Assessing mammal species richness and occupancy in a Northeast Asian temperate forest shared by cattle

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Funding information
This work was supported by the National Natural Science Foundation of China, Grant/Award Number: 31971539, 31270567; National Key Research and Development Program of China, Grant/Award Number: 2016YFC0500106.

Abstract
Aim: Asian forests are becoming increasingly degraded and fragmented by the extensive intensification of anthropogenic activities; these activities threaten wildlife and ecosystem sustainability. Facing a defaunation crisis, managers need more information on species assemblages to guide conservation efforts. We tested the relative influence of natural and anthropogenic factors on mammalian species richness and occupancy in temperate forests in Northeast Asia.

Location: Northeast China.

Methods: Camera-trapping data and multispecies occupancy models were used to estimate the species richness of a terrestrial mammal community in a working landscape and assess community-, group-, and species-specific responses to natural and anthropogenic features while accounting for imperfect detection. Species were grouped based on body size, diet and activity pattern.

Results: We deployed 138 cameras and photographed 21 mammalian species over 22,976 trap days across the China–Russia border. Both natural and anthropogenic correlates varied in their importance in predicting the presence of different animals. Vegetation cover and cattle were found to have significantly positive and negative influences on community-level mammalian occupancy, respectively. The positive relationship with vegetation cover was most evident for large or diurnal species; the negative relationship with cattle was most evident for diurnal and wild ungulate species. Large species occupancy was also negatively associated with human settlements. The predicted richness across each station varied from 5 to 14 unique species, and species had a mean occupancy probability of 0.45 (95% credible interval = 0.09–0.86). Species richness was generally the lowest in livestock grazing areas and close to human settlements. Human influence is more important than the influences of vegetation and environmental variables.

Main conclusions: Our results highlight that livestock grazing was the primary human disturbance that had a negative impact on species occupancy and richness. Multispecies occupancy models helped to identify drivers of biodiversity declines and will inform conservation strategies in human-dominated landscapes in Northeast Asia.

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Asian forests. We suggest that landscape conservation planning seeks to maximize forest protection and ecosystem services such as biodiversity and carbon storage.

**KEYWORDS**
camera trapping, cattle grazing, China, community occupancy, conservation, hierarchical modelling, species richness

1 | INTRODUCTION

Ecosystem integrity is often contingent upon the functional assemblages of mammals consisting of different guilds and body sizes (Estes et al., 2011; Lacher et al., 2019; Ripple et al., 2014). However, many natural terrestrial areas are being altered by humans, and elevated human–wildlife conflict has become a common problem worldwide (van Eeden et al., 2018; Treves & Karanth, 2003). Anthropocene defaunation, the emptying of ecosystems of wildlife, is currently a global phenomenon of human-induced animal biodiversity loss (Dirzo et al., 2014; Sandom et al., 2017). Intensification of human activities has simultaneously led to declines in top carnivores, small predators and herbivores in many regions of the world, even protected areas (Ripple et al., 2014; Sandom et al., 2017; Yackulic et al., 2011). As a result, these losses further influence ecosystem functions, including nutrient cycling, carbon storage, seed dispersal, trophic regulation and ultimately the maintenance of forest structure (Estes et al., 2011; Lacher et al., 2019; Sobral et al., 2017). As is occurring elsewhere, Asian mammals, especially large carnivores and their primary prey species, are threatened or declining due to human activities; these impacts have important consequences for ecosystem sustainability (Gallego-Zamorano et al., 2020; Pimm et al., 2014; Tilker et al., 2020). For example, top predators such as tigers (Panthera tigris), leopards (P. pardus) and Asiatic lions (P. leo persica) have suffered significant contractions of their numbers and ranges (Dinerstein et al., 2007; Singh & Gibson, 2011; Wolf & Ripple, 2017). Attempts to recover threatened populations of Asian mammals often involve incorporating areas that are utilized by livestock and people (Carter et al., 2012; Soofi et al., 2018; Xiao et al., 2018); thus, there is a need to reconcile conservation and development. Accordingly, managers require reliable information on species assemblages to guide conservation efforts in multi-use areas in Asia (Tilker et al., 2020). This action is urgently needed to ensure the long-term viability of regional native wildlife. Although studies have assessed mammalian communities in Southeast Asian (Brodie et al., 2015; Tilker et al., 2020; Wearn et al., 2017), to date, knowledge of the status and distribution of mammalian communities in Northeast Asian forest ecosystems is limited.

Temperate mixed forests in Northeast Asia support diverse fauna and provide habitat to endangered Amur tigers (P. t. altaica) and leopards (P. p. orientalis). However, defaunation in this area has been particularly severe due to multiple anthropogenic threats. Large- and medium-sized animals in Northeast China are threatened by habitat degradation, rapid land use change, hunting and human–wildlife conflict (Li et al., 2017; Soh et al., 2014; Wang et al., 2016). A particular threat in Northeast Asia is the previously underestimated impact of increased livestock grazing. As an alternative to logging, livestock grazing within the forest has become the most prevalent human disturbance and is the main driver of biodiversity loss in Northeast China (Wang et al., 2019). However, there is extensive potential habitat to expand the land base in the Changbai Mountains to support regional mammalian communities (Hebblewhite et al., 2012; Vitkalova et al., 2018). To increase mammalian species richness across the region, it is important to gain an understanding of the ecological and anthropogenic correlates that influence the region’s mammalian community. Previous studies on the impact of human activities on mammalian species distribution in Asia have mostly focused on the tropics and the impact of hunting and habitat loss (Brodie et al., 2015; Gallego-Zamorano et al., 2020; Harrison et al., 2016). Less is known about how species richness and occupancy respond to free-ranging livestock grazing, which is the dominant human activity in forests in Northeast China.

