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Human Footprint and Forest Disturbance Reduce Space Use of Brown Bears (*Ursus arctos*) Across Europe

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ABSTRACT

Three-quarters of the planet's land surface has been altered by humans, with consequences for animal ecology, movements and related ecosystem functioning. Species often occupy wide geographical ranges with contrasting human disturbance and environmental conditions, yet, limited data availability across species' ranges has constrained our understanding of how human pressure and resource availability jointly shape intraspecific variation of animal space use. Leveraging a unique dataset of 758 annual GPS movement trajectories from 375 brown bears (*Ursus arctos*) across the species' range in Europe, we investigated the effects of human pressure (i.e., human footprint index), resource availability and predictability, forest cover and disturbance, and area-based conservation measures on brown bear space use. We quantified space use at different spatiotemporal scales during the growing season (May–September): home range size; representing general space requirements, 10-day long-distance displacement distances, and routine 1-day displacement distances. We found large intraspecific variation in brown bear space use across all scales, which was profoundly affected by human footprint index, vegetation productivity, and recent forest disturbances creating opportunity for resource pulses. Bears occupied smaller home ranges and moved less in more anthropized landscapes and in areas with higher resource availability and predictability. Forest disturbances reduced space use while contiguous forest cover promoted longer daily movements. The amount of strictly protected and roadless areas within bear home ranges was too small to affect space use. Anthropized landscapes may hinder the expansion of small and isolated populations, such as the Apennine and Pyrenean, and obstruct population connectivity, for example between the Dinaric Pindos population and the Alpine or Carpathian population. Our findings call for actions to maintain bear movements across landscapes with high human footprint, for example by maintaining forest integrity, to support viable bear populations and their ecosystem functions.

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1 | Introduction

Anthropogenic effects, including climate change, land conversion, fragmentation, and human disturbance affect all aspects of animal ecology (Abrahms et al. 2023; Gaynor et al. 2018; Humphries, Thomas, and Speakman 2002; Prugh et al. 2008). Movement is an integral part of animal ecology and evolution, facilitating ecosystem interactions, population connectivity, and species' geographic distribution (Nathan et al. 2008; Nathan et al. 2022). Movement facilitates range shifts and allows animals to adapt to climate and global changes (Ellis-Soto, Wikelski, and Jetz 2023; Kauffman et al. 2021). Understanding why space use varies within species has received considerable attention (Shaw 2020), however, due to the lack of movement data availability across species' ranges, the majority of studies have focused on single populations or limited geographic extents (Saïd and Servanty 2005). This has restricted our understanding of intraspecific variation in animal movement (Kays et al. 2015). To address this issue, comparative studies integrating large-scale spatial data have contributed toward gaining an understanding of the ecological drivers of animal movements at continental and global scales (Morellet et al. 2013; Mumme et al. 2023; Tucker et al. 2018; Tucker et al. 2023).

How animals use space is largely determined by their motivation and capabilities to move, paired with the prevailing environmental conditions they are exposed to (Morellet et al. 2013; van Beest et al. 2011). Within a species, state-dependent variables, such as body size, sex, age, or reproductive status, affect energetic needs and the motivation to move (Nilsen, Herfindal, and Linnell 2005; Tucker, Ord, and Rogers 2014). However, because many species have wide geographic distributions that span over contrasting environmental conditions, populations of a given species may exhibit different patterns of space use, with resource availability and seasonality being the most commonly reported factors underlying intraspecific space use variation (Mcloughlin, Ferguson, and Messier 2000; Olsson et al. 2006; Teitelbaum et al. 2015). In general, where resources are more predictable and abundant, animals tend to occupy smaller ranges, because they can satisfy their energetic requirements within a smaller area (Morellet et al. 2013). Additionally, climatic variables, such as temperature, snow cover, and terrain topography, can also influence animal space use (Morellet et al. 2013; Rivrud, Loe, and Mysterud 2010; Valderrama-Zafra et al. 2024; van Beest et al. 2011).

The increasing pressure of human activities on natural habitats alters resource availability, causes habitat loss, and disrupts connectivity, with profound impacts on animal movements. Linear infrastructure (e.g., roads and fences), forestry, agriculture, hunting, recreation, and other human pressures have permeated into natural areas to such an extent that approximately 75% of the Earth's land surface shows measurable anthropogenic effects (Oscar Venter et al. 2016). Human pressures have been summarized into an overall index of human footprint (HFI), including infrastructure, human density, land use change, urbanization, and light pollution (Barnosky et al. 2012; Newbold et al. 2015; Venter et al. 2016). Linear infrastructure can act as barriers, disrupt the connectivity of habitats, and, together with changes in resource availability through forestry, agriculture, or artificial feeding, alter animal movements and home range sizes (Bischof,

Steyaert, and Kindberg 2017; Fahrig 2007; Jerina 2012; Main et al. 2020; Passoni et al. 2021; Selva et al. 2017). While there is a global trend of animal movements being reduced with increasing human footprint (Main et al. 2020; Tucker et al. 2018), how animals respond to human pressure depends largely on the nature of the disturbance, the species' life history, and individual personality (Dammhahn, Lange, and Eccard 2022; Doherty, Hays, and Driscoll 2021). For example, animals may move further distances in response to direct human disturbances, such as hunting or recreation due to "fear effects" (Doherty, Hays, and Driscoll 2021).

The scale and ubiquity of disrupted animal movements, in combination with habitat fragmentation, is a major conservation issue worldwide. In some areas of the world, such as in the contiguous United States, parts of Asia and Africa, wildlife mainly persists in protected wilderness away from human habitation and large enough to accommodate animals' spatial needs (Chapron et al. 2014; Packer et al. 2013; Veldhuis et al. 2019). This is especially true for species that have traditionally been the subject of socio-political conflicts when sharing space with humans, like large carnivores, which generally occur at low densities and have large spatial requirements (Bautista et al. 2017). Yet, in the highly fragmented and human-dominated landscape of Europe, large carnivores are currently increasing in numbers and recolonizing former ranges due to favorable conservation policies, the depopulation of rural areas, and increases in forest cover (Chapron et al. 2014; Cimatti et al. 2021; Passoni, Coulson, and Cagnacci 2024; Reinhardt et al. 2019). This remarkable comeback is only possible due to several behavioral adaptations of large carnivores living in human-dominated landscapes, for example, to avoid humans spatially and temporally (de Gabriel Hernando et al. 2020; Lamb et al. 2020; Ordiz et al. 2011). However, comparative studies evaluating large carnivore behavior along gradients of human disturbance are still lacking.

In this study, we aim to evaluate intraspecific variation in space use patterns of one of the most abundant large carnivores in Europe, the brown bear (*Ursus arctos*), across contrasting environmental and anthropogenic conditions (Figure 1). An earlier multi-population study of brown bear space use from North America has demonstrated substantial intraspecific variation in home range size and overlap, primarily linked to natural food availability (Mcloughlin, Ferguson, and Messier 2000), but no comparative study has determined the drivers of variation in space use patterns across the highly anthropogenic landscape in Europe. With approximately 18,000 individuals, European brown bears are distributed across ten populations with generally increasing or stable trends during recent years (Kaczensky et al. 2021). Their range spans from the highly anthropized landscapes in southern and central Europe to the comparatively remote boreal forests in northern Europe. Similar to other large carnivores, brown bears act as mobile links in natural ecosystems and can play a significant role in ecosystem dynamics by facilitating seed dispersal and plant regeneration (García-Rodríguez, Albrecht, Szczutkowska, et al. 2021; García-Rodríguez, Selva, Zwijacz-Kozica, et al. 2021; Hämäläinen et al. 2017; Steyaert, Hertel, and Swenson 2019), protecting plants from herbivorous insects (Grinath, Inouye, and Underwood 2015), shaping ungulate prey densities (Swenson et al. 2007; Tallian et al. 2021), providing a nitrogen influx into riparian forests (Deacy et al. 2017;
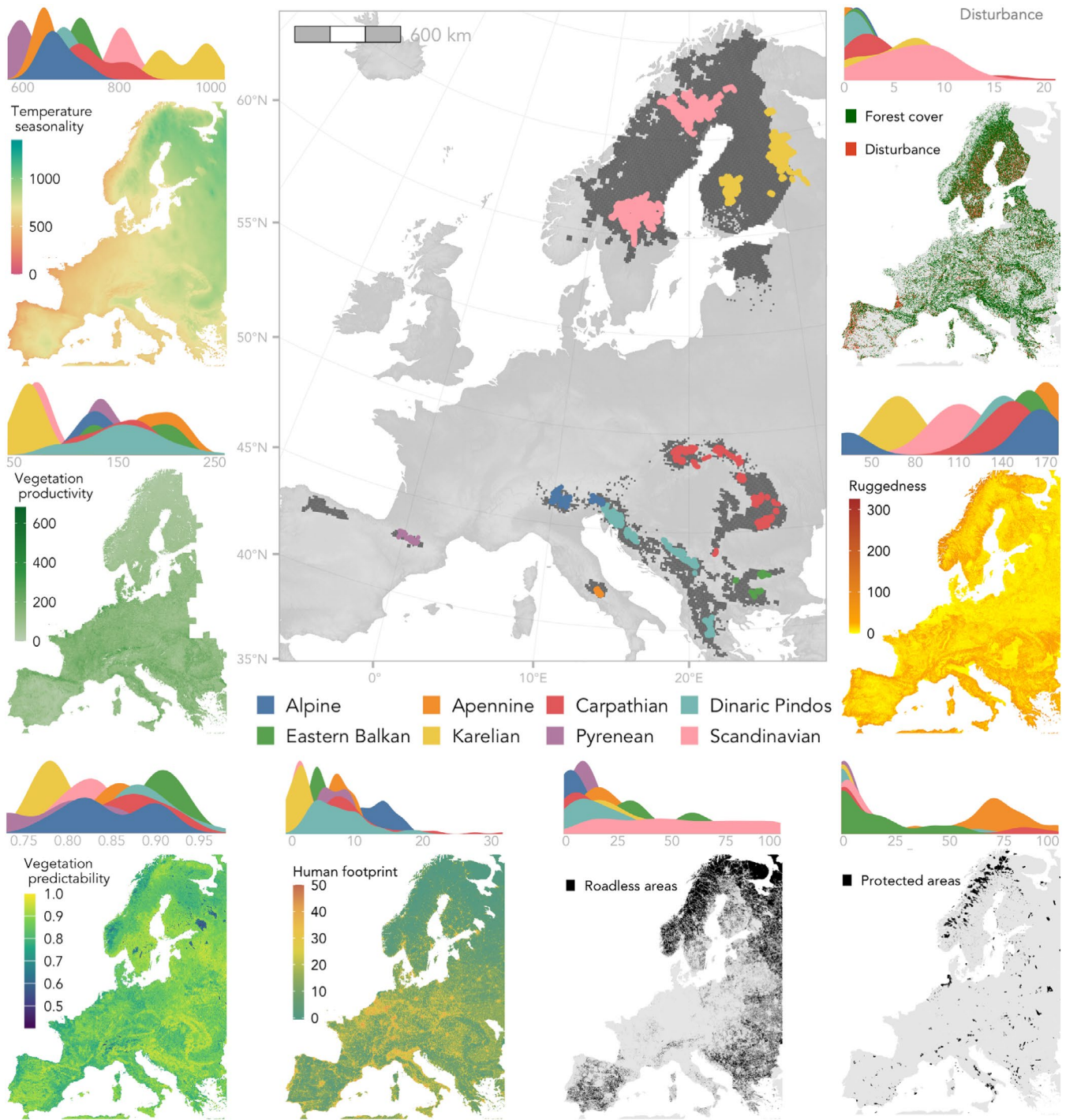
FIGURE 1 | Within the BearConnect initiative, we compiled GPS movement data from eight of the ten extant brown bear populations in Europe. Using data from the summer growing season (May–September) we estimated individual home ranges (main panel, colored by population) which covered a substantial amount of the current permanent occurrence range of the brown bear in Europe (main panel dark gray, Kaczensky et al. 2021). For each home range we extracted the median temperature seasonality (Bio4 in WorldClim, Fick and Hijmans 2017), median annual vegetation productivity (Copernicus 2020), median vegetation predictability (estimated from MODIS NDVI with equations by Colwell (1974)), median human footprint index (Venter et al. 2016), proportion of roadless (Ibisch et al. 2016) and strictly protected areas (World Database on Protected Areas), median terrain ruggedness index (calculated from a European digital elevation model), and proportion of forest cover and disturbance (Senf and Seidl 2021). Density plots show the distribution of covariates for each population.

Helfield and Naiman 2006), or by removing carrion (Krofel, Kos, and Jerina 2012). However, some studies suggest that low carnivore population densities and human-induced altered space use patterns disrupt the role brown bears play in European ecosystems (Diserens et al. 2020; Kuijper et al. 2016).

We used 752 annual brown bear movement trajectories from the BearConnect movement database (bearconnect.org) to analyze the space use of brown bears across the species' geographical range in Europe. We summarized annual space use at three distinct spatiotemporal scales during the growing season

(May–September), when bears are active and not hibernating: home range size during the growing season, which represents the total area a bear traverses for foraging, resting, and mating and indicates the total space requirements of a bear in a given landscape. The 90th percentile of an individuals' 10-day displacement distances, which is indicative of its long-distance movement potential over longer time scales, and finally, the median (50th percentile) of an individuals' 1-day displacement distances, which is indicative of the routine distance it needs to travel to satisfy daily needs. We summarized a suite of spatially explicit covariates at the home range scale (Figure 1) to evaluate hypotheses about the drivers of intraspecific variation in space use.

First, we expected that bears can satisfy their energetic requirements across less space in resource-rich and stable, that is, predictable environments (Mcloughlin, Ferguson, and Messier 2000; Morellet et al. 2013). We therefore predicted smaller home range sizes and shorter movement distances in areas with higher annual vegetation productivity, higher vegetation predictability, and lower temperature seasonality. In addition, early successional or seral forests after an anthropogenic or natural forest disturbance may provide high quantity and pulsed food resources, such as berries, due to their open canopy and increased light availability at the ground level (Larsen et al. 2019; Lodberg-Holm et al. 2019; Nielsen et al. 2004). We therefore predicted that bears would occupy smaller home ranges when they encompass a higher proportion of recently disturbed forests in early successional stages (until 9 years after disturbance, Larsen et al. 2019).

Second, we expected that human pressures, as summarized by the human footprint index, significantly affect bear space use through barrier effects of human infrastructure but also through altered food availability close to human settlements (i.e., increase in food availability and predictability through agriculture or garbage) (Main et al. 2020; Mumme et al. 2023; Tucker et al. 2018). We predicted that bears would occupy smaller home ranges and move less in areas with a higher human footprint index. Conversely, we expected bears to move more in areas with higher forest cover, indicating contiguous, habitats with fewer barriers (Cimatti et al. 2021).

Third, we expected that area-based conservation measures, that is, protected areas or areas with restricted traffic access, have the potential to maintain the ecological integrity of habitats, especially in anthropized landscapes and, thus, may help sustain animal movements (Brennan et al. 2022; Hofmann et al. 2021; Jones et al. 2018). We tested the effect of two area-based conservation measures, the proportion of protected areas (WDPA Consortium 2004) as well as the proportion of roadless areas (Ibisch et al. 2016), within a bear's home range on its space use. Roadless areas are generally relatively undisturbed by humans and associated with fewer barriers, lower fragmentation, and increased landscape permeability (Bischof, Steyaert, and Kindberg 2017; Lamb et al. 2018). In comparison, the effects of protected areas are less clear (Geldmann et al. 2013), especially in Europe where the size of protected areas is commonly too small to contain brown bear home ranges (Woodroffe and Ginsberg 1998), where protected areas may be situated in resource poor habitats (Joppa and Pfaff 2009), or where protected areas are hotspots for recreational activities (Schägner

et al. 2016), which could ultimately promote or hinder animal movements. We predicted that bears move more when their home ranges encompass larger proportions of roadless areas, while the proportion of protected areas could either promote or restrict movements.

Last, we accounted for topography and for the sex of the individual. We expected that bears inhabiting home ranges with on average more undulated and rugged terrain would move slower and occupy smaller ranges as compared to bears inhabiting flatter terrain. Given the mating system and social organization of brown bears, we expected males to use larger areas than females (Nilsen, Herfindal, and Linnell 2005; Steyaert et al. 2012). Finally, after accounting for the main covariates, we quantified remaining space use differences between populations. In addition to these main covariates, we also explored the effect of age, reproductive class, and artificial feeding on space use, using subsets of our data for which such metadata were available, and we tested for sex-specific responses to our most influential environmental covariates.

2 | Methods

2.1 | Compilation and Filtering of Movement Data

As part of a large collaborative Biodiversa project (BearConnect), we compiled a database of all available GPS relocation data sets from brown bears across Europe. In total, movement data was compiled from eight of the 10 extant European brown bear populations (Kaczensky et al. 2021), spanning 13 countries between 2002 and 2018 representing 615 unique individuals monitored over 1411 tracking years. First, we split our data per individual and year (hereafter referred to as annual bear track). Because brown bears cease movement during winter hibernation, our analysis focused on the growing season (i.e., from May to September), assuming that all individuals were fully active during these months. The duration of GPS tracking, the GPS sampling intervals, and the success rate of GPS relocations varied greatly. We therefore only included annual bear tracks that covered at least 100 out of 153 days of the growing season (i.e., 3.5 months out of 5 months) and we resampled trajectories to a 1-day resolution, that is, retained 1 location per 24 hrs in an attempt to obtain unbiased and comparable data using the R package *amt* (Signer, Fieberg, and Avgar 2018). Our final dataset included space use information from 758 annual bear tracks of 375 individuals (211 females and 164 males) monitored for 1–13 years, though sample sizes varied substantially among populations (Figure 2a).

2.2 | Space Use Metrics

We calculated and summarized bear space use at three distinctive spatiotemporal scales during the growing season, leading to one value for each metric per annual bear track: home range size (representing overall space requirements), long-distance 10-day displacement (representing long-distance movements), and average 1-day displacement distance (representing routine daily movements). In Appendix S1, we explore the effects of environmental covariates on space use in continuous time, from 1-day to 10-day displacements for both, routine (50th percentile) and long-distance (90th percentile) movements.
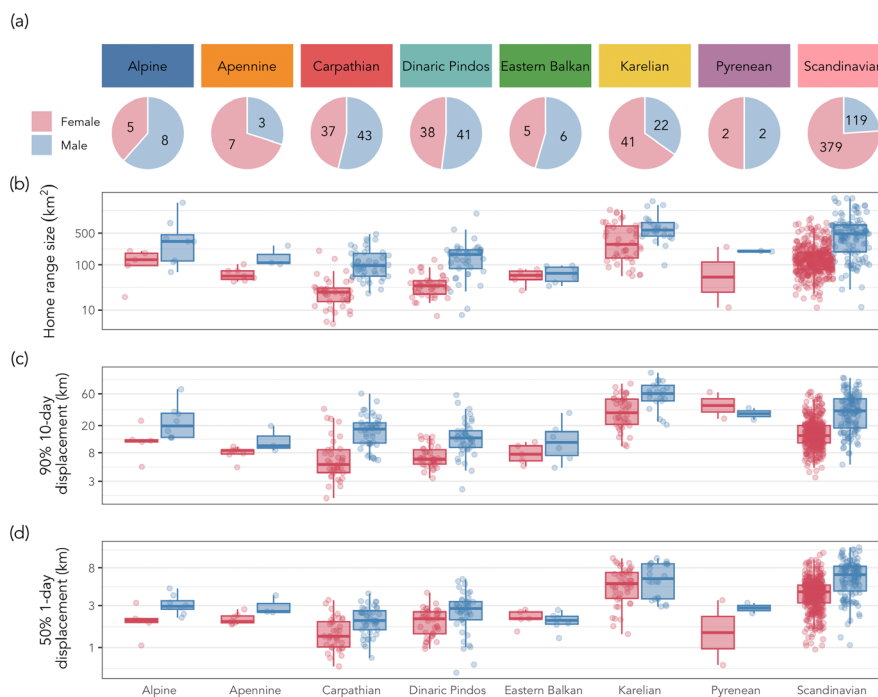
FIGURE 2 | Population and sex-specific sample sizes (n annual bear tracks) and respective distribution of space use metrics: Home range sizes (km²), 10-day and 1-day displacement distances (km), collected for eight European brown bear populations. Boxplots extend from the population and sex-specific 25th to 75th percentile, with the mean as horizontal line and the data range as whiskers. Male bears generally occupied larger home ranges and moved more than females. All space use metrics were log-transformed for analyses but *Y*-axis labels are given at the km²/km scale to facilitate interpretation.

2.2.1 | Home Range Size

We estimated year-specific home range size for each annual bear track (i.e., the spatially constrained area used by an individual during the summer growing season period between May and September). We used the time-local convex hull estimator at the 95% isopleth (T-LoCoH, R library "tlocoh") (Lyons, Turner, and Getz 2013), which progressively aggregates local convex hulls to build the home range polygon. We incorporated time and used the adaptive LoCoH method in our home range estimates. Due to the variability of movement patterns among the monitored animals, we selected the time parameter "s" and the parameter for defining neighboring points "a" using the graphical tools available in the T-LoCoH software (see the user guidelines by Lyons, Turner, and Getz (2013) for more details on the parameters' selection). Because topography can affect home range estimates (Monterroso et al. 2013), we calculated home range sizes taking into account the three-dimensionality of land topography. For this, we used the European Digital Elevation Model (EU-DEM) at a 25 m resolution, from the Copernicus Land Monitoring Service (originally downloaded from https://www.gpxz.io/blog/eudem), and the "surfaceArea" function from the R package "sp" to calculate home range size (Appendix S2). To avoid including annual bear tracks with non-sedentary spatial behavior (i.e., bears that did not occupy a home range during the growing season) in our analyses, we removed from our dataset 12 annual bear tracks that showed directed long-distance dispersal or atypical ranging behavior (Appendix S3).

2.2.2 | 10-Day and 1-Day Displacement Distances

We calculated displacement distances at 10- and 1-day temporal scales, as Euclidean distances between consecutive GPS locations of each annual bear track using the R package *adehabitatLT* (Calenge 2006). Missing GPS locations (i.e., data gaps) were accounted for by omitting erroneous distance calculations. At the 10-day scale, we summarized the 90th percentile of displacement distances for each annual bear track, representing a bears' capacity for long-distance movements over longer temporal scales (following referred to as 10-day long distance displacements). During binning the data, we allowed 1 day tolerance and obtained 11–17 successful 10-day displacements per annual bear track from which 90th percentiles were drawn. At the 1-day scale, we obtained 82–152 successful daily displacements per annual bear track from which we summarized the 50th percentile, that is, median displacement distance for each annual bear track, representing routine daily movements (Tucker et al. 2018). Given that bears are no central place foragers, that is, they do not return to a central point for resting, but instead move incrementally through their home range in search of food and pick resting places on the go, 1-day displacement distances are representative of daily space use.

2.3 | Environmental Covariates

We obtained spatial layers of eight environmental covariates related to food availability, human pressure, forest cover, area-based conservation measures, and topography (Figure 1). We

extracted and summarized the values of all pixels falling within each bear home range. Thus, every annual bear track was characterized by a single value for each of the tested covariates.

2.3.1 | Vegetation Productivity and Predictability

To capture differences in food resource availability, we extracted the total vegetation productivity from the European Environmental Agency's Vegetation Phenology and Productivity (HR-VPP) product suite (Copernicus 2020; Tian et al. 2021), which represents the growing season integral as the sum of all daily Plant Phenology Index values (PPI, range 0–3) between the dates of the season start and end in a given year. Higher values indicate higher annual productivity and/or longer growing seasons. These maps have a spatial resolution of 100 m and were compiled from finer resolution Sentinel-2A and Sentinel-2B satellite products (10 m resolution and 5-day revisit time). Annual raster maps were available for 2017–2023 and we summarized annual maps into a mean vegetation productivity layer, indicating long-term average vegetation productivity. We extracted the vegetation productivity of all cells falling into a home range and calculated the median with higher values indicating home ranges with overall higher vegetation productivity.

We also calculated the overall spatiotemporal vegetation predictability, using the Normalized Difference Vegetation Index (NDVI) derived from monthly MODIS imagery from 2007 to 2018 at a spatial resolution of 1 km. We applied the equations from Colwell (1974) to the NDVI time-series data using the *hydrostats* R package (Bond 2022). We obtained a unique grid of values that summarize the variability of NDVI values within a year through space and the inter-annual variability of NDVI values which allowed us to summarize the overall spatiotemporal heterogeneity of vegetation dynamics at the home range scale. We extracted vegetation predictability values at the home range scale, and calculated the median predictability for each annual bear track, with higher values indicating greater intra- and interannual variation in vegetation productivity.

2.3.2 | Temperature Seasonality

To account for latitudinal and altitudinal differences in seasonality, we extracted the median temperature seasonality within each bear's home range from the WorldClim version 2.1 climate data (Fick and Hijmans 2017). Temperature seasonality (BIO4 layer) is a measure of temperature change over the course of the year and is calculated as the standard deviation of the annual range in temperature, where larger values represent more seasonal environments and lower values more stable environments with more continuous food availability. The BIO4 layer represents the average temperature seasonality for the years 1970–2000. We used the BIO4 layer at a spatial resolution of 2.5 min (~21 km) as we wanted to capture large-scale latitudinal and altitudinal differences.

2.3.3 | Human Footprint Index

The human footprint index (HFI) map for 2009 was downloaded from the global map of anthropogenic impact at a 1 km resolution

that combines multiple sources of anthropogenic disturbance, including human population density, built-up areas, nighttime lights, crop- and pasture land use, roads, railroads, and waterways (Venter et al. 2018; Venter et al. 2016). HFI ranges from 0 to 50, with increasing values indicating increasing levels of human pressure. We extracted HFI values and calculated the median HFI within each home range.

2.3.4 | Total Forest Cover and Forest Disturbances

Senf and Seidl (2021) published a map of Europe's forests and identified forest disturbances from USGS Landsat satellite data across Europe between 1986 and 2016 at a spatial resolution of 30 m. The spatial product identifies forest cover (binary variable) and if and when a forest was disturbed between 1986 and 2016. Forest disturbances were defined as cleared forest patches due to either anthropogenic (e.g., forest management and logging) or natural causes (e.g., windfall, fire, and bark beetle outbreak (Senf and Seidl 2021)). Within a bear's annual home range, we calculated the proportion of forest cover and the proportion of forests in early successional stages after a disturbance, that is, disturbances occurring within 9 years before the year a bear track was recorded (Larsen et al. 2019). We excluded the year of disturbance for two reasons: (1) structural disturbance of the site likely does not lead to increased food availability in the first year and (2) we wanted to mitigate any effects of forestry activity on animal movement.

2.3.5 | Roadless and Protected Areas

We downloaded the protected areas with the highest degree of IUCN protection (i.e., Strict Nature Reserve—Ia, Wilderness Area—Ib, and National Park—II) as shape files from the World Database on Protected Areas (WDPA) and World Database on Other Effective Area-based Conservation Measures (WD-OECM), https://www.protectedplanet.net). These IUCN categories represent areas of high ecological integrity but potentially with high human disturbance through recreation (Jones et al. 2018). We calculated the proportion of the home range that was covered by protected areas. We further used the global map of roadless areas (shape file), which represents areas relatively free of barriers (Ibisch et al. 2016, downloaded from http://www.roadless.online/). Roadless areas were defined as land units that were at least 1 km away from any kind of mapped roads (Ibisch et al. 2016). We calculated the proportion of the home range that was covered by roadless areas.

2.3.6 | