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Abundance patterns of mammals across Russia explained by remotely sensed vegetation productivity and snow indices

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Abstract

Aim: Predicting biodiversity responses to global changes requires good models of species' distributions. Both environmental conditions and human activities determine population density patterns. However, quantifying the relationship between wildlife population densities and their underlying environmental conditions across large geographical scales has remained challenging. Our goal was to explain the abundances of mammal species based on their response to several remotely sensed indices including the Dynamic Habitat Indices (DHIs) and the novel Winter Habitat Indices (WHIs).

Location: Russia, the majority of regions.

Taxon: Eight mammal species.

Methods: We estimated average population densities for each species across Russia from 1981 to 2010 from winter track counts. The DHIs measure vegetative productivity, a proxy for food availability. Our WHIs included the duration of snow-free ground, duration of snow-covered ground and the start, end and length of frozen season. In models, we included elevation, climate conditions, human footprint index. We parameterized multiple linear regression and applied best-subset model selection to determine the main factors influencing population density.

Results: The DHIs were included in some of the top-twelve models of every species, and in the top model for moose, wild boar, red fox and wolf, so they were important for species at all trophic levels. The WHIs were included in top models for all species except roe deer, demonstrating the importance of winter conditions. The duration of frozen ground without snow and the end of frozen season were particularly important. Our top models performed well for all the species (R^2_{adj} 0.43–0.87).

Main Conclusions: The combination of the DHIs and the WHIs with climate and human-related variables resulted in high explanatory power. We show that vegetation productivity and winter conditions are key drivers of variation in population density of eight species across Russia.

KEYWORDS

animal abundance, dynamic habitat indices, Russia, Winter Habitat Indices, winter track counts

1 | INTRODUCTION

Population densities of wild species vary greatly in space and time (Currie et al., 1993). Environmental conditions and human activities strongly influence population density (Melis et al., 2009; Muhly et al., 2013), and discerning the relative importance of these factors is important for better understanding of broad-scale biogeographic pattern of species' abundances and distributions. Remote sensing offers many advantages as a tool to explain broad-scale population density patterns because satellite data provide consistent information about habitat conditions including land cover, primary productivity, snow cover, soil freeze-and-thaw status and human disturbances across large areas (Kerr & Ostrovsky, 2003; Turner, 2014; Turner et al., 2003).

Understanding what causes variation in population densities is a central question in ecology and biogeography. Food availability is an important bottom-up factor, and plant productivity influences the density of herbivores (Oksanen et al., 1981; Scherber et al., 2010). In tri-trophic systems (i.e. plants, herbivores and carnivores), the relationships become less clear because herbivore densities may be influenced by both top-down and bottom-up effects (Oksanen et al., 1981; Ripple & Beschta, 2012). In such systems, carnivore densities may show a positive relationship with plant productivity while herbivore densities are relatively stable across productivity gradients (Oksanen et al., 1981; Ripple & Beschta, 2012). Remotely sensed estimates of plant productivity, especially the suite of MODIS vegetation products, provide great opportunities to explore such relationships. Ecological theory suggests that several aspects of annual productivity, especially a) the cumulative productivity throughout the year, b) the minimum productivity and c) the variation in productivity matter for biodiversity because they are related to the available energy hypothesis (Bonn et al., 2004; Hawkins et al., 2003; Mittelbach et al., 2001; Wright, 1983), the environmental stress hypothesis (Connell & Orias, 1964; Currie et al., 2004) and the environmental stability hypothesis (Hurlbert & Haskell, 2003; Williams & Middleton, 2008) respectively (Radeloff et al., 2019). That is why the three Dynamic Habitat Indices (DHIs, Coops et al., 2008) are cumulative productivity, minimum productivity and variation in productivity. Indeed, the DHIs are good predictors of the species richness of birds in North America (Coops, Waring, et al., 2009; Coops, Wulder, et al., 2009; Hobi et al., 2017) and Thailand (Suttidate et al., 2019), of butterflies in Canada (Andrew et al., 2012) and of moose abundance in Ontario, Canada and in Russia (Michaud et al., 2014; Razenkova et al., 2020).

In middle and high latitudes, population densities are quite sensitive to winter habitat conditions because food is less available, while energetic demands are higher, which affects survival rates. The duration of both the frozen season and snow cover are important for wildlife, and frozen ground without snow cover is particularly challenging because of limited availability of accessible moisture, and because many northern species rely on snow cover for insulation (Gilg et al., 2012; Korslund & Steen, 2006; Reid et al., 2012; Shipley

et al., 2019; Sinclair et al., 2013). Also, the depth and density of snow cover affect animal movement, food availability and the ability of small mammals to tunnel. For example, the duration of snow cover affects hare abundance (*Lepus* spp.) (Pedersen et al., 2017), and distribution (Sultaire et al., 2016). Snow cover also determines moose distribution (Formozov, 2010), and ice-covered ground limits reindeer foraging (Hansen et al., 2011). Satellite data can detect both frozen ground (Zhu et al., 2017) and snow cover (Hall et al., 2002), thereby capturing key aspects of winter habitat conditions such as the duration of frozen ground with and without snow cover, and the start, end and length of the frozen season (Zhu et al., 2017, 2019). These Winter Habitat Indices (WHIs) provide exciting new opportunities to quantify the effects of winter habitat conditions and predict winter bird diversity well (Gudex-Cross et al., 2021).

Our study provides a unique opportunity to examine regional variation in population densities of wildlife, using unique abundance data that have been collected across Russia. The broad expanse of Russia encompasses large variation in population densities, environmental and climate conditions and anthropogenic activities. The aim of our work was to advance understanding of population densities of eight mammal species across Russia in response to several new remotely sensed indices. In particular, we explore how much variation in population densities is explained by indices for primary productivity, that is, the DHIs, and winter habitat conditions, that is, the WHIs, while including other frequently used remotely sensed indices for elevation, climate and anthropogenic activities. The newly released WHIs have never been related to any wildlife population data. Furthermore, the DHIs were originally designed to model species richness, and only a few studies have related the DHIs to abundance of large mammals. Assessment of the factors driving variability in population density across regions is important for understanding underlying mechanisms shaping those population patterns. We formulated expectations about how the newly released indices of DHIs and WHIs are related to densities of each of the eight mammal species (Table 1). In general, we expected positive relationships for all species between population density and cumulative DHI and minimum DHI, and negative relationships with variation DHI, especially for herbivores (Table 1). Further, we expected that with increasing severity of winter conditions (e.g. length of frozen season or duration of snow cover), population densities would decrease, except for carnivores which are not affected by snow in the same way as herbivores (Table 1).