Advances in non-invasive survey methods and statistical modelling techniques provide methods to address the status of mammalian communities and guild conservation actions. Camera traps have emerged as a powerful tool for surveys of forest-dwelling mammals and their conservation across the planet (Rich et al., 2017; Steenweg et al., 2017). This growth in camera trap use has been accompanied by important new statistical approaches, such as occupancy modelling to account for imperfect detection (MacKenzie et al., 2002; Rich et al., 2017). Currently, emerging conservation paradigms have shifted from single species to ecological communities. The multispecies occupancy model is a major step forward, as it allows investigators to simultaneously explore the ecological and anthropogenic variables that affect the distribution of single species, communities or functional groups while providing reliable inference for species that are not often found in ecological surveys (Easter et al., 2019; Rich et al., 2016; Tobler et al., 2015; Zipkin et al., 2009).

For the first time, we use a multispecies occupancy model to study the diversity and composition of terrestrial mammals in Northeast Asia. Using large-scale camera-trapping data, we estimated species richness and assessed how natural factors (i.e., terrain and vegetation) and anthropogenic pressure (i.e., cattle grazing and human settlements) influence the mammalian community-, functional groups- or species-level occupancy across a human-dominated landscape in Northeast China. We hypothesized that (1) mammalian richness will be lowest in areas influenced by human disturbance; (2) cattle grazing and settlements will have the strongest negative impacts on occupancy by large and diurnal species; and (3) species-specific responses of wildlife to natural covariates
will vary depending on their life history traits (e.g., body size, diet, activity pattern) or species' behavioural niches (Easter et al., 2019; Rich et al., 2016). This study was motivated by efforts to expand regional conservation efforts in China and the realization that human activities have a cascading impact on regional forest condition that likely influences entire mammalian communities.

2 | MATERIALS AND METHODS

2.1 | Study area

This research was conducted in the eastern part of Northeast Tiger Leopard National Park. The park was established in 2016 and located in the northern portion of the Changbai Mountains in China, adjacent to the Land of the Leopard National Park in south-western Primorsky Krai, Russia, to the east, and North Korea to the south-west (Figure 1). The study area forms the core of a potential recovery landscape for tigers and leopards in China (Hebblewhite et al., 2012; Wang et al., 2016). Breeding tigers and leopards currently have home ranges that span the China/Russia border and several breeding female tigers and leopards reside entirely in China (Ning et al., 2019; Vitkalova et al., 2018).

Elevations range from 5 to 1,477 m. The climate is characterized as temperate continental monsoon with an average annual temperature of 5.60°C (±1.30°C) and a frost-free period of 110–160 days/year. The annual average precipitation was 618 mm (±68 mm) during 1990–2010, with most precipitation occurring in the summer from June to August. Forest cover is >92%, and the majority of forests have been converted into secondary deciduous forests over the past 5 decades (Li et al., 2009). Within the park, over 62,300 people reside in 130 villages, and rely on farming, livestock grazing, forest

![Elevation map](image)

**FIGURE 1** Map of our camera-trapping study area in Northeast China, adjacent to Leopard Land National Park in Russia. The insert shows the location of the study area along the China–Russia border.
resource collection for their livelihoods. Free-range cattle grazing is one of the main economic activities in the study area, with cattle densities ranging from 8 to 12 livestock per km² (Li et al., 2017; Wang et al., 2016).

2.2 Camera trap survey

This study was a part of a long-term Tiger Leopard Observation Network (TLON) of camera traps along the border of Russia (Vitkalova et al., 2018; Wang et al., 2016; Yang et al., 2019) (Figure 1). A 6-month subset of data collected from May to October 2015 was analysed from the 138 camera stations. This period represents a high level of detection probabilities based on preliminary analysis of a multi-year dataset, which could be due to climate, food availability or animal non-hibernation. The camera array covered a minimum convex polygon of 5,712 km². On average, adjacent camera stations were 3.82 km (±1.94 km) apart. We maximized the detection probability by placing cameras at sites where wildlife was likely to travel (e.g., along ridges, valley bottoms, forest roads and near scent-marked trees). Cameras (LTL 6210M, Shenzhen, China) with no bait were fastened to trees approximately 40–80 cm above the ground and programmed to take videos 24 hr/day with a 1-min interval between consecutive 15 s videos. At most sites, we set pairs of cameras facing towards each other to provide redundancy in case of camera failure.

2.3 Covariates

We examined a suite of natural and anthropogenic covariates that could potentially influence the community-, group- or species-level space use by animals observed in this area. Based on previous studies (Hebblewhite et al., 2014; Li et al., 2017; Li, Wang, et al., 2019; Wang et al., 2018; Xiao et al., 2018; Yang et al., 2019), we explored whether weather, vegetation, elevation, ruggedness, cattle encounter rates, and the distance to the Russian border, river, as well as settlements and roads, might affect species occupancy. Distance from the Russian border was recorded to measure the potential that Russia serves as a source population location. We also tested for a quadratic effect of elevation and distance from roads and settlements to determine whether animals preferred intermediate levels of these covariates. We used ArcToolbox in ArcGIS 10.3 (ESRI Inc.) to calculate the distances from each camera to settlements, roads, river or international border, and obtained these GIS data layers from local forest management offices.

