribution and spread of Amur tigers and leopards (Jiang et al., 2014; Jiang et al., 2015; Li et al., 2009; Wang et al., 2017). According to our research, the distribution of Amur tigers and leopards is mostly influenced by environmental factors during the cold season. During the warm season, distinct patterns were observed: the population distribution of Amur leopards was primarily influenced by prey abundance and environmental factors, whereas the distribution of Amur tigers was affected by both prey availability and human disturbances.

The population distribution of Amur leopards is greatly influenced by tree density in the cold season. A higher population abundance of Amur leopards is observed in areas with high tree density. Research has shown that leopards achieve a better balance between energy expenditure and the likelihood of hunting prey in regions with dense vegetation (Pitman et al., 2013). In the harsh living conditions of the cold season in northeastern China, dense forests may enhance the hunting success rate of the Amur leopard, thereby reducing its energy consumption during hunting. During the warm season, the RAI of roe deer, elevation, and distance from larch forests are the main factors that affect the population distribution of Amur leopards. The RAI of roe deer has a threshold effect on Amur leopards, indicating that a specific level of roe deer abundance is essential to support the leopard population. This finding is

consistent with previous research that emphasizes the significance of roe deer abundance for the population distribution of Amur leopards (Qi et al., 2015). Moreover, the greater presence of Amur leopards at higher elevations during the warm season may also be attributed to the increased abundance of roe deer at those altitudes (Figure S1, Figure S4). In our results, the abundance of Amur leopards is higher in areas close to the larch forest, but there is no evidence that leopards prefer the larch forest, and further research is required.

During the cold season, the population abundance of Amur tigers was higher on sunny slopes and near roads, which can be attributed to snowfall. On sunny slopes and roads, Amur tigers experience less resistance from snow, which is more conducive to their movement (Jiang et al., 2014; Wang et al., 2023). During the warm season, the population of Amur tigers increased, and their primary distribution areas shifted. The prey factors influencing the population distribution of Amur tigers are the RAI of wild boar and roe deer. As the RAI of wild boar increases, the RAI of Amur tigers also tends to increase, emphasizing the importance of wild boar as a food source for Amur tigers (Sugimoto et al., 2016; Yang et al., 2018). The influence of roe deer on the Amur tiger was in the form of a threshold, indicating that roe deer was less important as food than wild boar (Sugimoto et al., 2016; Yang et al., 2018). Among other factors, human disturbance also strongly impacts the distribution of Amur tigers in the warm season. The Amur tigers exhibited varying responses to grazing and human activities. Our results are consistent with other studies indicating that grazing has a negative impact on the Amur tiger (Wang et al., 2016; Wang et al., 2018). However, the population abundance of Amur tigers increased due to the rise in human activities. This does not necessarily imply that human activities directly caused the increase in the Amur tiger population. Rather, it suggests that the habitats of Amur tigers and humans have gradually overlapped (Wang et al., 2018). Although Amur tigers can adjust their temporal niche to avoid encounters with humans (Yang et al., 2019), the recovery of the Amur tiger population and the increasing human activities will inevitably lead to severe human-tiger conflicts, which deserve attention.

It is important to note that while sika deer are considered important prey for Amur tigers and have shown a strong correlation in some studies (Wang et al., 2016; Wang et al., 2018), our results do not indicate a significant relationship between the RAI of Amur tigers and the RAI of sika deer. This could be attributed to the fact that Amur tigers may avoid hunting sika deer based on their food habits (Sugimoto et al., 2016; Yang et al., 2018), and sika deer may have a lower priority compared to other abundant prey. In studies of Amur leopards, prey selection generally includes all available prey species (Jiang et al., 2015; Wang et al., 2017). Therefore, sika deer alone may not exhibit a significant relationship with Amur leopards.

Our analysis reveals distinct distribution patterns of Amur tigers and leopards during the cold and warm seasons. Amur tigers tend to conserve energy during the cold season and may even utilize roads when human activities are reduced, whereas Amur leopards focus more on increasing their hunting success rate during this time. In the warm season, both Amur tigers and leopards tend to concentrate more in areas with abundant prey. Studies have shown that large carnivores can sustain high population densities in human-dominated landscapes (Athreya et al., 2013; Carter et al., 2012), with prey availability playing a significant role (Gehr et al., 2017). Thus, prioritizing the recovery of prey populations remains imperative for the preservation of these magnificent species (Wen et al., 2022). Grazing has a direct negative impact on the Amur tiger in the warm season, and it may have an indirect negative impact on the Amur leopard, as grazing also restricts the distribution of roe deer, which is the Amur leopard's main prey. The adverse impact of long-term grazing on the natural environment is evident to all (Feng et al., 2021; Li et al., 2017). Therefore, more attention should be paid to the management of grazing. In our results, we also observed a relatively lower abundance of wild boar compared to roe deer and sika deer. This can be attributed to the severe impact of African swine fever, which has reduced the wild boar population in recent years (Fekede et al., 2019; Ito et al., 2022; Luskin et al., 2023). Here, it is important to reiterate that wild boar serves as a significant food source for Amur tigers (Hayward et al., 2012; Miquelle et al., 2010), and special attention should be directed toward promoting the recovery of the wild boar population.