2 | MATERIALS AND METHODS

2.1 | Study area

The vast area of Russia provides an excellent opportunity to answer our research questions because Russia contains a wide range of vegetation types and climate conditions. Mountain ranges are located in the south (Caucasus Mountains), in eastern Siberia (Altai Mountains, Verkhoyansk Range, Sayan Mountains and

TABLE 1 Our expectations and predictions for the relationship between the densities for each species and the remotely sensed indices of habitat conditions (DHIs and WHIs)

Species	Dynamic habitat indices	Winter habitat indices	Reference
European hare (<i>Lepus europaeus</i>) (herbivore)	Positive relationship with cumulative DHI and minimum DHI because hares being herbivores require vegetation as food.	Negative relationship with duration of snow cover because European hare do not change their coat colour making them more prone to predation.	Sultaire et al. (2016), Mills et al. (2018)
Moose (<i>Alces alces</i>) (herbivore)	Positive relationship with cumulative DHI and minimum DHI because of the herbivore's dependence on vegetation as food.	A negative relationship with the duration of snow cover because it is harder to escape from predators in deep snow and food availability during winter.	Post et al. (1999), Razenkova et al. (2020)
Roe deer (<i>Capreolus pygargus</i> Pallas, <i>Capreolus capreolus</i> Linnaeus) (herbivore)	Positive relationship with cumulative DHI and minimum DHI because of the herbivore's dependence on vegetation as food.	A negative relationship with the duration of snow-covered ground because roe deer are not well adapted to severe winter condition, and snow depth is one of the limiting factors for the range of roe deer.	Mysterud and Østbye (2006), Danilkin (2008)
Brown bear (<i>Ursus arctos</i>) (omnivore)	Positive relationship with cumulative DHI and minimum DHI because plant productivity is a proxy for food availability for bears.	Negative relationship with duration of snow cover because snow cover limits food availability, and because bears prefer denning sites with less snow.	Pigeon et al. (2016), Berman et al. (2019)
Wild boar (<i>Sus scrofa</i>) (omnivore)	Positive relationship with cumulative DHI because of food availability.	A strong negative relationship with the duration of snow-covered ground and the length of the frozen season because boar frequently root in the ground to reach food, and cannot do so when the ground is frozen.	Melis et al. (2006), Massei et al. (2015)
Lynx (<i>Felis lynx</i>), red fox (<i>Vulpes vulpes</i>), wolf (<i>Canis lupus</i>) (carnivore)	Positive relationship with cumulative DHI and minimum DHI because higher plant productivity increases prey densities.	Positive relationship with duration of snow cover, because of their ability to move on top of snow, whereas their prey cannot.	Matyushkin and Vaisfeld (2003), Mech and Boitani (2003)

Chersky Range), in the Far East (Sikhote-Alin Mountains) and divide European from Asian Russia (Ural Mountains) (Figure S1a). The dominant climate is continental in European Russia and subarctic in Asian Russia, with a gradient of increasing annual mean temperatures from northeast to south, and the lowest temperatures are in Yakutia (Figure S1b). Annual mean precipitation also increases from north to south, and is highest in the Caucasus (southwestern Russia), and Primorsky, Khabarovsk and Kamchatka Krai (all in far eastern Russia Figures S1c and S2). Human population density is variable across Russia, with higher density in the European part (Figure S1d). Forest loss has occurred in recent decades mainly in the boreal forests (taiga), especially in Siberia (Krasnoyarsk Krai, Irkutsk, Yakutia) due to fire (Hansen et al., 2013). European Russia (Stavropol Krai, Krasnodar Krai, Orenburg, Saratov, etc.) and southern Siberia (Altai Krai, Novosibirsk) are well suited for agriculture (Lesiv et al., 2018).

2.2 | Data

2.2.1 | Wildlife population data for eight mammal species

We analysed eight mammal species with different life histories including European hare (*Lepus europaeus*), moose (*Alces alces*), roe

deer (*Capreolus pygargus* Pallas, *Capreolus capreolus* Linnaeus), brown bear (*Ursus arctos*), wild boar (*Sus scrofa*), lynx (*Felis lynx*), red fox (*Vulpes vulpes*) and wolf (*Canis lupus*). We obtained estimated abundance data for each species per year and per region from the Russian Federal Agency of Game Animals from 1981 to 2010 (Borisov et al., 1992; Gubar et al., 2007; Lomanov et al., 1996, 2000, 2004; Lomanova et al., 2011). The vast majority of the data were collected using Winter Track Counts (Kuzynkin, 1983; Lomanov et al., 2000), which have been conducted annually since 1981 for all of Russia, on approximately 30,000 transects (Gubar et al., 2007). The Winter Track Counts protocol involves counting animal tracks crossing fixed 8–12 km transects, which are visited after the hunting season and when snow is present. Each transect is surveyed on two subsequent days. On the first day, all prior tracks are removed, and on the second day, fresh tracks from the last 24 h are counted. Transects capture different types of land cover including forest, wetlands and open areas. The track counts are combined with a second survey of the daily travel distance of each species. Daily travel distances vary depending on factors such as snow depth, climate and human density or activity. Combining track counts and travel distances results in an estimate of the number of individuals of each species in each region and year in winter based on the equation: $D = \pi \times A/2 \times L$, where D is the average number of animals of a given species per 10 ha, A is the average number of times tracks of that species cross 10 km of transect, and L is the average daily travel distance of that

species (Chelintsev, 2000; Stephens et al., 2006). In addition, aerial surveys were conducted to validate Winter Track Counts in remote areas (Lomanov et al., 1996). For brown bear, which hibernates during winter, home range mapping and aerial surveys were employed (Gubar, 1990).

After the collapse of the Soviet Union in 1991, some regions of Russia were subdivided. In order to consistently analyse data for all thirty years of our study, we combined those separated regions to make them comparable to the pre-1991 administrative boundaries; in total, we analysed 71 regions. For each species, we excluded regions if three consecutive years of data were missing, and those that were outside of the range of a given species to avoid zero-inflated models (Table S1). Only red fox occurred in all 71 regions.

Data from 1996 for all species, and from 1997 for European hare and red fox, were not available, and some values for specific regions were missing in other years. In these cases, we applied linear interpolation thereby filling missing values based on the straight line between the two nearest dates for which data were available (Table S1). During our study period, wildlife populations changed rapidly, primarily to overexploitation (Bragina et al., 2015) during the politically unstable period after the Soviet Union collapse in 1991 (Figure S3), so we calculated the average of population densities for 1981–2010. We used linear interpolation to fill missing data because the average over the 30-years is potentially different from the average for the available years. For example, if a species had low population density values from 2000 to 2010 and there were missing data for this decade, the average of population density would be biased high, and if a species had high population density, then the average would be biased low.

We restricted the area for which we summarized the predictor variables to each species' range, and converted each species' abundance into density by dividing the average abundance from 1981 to 2010 by the area of suitable habitat (see below) that falls within the range of that species. To do so, we used range maps from the Russian Academy of Science for brown bear and European hare (Pavlov et al., 2002), from IUCN for lynx and wolf (IUCN, 2001), from Soviet literature for red fox (Heptner et al., 1967), wild boar and roe deer (Danilkin, 1999, 2002) and for moose, we drew from Lomanov et al. (1996). Roe deer species (*Capreolus pygargus Pallas* and *Capreolus capreolus Linnaeus*) are not differentiated in the game surveys, so we combined their ranges. Using a MODIS land cover map, we defined the land cover classes that can be considered as suitable habitat for each species (Table S2) and calculated the area of suitable habitat to determine regional population densities (Figure 1). We defined suitable habitat for each species based on literature (Baskin & Danell, 2003; Matyushkin & Vaisfeld, 2003) and expert knowledge (Tables S1 and S2).

2.2.2 | Dynamic habitat indices

The DHIs characterize three aspects of vegetative productivity: annual cumulative productivity (cumulative DHI), which is the overall

productivity throughout the year; annual minimum productivity (minimum DHI), which is the minimum value of productivity of a year; and seasonal variation (variation DHI) expressed as the coefficient of variation in productivity for a year (Figure S1e, Coops et al., 2008; Hobi et al., 2017; Radeloff et al., 2019). We calculated the DHIs from a time series of the 2003–2014 median values of the MODIS Fraction of Absorbed Photosynthetically Active Radiation (FPAR) data for each of the 46 dates of the 8-day MODIS product (Hobi et al., 2017; Radeloff et al., 2019) generated each year. The DHIs calculated from median productivity values (in this case FPAR) represent average annual vegetative productivity and eliminate year-to-year variation, which matched our study goal of investigating long-term averages of population density. We calculated mean values for each region within the suitable habitat of each species for the three DHIs.

2.2.3 | Land cover

We analysed the MODIS land cover product to map stable land cover for 2003–2012 (Friedl et al., 2010), as we expected higher abundance of most species in suitable habitat that was consistently available among years. For a given pixel, if one land cover type was present for more than half of that time, we treated it as stable (Figure S1f).

2.2.4 | Winter habitat indices

To include winter-related variables in our models, we used a recently developed dataset with 500-m spatial resolution that provided data for the duration of snow-covered ground (DWS WHI), the duration of snow-free frozen ground (DWOS WHI), the timing (start and end date) and the length of the frozen ground season from 2000 to 2012 (Figure S1g,h, Zhu et al., 2017, 2019). Zhu et al. (2017) derived these variables from combined 8-day MODIS snow cover product (MOD10A2) and the NASA MEaSUREs Global Record of Daily Landscape Freeze/Thaw Status dataset (FT-ESDR). The start of the frozen season was defined as the middle day of the first 15 consecutive days from September to February when ground was frozen ≥ 8 days. The end of the frozen season was defined as the middle day of the first 15 consecutive days from March to August when ground was thawed ≥ 8 days. The duration of snow-covered ground was defined as the number of days during the frozen season when frozen ground was covered by snow and the duration of snow-free frozen ground as the number of days when frozen ground was not covered by snow (Zhu et al., 2019). We calculated mean values for each region within the suitable habitat of each species for all winter-related variables. The duration of snow-free frozen ground and the duration of snow-covered ground were not available everywhere, so we calculated mean values for partially available data and assigned zero for areas affected by polar night.

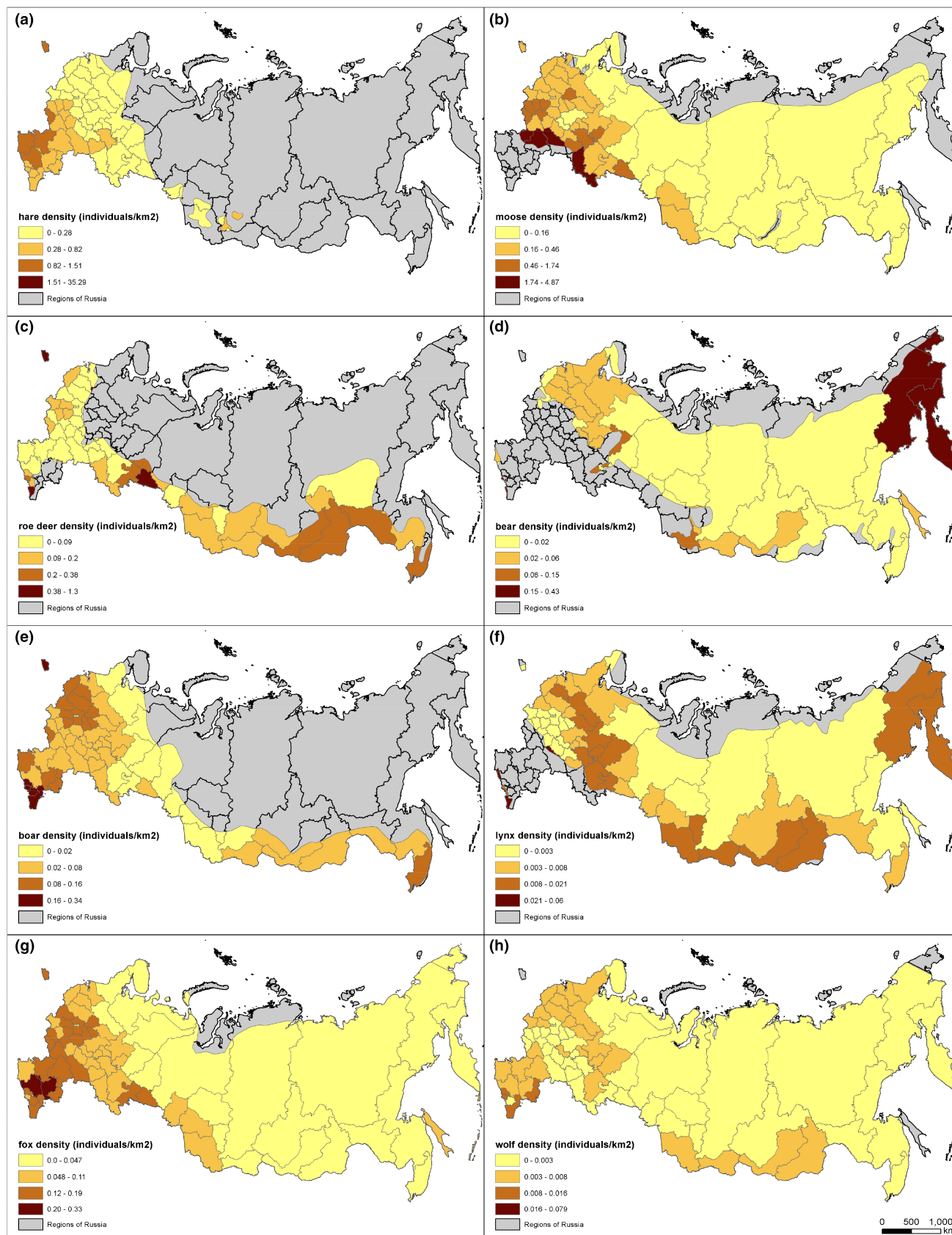


FIGURE 1 Average population density (individuals per 1 km²) over 1981–2010 period corrected by suitable habitat area within the range for each species. The species are European hare (*Lepus europaeus*), moose (*Alces alces*), roe deer (*Capreolus pygargus* Pallas, *Capreolus capreolus* Linnaeus), brown bear (*Ursus arctos*), wild boar (*Sus scrofa*), lynx (*Felis lynx*), red fox (*Vulpes vulpes*) and wolf (*Canis lupus*) across Russian's regions. The projection of the map is Albers equal area conic projection (Datum D European 1950).

2.2.5 | Elevation and bioclimatic variables

We used 1-km resolution elevation and bioclimatic data (Figure S1a–c, Hijmans et al., 2005). The elevation data are from the Shuttle Radar Topography Mission (SRTM), and bioclimatic data are from Worldclim.org. We calculated mean values for each region within the suitable habitat of each species.

2.2.6 | Human disturbance

As proxies of human disturbance, we included 1-km road density data (Hijmans et al., 2001), which are based on the Digital Chart of the World and include primary and secondary roads, and 1-km human footprint index (Figure S1d, Sanderson et al., 2002). The human footprint index is based on nine variables that capture human population pressure (population density), land use and infrastructure (built-up areas, nighttime lights, land use/land cover) and human access (coastlines, roads, railroads, navigable rivers). The human footprint index represents the cumulative human pressure on the environment, and higher values indicate greater pressure (Sanderson et al., 2002). We calculated the mean human footprint index value for each region within the range of each species, and road density for each region, defined as the length of roads within the region divided by its area.

2.2.7 | Statistical analyses

To model population densities, we applied multiple linear regression, best subset model selection, and for the top model 10-fold cross validation and hierarchical partitioning analysis. Best subset regression fits models using all possible combinations of independent variables, and ranks them by Bayesian information Criteria (BIC). Our dependent variable was population density, and explanatory variables were the cumulative, minimum and variation DHIs, road density, human footprint index, elevation, 19 bioclimatic variables, duration of snow-free frozen ground, duration of snow-covered ground and start, end and length of the frozen season. To ensure that the assumptions of linear regression model were met, that is, that the residuals of the model were normally distributed, we log-transformed the density of brown bear, lynx, moose, red fox, roe deer and wolf. We excluded outliers according to the Bonferroni outlier test (Table S1, Cook & Weisberg, 1982). We calculated Pearson's correlation coefficients among all explanatory variables and removed highly correlated variables while retaining the most important variables (Table S3, and described below. Also, see workflow of the statistical analysis Figure S4).

We conducted best subset regression analyses for each species to identify variables that were most frequently included in the top-twelve models. Then we calculated the percentage of the explanatory variables that were present in those models (Table S3). We then reduced the candidate set of explanatory variables by applying a three-step selection process: we selected variables that 1) appeared in most top-twelve models for all species or appeared in more than 8 models

for one species; 2) are ecologically important for each individual species; and 3) removed one of each pair of variables that had correlation coefficient >0.8 . After running best subset regression with all explanatory variables for all species (Table S3), we reduced the full set to the following subset: the three DHIs, human footprint index, elevation, isothermality, maximum temperature of the warmest month, precipitation of the wettest quarter, precipitation seasonality, duration of snow-free frozen ground, duration of snow-covered ground, start and end of the frozen season. Road density, mean temperature of warmest quarter and both precipitation of the wettest quarter and precipitation of the warmest quarter were removed due to high collinearity with human footprint, max temperature of the warmest month and precipitation of the wettest month, respectively (Table S3). Correlation was <0.8 among these remaining explanatory variables. We refitted models with the reduced set of explanatory variables and ranked them based on BIC. Most of the remaining explanatory variables were included in the top-twelve model of at least one species, but which variables were important varied greatly among species. For each species' top model, we plotted QQ plots to ensure that the residuals follow a normal distribution and calculated the variance inflation factor (VIF, where a VIF >10 indicates high multicollinearity) (Figure S5). To assess the predictive performance of the top model for each species, we performed a 10-fold cross validation and evaluated several metrics: the mean absolute error (MAE), the root mean squared error (RMSE), the standard deviation calculated of the coefficient of determination across the 10-folds of the cross validation (SD), and the average of coefficient of determination across the 10-folds of the cross validation (R^2). Low values for MAE, RMSE, SD and high values of R^2 are indications of the ability of model to predict actual observations. For the 10-fold cross validation, we split the data into 10 subsets, reserved one subset for testing our model and trained the model on remaining subsets, repeated that procedure 10 times and calculated the prediction statistics. Lastly, we ran hierarchical partitioning analysis of the top model to estimate the independent contributions of each variable to total variance explained (Chevan & Sutherland, 1991).

2.2.8 | Check for data quality

To test if the quality of Winter Track Counts data changed over time, we conducted several tests. We divided the data into three decades that captured the transition from planned to open-market economies: 1981–1990, 1991–2000 and 2001–2010. We assumed that data were of higher quality for the Soviet period (1981–1990), and that quality declined after the collapse of the Soviet Union. The years after the dissolution of the Soviet Union in 1991 were a time of instability for Russia. During this time major political and economic changes occurred, including the transition from state-command to open markets, land privatization (Lerman & Shagaida, 2007), farmland abandonment (Ioffe et al., 2004; Prishchepov et al., 2012), rising poverty rate (United National Statistics Division, 2016), as well as the rapid decline of wildlife populations due to overexploitation (Bragina et al., 2015). Due to all of these changes, Russian wildlife

management agencies may have been less effective than in prior decades. First, we calculated the correlation coefficients for average population densities for the entire study period (1981–2010) versus those averages for 1981–1990, 1991–2000 and 2001–2010. Second, we calculated the coefficient of variation (CV) for each year across all regions to see if CVs changed over time. We assumed that noisier data would correspond to higher CVs. A high CV could also reflect other patterns, for example, if European hare and lynx had cyclical population dynamics. However, neither of these two species exhibited a population cycle in our 30-year data, which is why we assumed that higher CVs indicated noisier data. Third, we calculated CVs for each of the three decades to see if there was a systematic difference among decades. This test, conducted for moose in Razenkova et al. (2020), found no difference among decades, and we checked other species here. Fourth, we checked if there was a significant difference between the CVs for three periods using a) the asymptotic test for the equality of coefficients of variation from k populations (Feltz & Miller, 1996), and b) the modified signed-likelihood ratio test (MSLRT) for equality of CVs (Krishnamoorthy & Lee, 2014). Finally, we checked for difference in the spatial autocorrelation of the residuals of the top models for the entire time period and for the three decades. To do so, we fitted non-parametric covariance function and plotted the spline correlograms with a 95% confidence interval, using 1000 permutations with a distance 5000km for seven species and 2000km for European hare (Bjørnstad & Falck, 2001). We chose a smaller maximum lag distance for European hare because this species occurs only in European Russia, which has smaller regions, and thus where correlations for longer lag distances could not be reliably calculated.

We performed all analyses in R 3.3.1 (R Core Team, 2016), including packages 'psych' to calculate correlation matrices (Revelle, 2017), 'leaps' to perform the best subset selection (Lumley, 2009), 'car' to run Bonferroni outlier test to identify outliers and calculate VIF for explanatory variables (Fox & Weisberg, 2016), 'caret' for cross-validation (Kuhn et al., 2021), 'hier. part' for hierarchical partitioning analysis (Walsh & Mac Nally, 2013), 'cvequality' to test for significant difference in CVs (Marwick & Krishnamoorthy, 2019) and 'ncf' to plot spline correlograms (Bjørnstad, 2020).

3 | RESULTS

For herbivores, we found that only moose density had positive relationships with cumulative DHI and minimum DHI. European

hare and roe deer did not have a strong positive relationship with either cumulative DHI or minimum DHI (Figure 2, Table 2). Among the WHIs, we found that the duration of snow-covered ground was an important variable only for European hare, but the duration of snow-free frozen ground was included in the top-twelve models for all herbivores, and the end of the frozen season was included in the top-twelve models for moose and roe deer density (Figure 2).

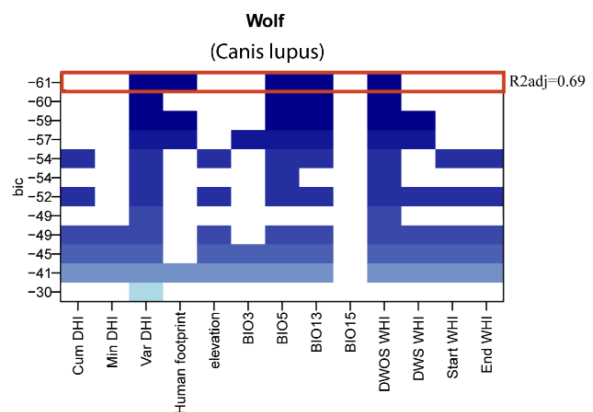
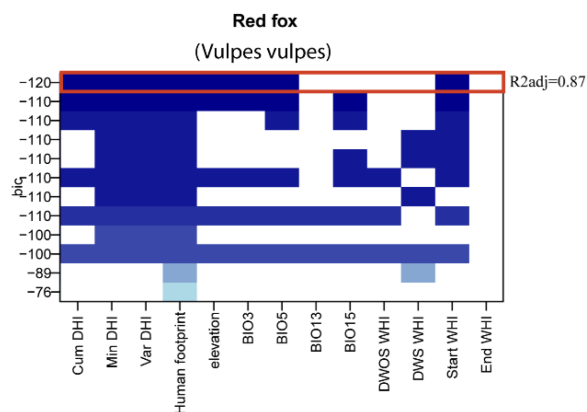
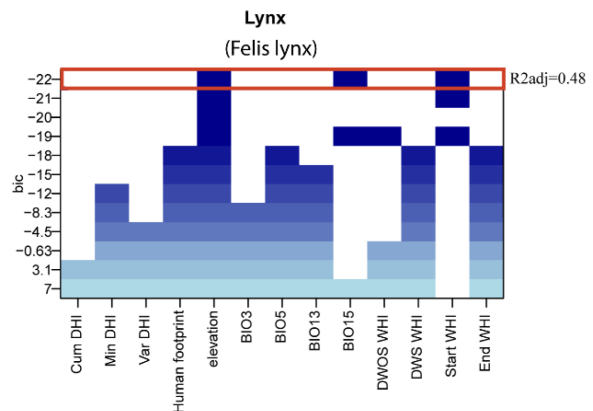
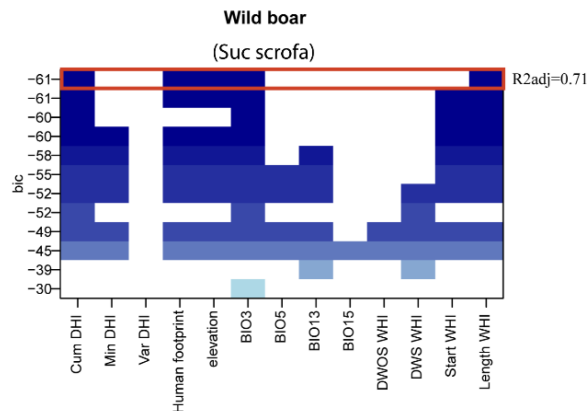
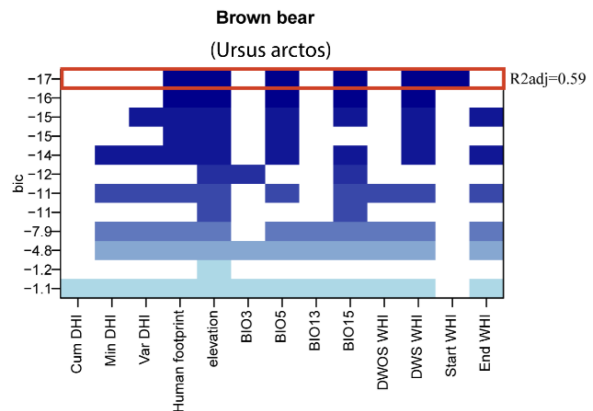
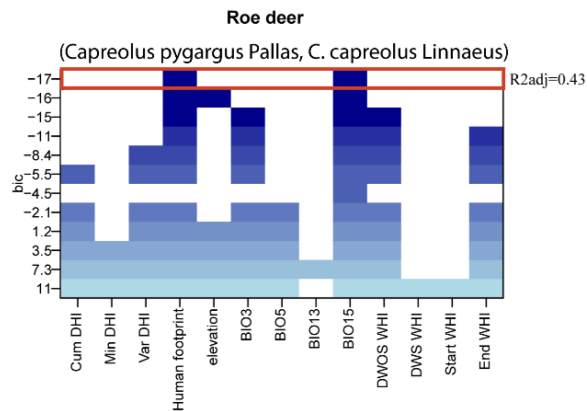
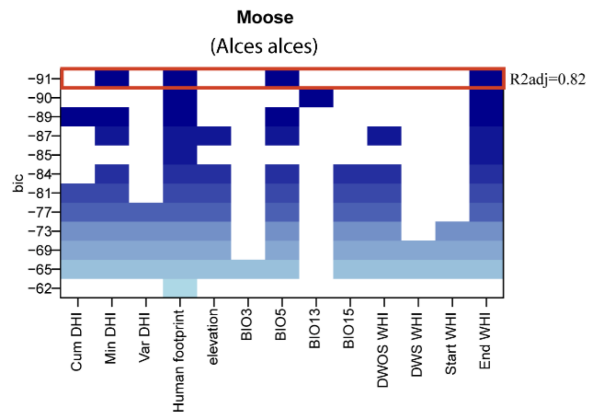
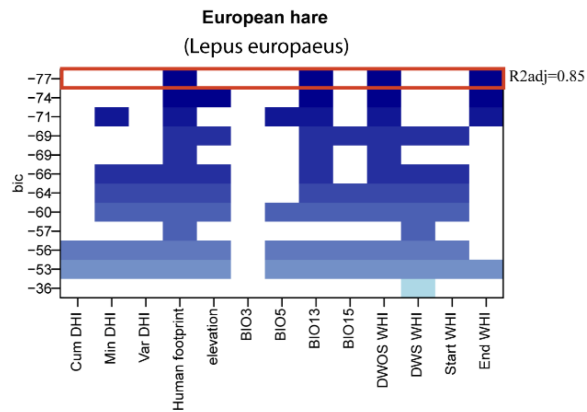
For omnivores, we found a positive relationship with cumulative DHI for wild boar, but not for brown bear (Figure 2, Table 2). Wild boar density was negatively associated with duration of snow-covered ground, while the density of brown bear was positively associated with duration of snow-covered ground. The density of brown bear was positively related to minimum DHI, however, minimum DHI was not a strong predictor and appeared in only five of the top-twelve models (Figure 2, Table 2).

We found that cumulative DHI was included in the top-twelve models for red fox and wolf, but not in the models for lynx. However, red fox density was negatively related to cumulative DHI (Table 2). Minimum DHI appeared in most of the top-twelve models for red fox, but in only six and three of the top-twelve models for lynx and wolf, respectively. The directionality of the relationship between minimum DHI and carnivore density varied in that there was a positive relationship for lynx, but negative relationships for red fox and wolf. Lynx and wolf had positive relationships with duration of snow-covered ground, while red fox had a negative relationship with this variable (Figure 2, Table 2).

Our top models explained medium to high levels of variation in population density of all eight species ($R^2_{adj} = 0.43\text{--}0.87$, Figure 2). With one exception, the VIF of all parameters in top models was less than 5, indicating an absence of multicollinearity in models (Table S4). The exception was red fox, in which both variation DHI and maximum temperature of warmest month had VIF = 5. While a VIF >10 indicates significant multicollinearity in the model, these VIF values of 5 are still relatively low. The evaluation metrics MAE, RMSE and SD calculated with the 10-fold cross validation varied among species; the lowest values of MAE and RMSE were for wild boar model and the highest values were for roe deer, brown bear and lynx models (Table S5), while SD was high for brown bear and lynx models. In comparisons of the R^2 across the 10-folds of our cross validation and the full models, we found that the biggest differences occurred for roe deer, brown bear and lynx indicating lower predictive power of those models.

The DHIs and WHIs complemented the environmental variables and human footprint index in our models of population density

FIGURE 2 Results of model selection showing which variables were included in the top-twelve models for all species when explaining average population densities for 1981–2010. Models were ranked based on the BIC criterion. R^2_{adj} is provided for the top model, highlighted with the red box. Bottom-axis labels: the Dynamic Habitat Indices (Cum DHI—cumulative DHI, Min DHI—minimum DHI, Var DHI—variation DHI), human footprint index, BIO 3—isoothermality, BIO5—maximum temperature of warmest month, BIO13—precipitation of wettest quarter, BIO15—precipitation seasonality, the Winter Habitat Indices (DWOS WHI—duration of snow-free frozen ground, DWS WHI—duration of snow-covered ground, Start WHI—start of the frozen season, Length WHI—length of the frozen season, End WHI—end of the frozen season). In the model for wild boar, we replaced end of the frozen season with length of the frozen season because length of frozen season was an ecologically more important variable for this species.



(Figure 3). The hierarchical partitioning analysis showed that different individual component of the DHIs and WHIs contributed substantially to the overall variance explained for the different species. Because we estimated independent contributions of each explanatory variable only for the top model, the set of explanatory variables was different for each species. The DHIs were included in the top model for moose, wild boar, red fox and wolf. The WHIs were included in the top models for all species except roe deer. Human

footprint index was included in models for all species except lynx, while elevation appeared in models for brown bear, wild boar, lynx and red fox. There was no consistency in which bioclimatic variables were included in models. Based on the hierarchical partitioning analysis, the duration of snow-free frozen ground had the highest independent contribution in the top model for European hare, while human footprint index had greatest contribution in moose and red fox top models, precipitation seasonality for roe deer, elevation for

TABLE 2 Summary of our expectations and actual relationships between the densities of each species and the remotely sensed indices of habitat conditions (expected/actual relationship) in the top-twelve models. The explanatory variables are Cum DHI—cumulative DHI, Min DHI—minimum DHI, Var DHI—variation DHI, DWOS WHI—duration of snow-free frozen ground, DWS WHI—duration of snow-covered ground, Start WHI—start of the frozen season, Length WHI—length of the frozen season, End WHI—end of the frozen season. (+)—positive regression relationship, (—)—negative regression relationship, NS—not significant relationship. There are few variables for which we had neutral expectation, and for these, we just include the actual relationship.

Species	Cum DHI	Min DHI	Var DHI	DWS WHI	DWOS WHI	Start WHI	Length WHI	End WHI
European hare (<i>Lepus europaeus</i>)	+ / NS	+ / NS		— / —				
Moose (<i>Alces alces</i>)	+ / +	+ / +		— / NS	—			—
Roe deer (<i>Capreolus pygargus</i> Pallas, <i>Capreolus capreolus</i> Linnaeus)	+ / +	+ / NS	—	— / NS	—			+
Brown bear (<i>Ursus arctos</i>)	+ / NS	+ / +		— / +				—
Wild boar (<i>Sus scrofa</i>)	+ / +			— / —		+	— / —	
Lynx (<i>Felis lynx</i>)	+ / NS	+ / +		+ / +				+
Red fox (<i>Vulpes vulpes</i>)	+ / —	+ / —	—	+ / —		+		
Wolf (<i>Canis lupus</i>)	+ / +	+ / —	—	+ / +	+			

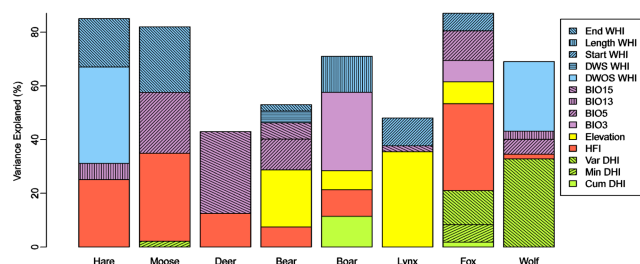


FIGURE 3 The results of hierarchical partitioning analysis of variables included in the top multiple regression model for each species explaining population density. The species are European hare (*Lepus europaeus*), moose (*Alces alces*), roe deer (*Capreolus pygargus* Pallas, *Capreolus capreolus* Linnaeus), brown bear (*Ursus arctos*), wild boar (*Sus scrofa*), lynx (*Felis lynx*), red fox (*Vulpes vulpes*) and wolf (*Canis lupus*) across Russian's regions. The explanatory variables are the Dynamic Habitat Indices (Cum DHI—cumulative DHI, Min DHI—minimum DHI, Var DHI—variation DHI), HFI—human footprint index, BIO3—isoothermality, BIO5—maximum temperature of warmest month, BIO13—precipitation of wettest quarter, BIO15—precipitation seasonality and the Winter Habitat Indices (DWOS WHI—duration of snow-free frozen ground, DWS WHI—duration of snow-covered ground, Start WHI—start of the frozen season, Length WHI—length of the frozen season, End WHI—end of the frozen season). The length of the frozen season was only included for wild boar because length of frozen season was an ecologically more important variable for this species.

brown bear and lynx, isothermality for wild boar and variation DHI contributed most in the wolf top model (Figure 3).

3.1 | Checks of winter track counts data quality

Within each species, the average population densities for the entire 30-year study period and for each decade were highly correlated (0.73–0.99, Table S6), suggesting that our choice to model the 30-year averages did not affect our results substantially. Annual coefficients of variation of population densities across all regions varied over time but we did not observe consistent trends (Figure S6). Similarly, in the CV, there was some variation among the three decades for most species but no major differences or trends, except in the last decade for wolf when the CV was especially high (Figure S7). This was confirmed in our statistical tests. Based on the asymptotic test for the equality of coefficients of variation from k populations and MSLRT for equality of CVs, we did not find significant differences between CV for different decades for any species (all $p > 0.16$; Table S7). Lastly, we did not find differences among the spatial autocorrelation of the residuals of the top models calculated on 30-year data and the three decades separately (Figure S8). Spatial autocorrelation was rare in our models, occurring only at shorter lag distances for lynx in two periods. In summary, we did not find evidence

that the data quality of the Winter Track Counts differed among the three decades.

4 | DISCUSSION

4.1 | Relationships between population density and explanatory variables

The main goal of our study was to explain variation in population density for eight mammals that occupy different trophic levels, that is, herbivores, omnivores and carnivores, using newly developed remotely sensed indices that characterize primary productivity (DHIs) and winter conditions (WHIs) along with more traditional variables representing elevation, climate and human pressure. We expected that the DHIs would be positively correlated with all species and especially so for herbivores, as high cumulative and high minimum DHI are likely to be associated with more food resources. Surprisingly though, the only herbivore that had a strong positive relationship with the DHIs was moose, while all carnivores exhibited strong relationships with DHIs (wolf positively related to cumulative DHI, fox negatively related to cumulative DHI and minimum DHI and lynx positively related to minimum DHI). These relationships suggest that primary productivity influences prey availability for carnivores. Such bottom-up effects are more pronounced when a population reaches carrying capacity, or prey are sparse, and weaker when population levels are low or prey are abundant (Currie et al., 1993; Lawton, 1990). While population density depends strongly on the quality and quantity of available food throughout the year, winter is often a time of high mortality, and both snow cover and extremely low temperatures can be important limiting factors (Danilkin, 2008). Our results highlighted the usefulness of WHIs; they appeared in the top models for every species except roe deer. We predicted a negative relationship with duration of snow-covered ground for herbivores and omnivores and a positive relationship for carnivores. Interestingly, the directionality of the relationship between population density and duration of snow-covered ground varied among species and even within one trophic level. For example, some of our omnivore (brown bear) and carnivore (lynx and wolf) species had positive relationships with the duration of snow-covered ground, while others (wild boar and red fox) had negative relationships. These findings may reflect differing morphology, that is, wolves and lynx, have physical adaptations for moving through and over snow (Telfer & Kelsall, 1984), whereas wild boar do not (Formozov, 2010). Overall, we found that the WHIs contributed substantially, and the DHIs somewhat, to our multivariate models, and both WHIs and DHIs provided complementary information to variables characterizing climate and human disturbance.

Interestingly, all carnivores except lynx had stronger relationships than herbivores did with the DHIs. However, our finding that the effect of primary productivity was not significant for European hare and lynx may be due to the strong declines in populations of both species. For lynx, these declines coincide with low prey

population (e.g. mountain hare [*Lepus timidus*] Newey et al., 2007), which may have weakened bottom-up effects (Figure S3). Lynx population dynamics are often cyclical, depending on the cycles of prey species (Matyushkin & Vaisfeld, 2003), and the reproductive rate of lynx responds strongly to prey population size (Okarma et al., 1997), hence, long-term averages of lynx densities may not correlate with long-term vegetation and climate indices. One potential reason the DHIs were not as important for roe deer as for the other species is that we had to analyse the two roe deer species jointly because the game surveys do not distinguish between them, but the two species differ somewhat in size and habitat preferences (Danilkin, 1999), and grouping them may have obscured the relationships of the individual species.

In middle to northern latitudes and high elevations, snow cover is one of the limiting factors for animals. For some species, the northern range boundary is limited by snow depth. For example, distribution is constrained by snow depth of 50 and 60 cm for European and Siberian roe deer, respectively (Danilkin, 1999; Grøtan et al., 2005). In general, our winter-habitat-index related results indicate that the degree of adaptation to winter conditions greatly affects patterns of wildlife population densities in Russia.

Climate affects both the distribution and demographics of wildlife populations (Ehrlén & Morris, 2015; Michaud et al., 2014; Skidmore et al., 2003). Indeed, temperature and precipitation were included in all top-twelve models for all species, but elevation was only included in some. Mountainous regions are characterized by a combination of complex landscape elements, often including open shrub lands. Usually, mountains are less developed, have lower human population densities and contain fewer roads than flat areas, which is why elevation can be a proxy of human absence. Given this, we speculate that elevation appeared in top-twelve models for brown bear and lynx because they avoid human-dominated areas (Martin et al., 2010; Nellemann et al., 2007; Oriol-Cotterill et al., 2015).

Human activities can greatly affect densities, both by bottom-up mechanisms when food availability is altered due to land use change (Foley et al., 2005; Kehoe et al., 2015), or top-down effects including overharvesting or poaching (Muhly et al., 2013; Okarma et al., 1997). The human footprint index was included in our top models for all herbivores, omnivores and carnivores except lynx, but often had a positive relationship with density. We caution that this is likely not a causal relationship, but may be due to both human populations and wildlife densities being higher in areas with high vegetative productivity, a phenomenon which may be especially highlighted in our broad-scale approach that summarizes data per region and thus excludes finer scale variation in human populations and animal densities. Some of the species are well-adapted to human-modified landscapes and can occur in agricultural land, including roe deer and wild boar (Geisser & Reyer, 2004; Putman & Moore, 1998). An indicator of strong negative, top-down effects of humans on wildlife populations was the rapid drop in animal population for all species except wolf during the politically unstable period after the collapse of the Soviet Union (Figure S3, Bragina et al., 2015).

4.2 | Caveats and limitations

When interpreting our results, it is important to keep in mind that we modelled average population density over 30 years versus average habitat conditions at the scale of administrative regions of Russia, which are rather coarse temporal and spatial resolutions. Furthermore, some of our data on habitat conditions was collected over different time spans than the wildlife data due to limitations in data availability. That spatiotemporal mismatch between modelled population densities and our predictor variables in all likelihood affected our results. However, we decided to analyse wildlife population density data for all years, and not just the years that matched the DHIs and WHIs, because population densities changed considerably for most species over time (Figure S3), and the average for the 30-year time series provided more robust estimates. Given the high correlation of population densities among decades (Table S6) that decision in all likelihood had a small effect on our results. Furthermore, by analysing averages, we may have missed the effects of extreme weather events. Another potential limitation is that our mammal abundance data are only publicly available at the scale of administrative regions, and have much lower spatial resolution than our remotely sensed data. Moreover, the Winter Track Counts data can only be collected when the ground is snow covered (Mirutenko et al., 2009). The number of transects has changed over time with the highest number in 1981 (about 30,500 transects), and the lowest in 1992 (about 26,600) (Gubar et al., 2007). Sampling density is likely uneven across Russia, both because survey regions are smaller in European Russia, necessitating a higher density of transects for accurate estimates there, and because many areas in Asian Russia are very remote and human population density is low making it logistically difficult to maintain a dense network of transects. Unfortunately though, we did not have access to tallies of the number of transects by region. Furthermore, data quality may have been affected by the political upheaval after the collapse of the Soviet Union. We did not find evidence for systematic changes in data quality over time (Table S7, Figures S6 and S7), but we cannot rule out such differences in individual regions. One limitation of the WHIs variables, especially duration of snow-free ground and the duration of snow-covered ground, is that they rely on optical satellite data, which do not provide observations during polar night, which affects Russia's North. That is why we had to assign zero to the areas affected by polar night, and that may have reduced the explanatory power of our models and importance of these variables in modelling population density. Despite these limitations, our remotely sensed indices had high explanatory power and our models were statistically significant. Had better spatial data for population density been available, relationships may have been even stronger, given the much higher spatial resolution of remotely sensed data.

Knowing which factors determine population densities is important for understanding the underlying mechanisms that shape biodiversity patterns and how species respond to human-dominated landscapes at broad scales. We found that the DHIs and the WHIs had substantial independent contributions in explaining variation

of population density for all eight species across Russia. The DHIs provide three measures of vegetation productivity that are relevant for species across different trophic levels because they represent different aspects of productivity, which is a direct measure of available food for herbivores and omnivores, and an indirect measure of available food and habitat quality for carnivores. This kind of information can be useful for better understanding the species–energy relationship (Evans et al., 2005, 2006), and habitat use (Garrouette et al., 2016; Michaud et al., 2014; Peek et al., 1976). The WHIs capture important characteristics of snow cover dynamics and characterize winter severity (Gudex-Cross et al., 2021; Zhu et al., 2017, 2019), which influence spatial distribution of plants and animals (Zhu et al., 2017). Combining the DHIs and the WHIs provided important information about environmental conditions that limited population densities and species distributions.

5 | CONCLUSIONS

In summary, remote sensing-based DHIs and WHIs explained population density of mammals of different trophic levels across Russia well. We found that the combination of our remote sensing indices together with climate and human-related variables resulted in models with high explanatory power. The DHIs provided valuable information about primary productivity while the WHIs provided important information about habitat conditions during the harsh time of the year, which not only limits the range of some species but also the number of individuals an area can support. The DHIs and WHIs were originally developed to explain species richness patterns, but have also proven to be useful in distribution models of individual species (Razenkova et al., 2020; Suttcliffe et al., 2019). Their potential to contribute to understanding patterns of population density and population dynamics of different taxa and in different regions of the world is high.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All the remote sensing datasets that we analysed have global coverage, and the data are freely available at <https://silvis.forest.wisc.edu/>. Animal data are available at <https://doi.org/10.5061/dryad.p2ngf1vvm>.

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BIOSKETCH

Our multidisciplinary research team has experience in wildlife ecology, conservation, remote sensing, and statistics and collaborates to test the usefulness of remotely sensed data for explaining the spatial pattern of species diversity and species abundance at broad scales. The application of these indices helps to identify the factors that shape the current species distribution at broad scale.

Author contributions: E.R., A.M.P., A.M.A., E.V.B., L.M.B., N.C.C. and V.C.R. developed the ideas, V.C.R. secured funding, L.M.B. facilitates access to the winter track count data, M.D., M.L.H. and L.Z. processed satellite imagery, E.R. and M.K.C. conducted statistical analyses, E.R. and V.C.R. wrote the first draft of the manuscript and all authors contributed to interpretation and writing of the final draft.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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