We assessed vegetation characteristics using the normalized difference vegetation index (NDVI) and tree basal area. NDVI was derived from the 250 m Moderate Resolution Imaging Spectroradiometer (MODIS) imagery (product MOD13Q1) of the study area. Based on a visual evaluation and land cover categories using an unsupervised classification method for 2015 MODIS NDVI, NDVI values significantly differed between habitat types based on tree cover (ANOVA test, \( F = 42.02, p < .05 \)), and we thus used NDVI as a proxy for habitat type, cover and forage availability (Easter et al., 2019; Harihar et al., 2014). We calculated the average NDVI in 2015 from a 1 km buffer surrounding each camera station. To derive the tree basal area, we established two orthogonal 100 m transects centred on each camera station in the summer of 2015. We randomly generated 4 sampling points along each 50 m transect in four directions from the centre. At these 16 sampling points, we used the point-centred-quarter method (Thornton et al., 2011) to measure the diameter at breast height (d.b.h) of trees ≥10 cm to calculate the total basal area of all tree species.

Elevation at each station was recorded using handheld GPS receivers. Ruggedness was generated using a topographic position index calculated using a circular neighbourhood with a 1-km radius from the Shuttle Radar Topography Mission (SRTM) 30-m digital elevation model. Annual mean temperature and annual precipitation were downloaded from the WorldClim database (http://www.worldclim.org/bioclimate). Cattle encounter rates at each camera station were the number of detections per 100 camera trap days using a 30-min period of independence per record for the entire sampling period (O’Brien et al., 2003).

Several variables may influence an animal’s detection rate, such as obstruction of the camera by vegetation or human disturbance. Every 10 m along transects, we used the line intercept method to determine the proportion covered with shrubs (woody vegetation between 0.5 m and 2 m in height) to derive undergrowth transparency (i.e., habitat visibility), with a value of 100 indicating maximum visibility and 0 indicating complete invisibility. We included a binary variable for a camera that was placed on an active dirt road (i.e., an obvious pathway for people and vehicle movement) (Easter et al., 2019; Tobler et al., 2015). We used an additional binary variable to indicate whether a trap consisted of a pair of cameras. Finally, we included human encounter rates because human activity may alter animal detection (Easter et al., 2019; Wang et al., 2018).

We tested for collinearity among covariates using two methods. First, a variance inflation factor (VIF), which measures multicollinearity among variables, was calculated for all covariates; those with a VIF < 3 were retained in the model. Then, Pearson’s correlation coefficients (\( r \)) were calculated to further exclude highly correlated variables with \( |r| > .7 \) (Dormann et al., 2013).

2.4 Modelling framework

For the community analysis, we used a hierarchical Bayesian multispecies model to assess mammalian richness and the influence of natural and anthropogenic variables on occupancy of each species at the scale of the camera trap station (Boron et al., 2019; Rich et al., 2016; Tobler et al., 2015; Zipkin et al., 2009). Multispecies models combine data across species to inform the occurrence probabilities of animals observed while still accounting for imperfect detection and improved parameter estimates for rare species...
(MacKenzie et al., 2002; Zipkin et al., 2009). These community-level models also allow for the grouping of different species for further testing of hypotheses for group-level effects (Easter et al., 2019; Rich et al., 2016). Before analysis, following Boron et al. (2019), we discarded data from red deer Cervus canadensis, brown bear Ursus arctos, and Eurasian otter Lutra lutra as these species were recorded once and the lack of data limits the inferences that can be made with regard to occupancy (Table 1).

We used a multispecies version of the Royle–Nichols (RN) occupancy model (Royle & Nichols, 2003; Tobler et al., 2015) with known species richness (Van der Weyde et al., 2018) for 18 species in our study area. The RN model effectively addresses the high level of spatial heterogeneity often found in camera trap data due to variation in the local abundance or non-random movement of animals. For each camera station, we pooled our data into 14-day sampling periods to further reduce heterogeneity and avoid over-dispersion caused by short periods of high activity. This approach resulted in 13 sampling occasions in our study area. Our observed data were represented by a summarized detection matrix $y_{ij}$ that contains the number of 14-day windows where species $i$ was detected at station $j$ at least once.

We connected occurrence and detection process of observed data through an additional hierarchical component that modelled coefficients from a community-level distribution governed by hyper-parameters. Consequently, species-specific parameter estimates are treated as random effects and are a function of individual detection histories and average community-level responses, which improves estimation precision even for infrequently observed species (Boron et al., 2019). We modelled the abundance $a_{ij}$ of each species $i$ at each station $j$ using a Poisson distribution with a rate parameter $\lambda_{ij}$ so that $a_{ij} \sim \text{Poisson}(\lambda_{ij})$ (Royle & Nichols, 2003; Tobler et al., 2015). However, we did not interpret $a_{ij}$ as true abundance and only used this formulation to cope with spatial heterogeneity in the detection history. Occupancy $\Psi_{ij}$ is defined as the probability of at least one individual occurring at a given station:

$$\Psi_{ij} = 1 - e^{-\lambda_{ij}}$$

We use the term occupancy to indicate the probability that a species uses the area at each camera station (i.e., intensity of use). Because annual mean temperature was highly correlated to elevation ($r = .90$) (Table S1), we did not include it. To reduce the number

| Common name       | Scientific name          | IUCN red list | Body size | Activity pattern | Detections | Occupancy (95% BCI)          |
|-------------------|--------------------------|---------------|-----------|------------------|------------|-----------------------------|
| Amur tiger        | Panthera tigris altaica  | EN            | Large     | Night            | 126        | 0.32 (0.22–0.46)            |
| Amur leopard      | Panthera pardus orientalis | CR           | Large     | Day              | 82         | 0.36 (0.26–0.49)            |
| Wild boar         | Sus scrofa               | LC            | Large     | Day              | 534        | 0.89 (0.83–0.95)            |
| Roe deer          | Capreolus pygargus       | LC            | Large     | Day              | 1,124      | 0.96 (0.93–0.99)            |
| Sika deer         | Cervus nippon            | LC            | Large     | Day              | 508        | 0.57 (0.49–0.69)            |
| Red deer          | Cervus canadensis        | LC            | Large     | –                | 1          | Recorded once               |
| Black bear        | Ursus thibetanus         | VU            | Large     | Day              | 46         | 0.58 (0.35–0.86)            |
| Brown bear        | Ursus arctos             | LC            | Large     | –                | 1          | Recorded once               |
| Red fox           | Vulpes vulpes            | LC            | Small     | Night            | 291        | 0.38 (0.30–0.49)            |
| Asian badger      | Meles leucurus           | LC            | Small     | Night            | 551        | 0.79 (0.73–0.86)            |
| Raccoon dog       | Nyctereutes procyonoides | LC            | Small     | Night            | 125        | 0.50 (0.40–0.64)            |
| Musk deer         | Moschus moschiferus      | VU            | Small     | Day              | 19         | 0.17 (0.06–0.40)            |
| Siberian weasel   | Mustela sibirica         | LC            | Small     | Night            | 154        | 0.58 (0.47–0.72)            |
| Sable             | Martes zibellina         | LC            | Small     | Day              | 8          | 0.14 (0.02–0.44)            |
| Yellow-throated marten | Martes flavigula     | LC            | Small     | Day              | 86         | 0.52 (0.40–0.69)            |
| Leopard cat       | Prionailurus bengalensis | LC            | Small     | Night            | 70         | 0.54 (0.37–0.75)            |
| Eurasian otter    | Lutra lutra              | NT            | Small     | –                | 1          | Recorded once               |
| Eurasian red squirrel | Sciurus vulgaris        | LC            | Small     | Day              | 224        | 0.62 (0.51–0.75)            |
| Siberian chipmunk | Tamias sibiricus         | LC            | Small     | Day              | 214        | 0.60 (0.51–0.71)            |
| Amur hedgehog     | Erinaceus amurensis      | LC            | Small     | Night            | 21         | 0.29 (0.15–0.54)            |
| Manchurian hare   | Lepus manschuricus       | LC            | Small     | Night            | 989        | 0.76 (0.72–0.80)            |

Note: Occupancy probabilities were estimated under a hierarchical multispecies RN occupancy model, and values shown are the posterior means (with 95% Bayesian credible intervals) across all camera trap stations. IUCN status: CR, critically endangered; EN, endangered; LC, least concern; NT, near threatened; VU, vulnerable.
of modelled predictor variables and avoid overfitting models, we first ran single covariate models using each covariate that we selected a priori, and evaluated their importance by assessing effect sizes for each species in the community. Neither ruggedness, precipitation nor the distance to a road were significant for any of the species studied, so we dropped these variables from the model. Proximity to river did not show strong effects on species-level occupancy (except Asian badger). Because we were unable to account for seasonal water sources, we did not include distance to river in the final model. Several other studies showed that distance to water had a weak effect on species richness and occupancy of carnivore and ungulate at regional or global scales (Rich et al., 2016, 2017). Thus, eight covariates were added as a linear model with a log link:

$$\log(\hat{p}_i) = a_0 + a_1 (\text{elevation}) + a_2 (\text{elevation}^2) + a_3 (\text{distance to border}) + a_4 (\text{basal area}) + a_5 (\text{NDVI}) + a_6 (\text{distance to settlement}) + a_7 (\text{distance to settlement}^2) + a_8 (\text{cattle detection rate})$$

The probability $r_{ij}$ that an individual of species $i$ was detected at station $j$ was modelled as a function of 4 covariates. Our data $y_{ij}$ then come from a binomial distribution with the probability $p_{ij} = 1 - (1 - r_{ij})^{a_9}$, being the probability that at least one individual is detected and $k_i$ indicating the number of sampling occasions when each camera was active:

$$\log(\hat{r}_{ij}) = \rho_0 + \rho_1 (\text{human detection rate}) + \rho_2 (\text{undergrowth transparency}) + \rho_3 (\text{camera}) + \rho_4 (\text{trail})$$

and,

$$y_{ij} \sim \text{Binomial}(k_i, 1 - (1 - r_{ij})^{a_9})$$

We also hypothesized that body size and activity pattern may influence how a species responds to the respective covariates. Body size groups included small (0–20 kg, 12 species) and large-sized species (>20 kg, 6 species), and activity patterns included day (9 species) and night (9 species) (Tables 1 and S2). Activity patterns were based on the proportion of independent events recorded by the camera during the night (from sunset to sunrise) and day (from sunrise to sunset). Species were classified as diurnal (>60% of events at day) and nocturnal (<40% of records at day) (Table S2). Prior to analysis, we converted the clock time of each event to "sun time" based on dates and locations, and then, we adjusted sunrise and sunset to $\pi/2$ and $3\pi/2$, respectively. We also extracted activity pattern data from a comprehensive database, ELTONTRAITS v.1.0 (Wilman et al., 2014) to supplement and validate our data, especially for species that were detected infrequently. Given that animals could adjust their daily activity based on human pressures (Gaynor et al., 2018), we further evaluated the effects of humans on animal activity pattern to check the feasibility of designation of diurnal or nocturnal species (Appendix S1). Combining diet and body size, we further grouped species into four different taxonomic or functional groups: large carnivores (order Carnivora, 3 species), small carnivores (order Carnivora, 7 species), ungulates (order Artiodactyla, 4 species) and other foragers (orders Rodentia, Erinaceomorpha and Lagomorpha, 4 species). Following Rich et al. (2016), we assumed species-level parameters to be governed by both a group-level and community-level hyper-parameter and modelled the group-level and species-level parameters for the respective variable.

All continuous covariates were scaled to a mean of 0 and a standard deviation of 1. We modelled species-specific coefficients as random effects coming from a normally distributed, community hyper-parameter with a common mean and standard deviation (Rich et al., 2016; Zipkin et al., 2010). We used vague priors for all parameters. The significance of covariates was assessed by testing if the 95% Bayesian credible intervals (BCI) overlapped 0. The model was run in JAGS v4.3.0 using the R2Jags package in R (Su & Yajima, 2015). We ran three chains of 150,000 iterations with a burn-in of 50,000 and a thinning rate of 50. Model convergence was then assessed using the Gelman–Rubin statistic, where R-hat values <1.1 indicate good convergence (Gelman & Hill, 2007). We checked the adequacy of the model by using a Bayesian $p$ value based on the $\chi^2$ discrepancy in Pearson’s residuals (by comparing the observed residuals to residuals from data simulated under the model), with $p > .05$ or $p < .05$ considered a good fit (Gelman & Hill, 2007; Tobler et al., 2015). We also calculated a “lack-of-fit” statistic with values close to 1 suggesting a good model fit (Kéry & Schaub, 2012).

We estimated species richness using a station-level occurrence matrix $z_{ij}$ governed by the occupancy parameter $\Psi_{ij}$ ($z_{ij} = 1$ for present and 0 absent) by summing the number of estimated species at the level of individual camera stations. We further inferred station-level associations of richness with eight occupancy covariates by variance partitioning analysis using the R package "modEvA" (Barbosa et al., 2020). We combined variables into the three groups: "vegetation"—including NDVI and tree basal area, "human influence"—including distance to settlement and its square term and cattle detection rates, and "environment," consisting of elevation and its square term and distance to the border. We only allowed for the comparison of the unique and shared proportions of the variance explained by three factor groups. We conducted variance partitioning for mammalian species richness on a generalized linear model (GLM) with a Poisson family using the pseudo $R^2$ values obtained from the GLMs. To elucidate the spatial trend of mammalian richness in our study, we used empirical Bayesian kriging interpolation to map the model-predicted richness for the entire community at each station in ARCGIS 10.3. We used Moran’s I global indexes to examine the spatial autocorrelation of predicted richness at each station and calculated Moran’s I using the moranI function from the R package lctools. Spatial autocorrelation was evident for animal richness when the number of neighbours ranged from 2 to 4 (Moran’s I range = 0.12–0.24, z-scores between 2.24 and 3.24 at 95% confidence level). Thus, we can conduct interpolation.
3 | RESULTS

We recorded 5,175 detections of 21 mammal species over 22,976 trap days from ten taxonomic families and five orders (Table 1). Cameras were active for an average of 166 ± 28 (mean ± SD) trap nights. On average, camera stations detected 7 species (range 1–13). The species accumulation curves indicated that we likely recorded most species in our study area (Figure S1). Approximately half of the detected species (11 of 21) were listed as protected species by the Chinese Wildlife Conservation Law. Four species were categorized by the IUCN (2017) as globally threatened (vulnerable, critically endangered or endangered), and one species was categorized as near threatened. Roe deer Capreolus pygargus (n = 1,124) and Manchurian hare Lepus manchuricus (n = 989) were the most frequently detected species across stations, and Musk deer Moschus moschiferus (n = 19), sable Martes zibellina (n = 8) and Amur hedgehog Erinaceus amurensis (n = 21) were the least frequently detected (Table 1).

3.1 | Community-level and group-level summaries

The goodness-of-fit test showed a good fit of the full RN community model (Bayesian p = .89, lack-of-fit = 1.08). Posterior distributions for community-level hyper-parameters indicated a strong quadratic relationship between elevation, distance to settlement and occupancy (Table 2). NDVI and cattle were found to have significantly positive and negative influences on the community-level mammalian occupancy, respectively (Table 2). The use of paired cameras and off the road placement of cameras significantly improved the detection of most species; however, human detection rate and understory cover had unclear effects on the community detection probabilities (Table 3).

Model-predicted species richness at each camera trap ranged from 5 to 14 species (Table S3). Cattle presence had a significantly negative impact on species richness (Figures 2 and 3; Table S4). Richness was greater at intermediate elevations (approximately 6.5 km) and had a significantly positive relationship with NDVI. Variance portioning analysis further identified that human influences on all mammals accounted for a higher (21%) proportion of the variation than vegetation and environmental factors (6% and 6.8%, respectively) (Figure 4).

At the group level, the quadratic relationship between distance to settlement and occupancy was significant for both small and nocturnal species, and distance to settlement also had a significant, positive association with the occupancy of large species (Table 3). Large diurnal species had a positive relationship with increased NDVI and a negative relationship with an increased probability of cattle presence (Table 3). Elevation (including a squared term), distance to border and basal area were not related to the occurrence of any of these groups.

### TABLE 2 Community-level summaries of the hyper-parameters for occupancy (α1 to α8) and detection (β1 to β4) covariates hypothesized to influence the occupancy probabilities of 18 mammal species in Northeast China

| Community-level covariate | Mean | SD  | 95% BCI |
|---------------------------|------|-----|---------|
| α1_i Elevation            | 0.06 | 0.15| -0.22   |
| α2_i Elevation^2          | -0.10| 0.05| -0.22   |
| α3_i Distance to border   | -0.04| 0.15| -0.34   |
| α4_i Basal area           | 0.03 | 0.04| -0.05   |
| α5_i NDVI                 | 0.09 | 0.04| 0.01    |
| α6_i Distance to settlement| 0.15 | 0.10| -0.06   |
| α7_i Distance to settlement^2| -0.11| 0.03| -0.18   |
| α8_i Cattle detection rate| -0.16| 0.05| -0.25   |
| β1_i Human detection rate | 0.11 | 0.10| -0.08   |
| β2_i Undergrowth transparency| 0.09 | 0.05| -0.01   |
| β3_i Paired camera        | 0.65 | 0.14| 0.39    |
| β4_i Active road          | -0.40| 0.18| -0.78   |

Note: We present the posterior mean, standard deviation (SD) and 95% Bayesian credible intervals (95% BCI). Bold denotes covariates with significant effects on community occupancy.

3.2 | Species-level summaries

The mean detection probabilities (mean = 0.08, BCI = 0.01–0.26) showed high levels of heterogeneity among species, ranging from 0.02 for black bear (Ursus thibetanus) and leopard cat (Prionailurus bengalensis euptilurua) to 0.20 for Manchurian hare (Table S5). The mean probability of occupancy across all species and camera stations was 0.45 (95% BCI = 0.09–0.86), but occupancy also varied dramatically among species, ranging from 0.14 for sable to 0.96 for roe deer with 6 species having a probability of occurrence <0.5 (Table 1). There was a correlation between the detection probabilities and occupancy (r^2 = .37, p < .001).

Of the 18 species presented in the occupancy model, 10 were strongly (i.e., 95% BCI did not overlap zero) related to elevation (6 positively and 4 negatively), 6 to distance from the border (3 positively and 3 negatively), and 3 to distance into settlement (all positively) (Figure 5 and Table S6). A further four and six species were negatively influenced by the squared term of these two variables. Consistent negative impacts of cattle grazing on occupancy were documented for all species, and this trend was significant for ten species. In contrast, only roe deer and Amur leopard demonstrated a strong preference for areas dominated by high tree basal area and NDVI, respectively. Finally, the detection probabilities of three (Amur tiger, red fox Vulpes vulpes and Siberian weasel Mustela sibirica) of 18 species were strongly related to the detection rate of humans (Table S7).
### TABLE 3  Assemblage-level summaries (posterior mean and 95% Bayesian credible intervals are in parentheses) of the hyper-parameters for each occupancy covariate in Northeast China

| Assemblage       | Elevation    | Elevation² | Distance to border | Basal area | NDVI       | Distance to settlement | Distance to settlement² | Cattle detection rate |
|------------------|--------------|------------|--------------------|------------|------------|------------------------|-------------------------|-----------------------|
| **Body size**    |              |            |                    |            |            |                        |                         |                       |
| Small            | 0.10 (−0.35−0.55) | −0.12 (−0.34−0.07) | 0.08 (-0.19−0.37) | 0.14 (-0.02−0.32) | 0.05 (-0.09−0.18) | 0.02 (-0.22−0.25) | -0.14 (-0.26 - -0.03) | -0.12 (-0.28−0.03) |
| Large            | 0.14 (-0.53−0.79) | 0.07 (-0.24−0.36) | -0.40 (-0.82−0.03) | -0.02 (-0.27−0.26) | 0.27 (0.05−0.50) | 0.40 (0.05−0.75) | -0.03 (-0.21−0.17) | -0.24 (-0.51−0.03) |
| **Activity pattern** |              |            |                    |            |            |                        |                         |                       |
| Day              | 0.30 (-0.17−0.80) | 0.02 (-0.19−0.22) | -0.12 (-0.48−0.23) | 0.09 (-0.11−0.31) | 0.19 (0.03−0.36) | 0.06 (-0.27−0.41) | -0.08 (-0.22−0.07) | -0.19 (-0.39−0.01) |
| Night            | -0.12 (-0.58−0.34) | -0.19 (-0.41−0.02) | 0.07 (-0.28−0.43) | 0.12 (-0.07−0.34) | 0.01 (-0.15−0.17) | 0.20 (-0.12−0.54) | -0.15 (-0.29−0.01) | -0.11 (-0.30−0.06) |
| **Functional group (combining diet and size)** |              |            |                    |            |            |                        |                         |                       |
| Small carnivore  | -0.24 (-0.84−0.40) | -0.17 (-0.46−0.13) | 0.21 (-0.20−0.63) | 0.20 (-0.04−0.46) | 0.01 (-0.19−0.19) | 0.11 (-0.21−0.42) | -0.20 (-0.37−0.04) | -0.15 (-0.40−0.07) |
| Large carnivore  | 0.23 (-0.73−1.21) | -0.22 (-0.71−0.23) | -0.26 (-0.94−0.45) | -0.10 (-0.54−0.33) | 0.37 (0.03−0.81) | 0.95 (0.40−1.54) | -0.34 (-0.66−0.03) | -0.32 (-0.84−0.17) |
| Ungulate        | 0.26 (-0.56−1.12) | 0.09 (-0.34−0.49) | -0.36 (-0.92−0.20) | 0.11 (-0.22−0.48) | 0.24 (-0.02−0.52) | 0.01 (-0.42−0.43) | 0.11 (-0.13−0.38) | -0.22 (-0.46−0.01) |
| Other forager    | 0.49 (-0.30−1.28) | 0.03 (-0.32−0.38) | -0.03 (-0.49−0.46) | 0.07 (-0.23−0.41) | 0.09 (-0.14−0.31) | -0.09 (-0.46−0.31) | -0.09 (-0.27−0.11) | -0.10 (-0.39−0.18) |

*Note: Coefficients in bold indicate the 95% Bayesian credible intervals that do not overlap 0.*
4 | DISCUSSION

We analysed camera-trapping data using a multispecies occupancy model and examined the relative influences of natural and anthropogenic factors on mammal persistence in a temperate mixed forest in Northeast Asia shared by cattle and people. We demonstrated that anthropogenic features are of higher importance than natural features in determining local species occurrence patterns of different functional groups. Following our predictions, human disturbance has highly degraded animal communities, with overall richness being generally the lowest in the forested areas grazed by livestock. Our results provide a baseline understanding of the distribution and composition of the mammal community in the area, and suggest that managers need to develop land use incentives that reduce free-range cattle grazing and which could help refine strategies for improving wildlife conservation in multi-use landscapes.

4.1 | Determinants of species richness and occupancy

Our study showed that livestock presence and proximity to human settlements have a strong negative influence on species richness and occupancy; this finding supports our first and second hypotheses. These two disturbance factors are ubiquitous around the world (Robinson et al., 2014). Unsurprisingly, these factors have generated a significant loss of animal biodiversity on multiple trophic levels (Filazzola et al., 2020; Steinfeld et al., 2006; Tilker et al., 2020), as revealed by our results. Many studies in Asia and elsewhere also emphasize the negative effects of a high human footprint on wildlife occurrence and richness estimates (Easter et al., 2019; Harihar et al., 2014; Koerner et al., 2017; Macedo et al., 2018; Ripple et al., 2016). For example, Easter et al. (2019) and Koerner et al. (2017) found that mammal richness declined significantly with proximity to a village in Africa, indicating that the top-down force of hunting strongly affects the large wildlife community composition and structure. In the Terai Arc Landscape in South Asia, protected areas with settlements harbour lower densities of large carnivores and their ungulate prey than inviolate protected areas (Harihar et al., 2009, 2014) and have increased nocturnal activity of many species.

Similarly, we confirmed previous findings (Wang et al., 2017, 2018) that a strong negative impact of human settlement on predator-prey system (Figure 5). Hunting pressure near villages along with cattle grazing may decrease species richness and presence. For example, Soh et al. (2014) showed that low overall ungulate densities were associated with proximity to snares and villages in our study area. Furthermore, in the winter of 2017, approximately 420 snares were seized near villages in the eastern portion of our

![FIGURE 2 Estimated relative species richness at 138 camera stations in Northeast China in relation to (a) elevation, (b) distance to settlement, (c) NDVI and (d) cattle detection rate (mean detections per 100 trap nights)](image-url)
Our covariate responses suggest that impact by domestic cattle is much greater on large carnivores and their ungulate prey, including wild boar, roe deer and sika deer, confirming that livestock grazing can influence the trophic structure of ecological communities, in particular trophic levels directly dependent on plants, such as herbivores (Filazzola et al., 2020). Similar results were also observed in Indonesia; Pudyatmoko (2017) reported that large carnivores and herbivores were absent in areas with livestock. Cattle \( n = 1,548 \) detections) were photographed at 44% of all stations, with 73% recorded during the day in our study area; it has been widely observed that overlap with cattle in space and time greatly intensifies pressure on diurnal wildlife such as ungulates (Gaynor et al., 2018).

In grazing areas, cattle, which weigh >300 kg, reduce the plant biomass in the shrub–herb layer by ~24% (Wang et al., 2019), thus reducing habitat quality for the large wild ungulates (Yang et al., 2018). The cattle density was ca. 4–6 times the density of the three wild ungulates (derived from the north of the study area, wild boars 0.53 individuals/km\(^2\), roe deer 1.22 and sika deer 0.15) (Qi et al., 2015). Camera-trapping data also showed that the detections for cattle were 1.4–3.0 times greater than those for three major prey species. These data are in accordance with earlier findings in Africa and North America that showed the impact of resource competition by livestock on large wildlife (Schieltz & Rubenstein, 2016; Stewart et al., 2002). The impact of livestock on large ungulates in turn has a cascading impact on large carnivores by reducing the distribution of their major prey. In western and southern Asia, grazing by domestic livestock may also reduce the distribution and abundance of large prey, thereby decreasing the density and even resulting in local extirpation of tigers and leopards (Madhusudan, 2004; Punjabi

![FIGURE 3](image)

**FIGURE 3** Empirical Bayesian kriging interpolation of the model-predicted number of mammalian species at each station from the full RN community model and the spatial patterns of the detection rate per 100 days for cattle (red point) from May 2015 to October 2015. Black points represent camera traps where cattle were not observed.
4.2 Conclusions and management implications

Our study identified the determinants of community, group and species occupancy and determined the areas that are most likely to support the highest levels of species richness. Our results underscore the importance of anthropogenic factors in limiting species occurrence and provide a starting point for landscape-level conservation planning. Cattle grazing areas have probably the greatest resistance to the movement of wide-ranging and sparsely distributed mammals (Wang et al., 2016). Reducing grazing or shifting to stall-feeding will also greatly reduce tiger predation on free-roaming cattle (Soh et al., 2014). Thus, management should be directed to developing alternative human livelihoods that promote biodiversity and create recreational opportunities. Given the socio-economic complexities in this region and their importance as part of the national biodiversity and ecosystem services network (Xu et al., 2017), landscape conservation planning is needed not only for the tiger–leopard landscape but also for the entire Changbai Mountain landscape. Planning at this scale is especially important because this landscape contributes to regional biodiversity as well as to the national goal of increasing ecological services critical to the well-being of the Chinese people.

However, shifting local livelihoods from forestry and cattle grazing will require retraining forest rangers to serve as technicians to monitor regional biodiversity, patrol and manage the expanding tiger–leopard landscape (McLaughlin, 2016). These livelihood changes are already being implemented, and a key part of planning is to develop and test incentives to encourage a proportion of the existing forest ranger labour force to shift to urban employment where there is great access to education and health services. The remaining forest rangers need to be retrained to patrol and monitor biodiversity and operate the expanding remote animal and ecosystem monitoring system. As rangers acquire new skills, they are likely to also feel increased professional pride (Gurung et al., 2009).
Rural agricultural communities also need incentives to shift to urban areas or to transition from free-range cattle grazing to stall-feeding livestock and to develop a more diverse rural economy that provides regional and national opportunities for recreation and protected area tourism. Central government assistance via the creation of incentives and policies that support provincial government initiatives will be required to accomplish these changes in the livelihood of rangers and local farmers. These changes can be centered on the new electronic monitoring system being developed by the National Forestry and Grassland Administration and academic institutions (Li, Zhao, et al., 2019). As China continues to develop economically, networks of connected, rural working conservation landscapes such as the Northeast Tiger Leopard National Park provide needed ecological services and green spaces for an increasingly urbanized national population.

The recovery of tigers and leopards and the expansion of their ranges into the Changbai Mountains are of particular importance to efforts to establish a network of national biodiversity and ecosystem service landscapes. These species have wide charismatic appeal, both nationally and internationally, that can increase support
for this initiative. Furthermore, China’s focus on tiger and leopard recovery and its cooperation with Russia (Feng et al., 2017; Vitkalova et al., 2018) in creating a transboundary tiger landscape will increase China’s growing leadership in demonstrating that biodiversity and human well-being are essential to developing an ecologically sustainable global system.

ACKNOWLEDGEMENTS

We thank Francesca Cuthbert and the anonymous referees for their comments and suggestions that greatly improved our manuscript. This work was supported by grants from the National Natural Science Foundation of China (31971539, 31270567) and the National Key Research and Development Program (2016YFC0500106). J.L.D. Smith’s contribution to this research was supported by the USDA National Institute of Food and Agriculture. Our camera-trapping protocol was approved by the Chinese National Forestry and Grassland Administration. Non-invasive camera-trapping technology did not involve direct contact with animals.

CONFLICT OF INTEREST

The authors declare no conflicts of interest associated with this study.

PEER REVIEW

The peer review history for this article is available at https://publo ns.com/publon/10.1111/ddi.13237.

DATA AVAILABILITY STATEMENT

The data supporting the results are available on the DRYAD digital repository https://doi.org/10.5061/dryad.2jm63xsnp.

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**BIOSKETCH**

This work was a part of a long-term Tiger Leopard Observation Network (TLON) of camera traps along the border of Russia. The research team includes specialists working on biology, ecology, taxonomy, conservation and management of animal community in Northeast Asia.

Author contributions: T.W., J.F. and J.G. conceived the ideas and designed methodology; J.F. and T.W. analysed the data; T.W. and J.L.D.S. led the writing of the manuscript, with input from all authors; all authors contributed to interpretation of results, contributed critically to the drafts and gave final approval for publication.

**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section.

**How to cite this article:** Feng J, Sun Y, Li H, et al. Assessing mammal species richness and occupancy in a Northeast Asian temperate forest shared by cattle. *Divers Distrib.* 2021;27:857–872. https://doi.org/10.1111/ddi.13237