4.3. Differences in adaptation of big cats and ungulates to human land uses during warm and cold seasons

Human land uses have been extensively documented to have a significant detrimental effect on the distribution of large mammals (Linke et al., 2013; Paudel and Kindlmann, 2012). Moreover, animals exhibit varying sensitivity to changes in human activity intensity in these areas across different periods or seasons (Farmer et al., 2022; Houle et al., 2010; Polfus et al., 2011). Among the three ungulate species in this study, only the wild boar population distribution showed significant changes between the cold and warm seasons (Fig. 2). The distribution of the wild boar population was significantly limited near villages and croplands during the warm season (Fig. 4), possibly due to increased human activities during that period (Ohashi et al., 2013; Rosalino et al., 2022).

For big cats, our results show that roads have a stronger impact on Amur tigers during the warm season (Fig. 4). Roads have long been recognized as a significant influence on the distribution patterns of Amur tigers (Hebblewhite et al., 2014; Jiang et al., 2014). However, the adverse effects on Amur tigers were mainly observed during the warm season in our result. Interestingly, we found that Amur tigers even utilized roads during the cold season, indicating a certain level of fear response due to increased traffic and other human activities in the warm season (Wang et al., 2023).

In our study area, there is a vast forest road network and a main road that is surrounded by croplands and villages throughout the entire region. The presence of these human land uses has led to the division of the study area into northern and southern habitats (Fig. 1). While previous studies have suggested that composite areas consisting of villages, croplands, and roads do not completely impede the movement of Amur tigers and leopards (Wang et al., 2016), our results highlight the inevitable impact of these complex human land uses on the population distribution patterns of Amur tigers and ungulates during the warm season. The Hunchun area is of great significance as a habitat for Amur tigers and Amur leopards in China, and it borders the Southwestern Primorsky Krai habitat in Russia (Li et al., 2017; Vitkalova et al., 2018). Due to its unique geographical location, the Hunchun area serves as a crucial link in the communication and spread of tiger and leopard populations between China and Russia (Qi et al., 2021; Vitkalova et al., 2018).

Although the limitation of monitoring means we cannot accurately investigate the intensity of human disturbance in human land uses, according to our camera monitoring data, the RAI of human disturbance is significantly higher in the warm season than in the cold season (Figure S6). This trend is observed only in forest areas with fewer human activities. Therefore, we have reason to believe that the relative increase in human activity in primary human land use areas will be even more pronounced in the warm season. High-intensity human activity during the warm season may act as a primary factor triggering avoidance behaviors in various species.

Consequently, it is imperative to plan the control of human disturbances in protected areas according to the varying intensity of human activity in different seasons. In areas with more human disturbances, habitat restoration and corridor construction are important tasks (Charles et al., 2023; Miquelle et al., 2015; Qi et al., 2021). Additionally, animal early warning systems should be established to reduce the risk of human-animal conflict (Figel et al., 2023). These measures aim to mitigate the adverse effects of human disturbances on big cats and ungulates by reducing the impact of human disturbances on the spatial distribution of their populations, ultimately promoting the conservation and recovery of these species.

CRediT authorship contribution statement

Zeyang Zhou: Investigation. **Yumiao Tian:** Investigation. **Nathan James Roberts:** Writing – review & editing. **Yonglu Cui:** Investigation. **Qi Qi:** Investigation. **Guangshun Jiang:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Data curation, Conceptualization. **Zhaoyue Li:** Investigation. **Eryan Yang:** Investigation. **Wannian Cheng:** Investigation. **Feng Shan:** Investigation. **Jinzhe Qi:** Investigation. **Yan Zhao:** Investigation. **Dusu Wen:** Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Zhigang Cheng:** Investigation. **Ying Wang:** Investigation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2024.e02881](https://doi.org/10.1016/j.gecco.2024.e02881).

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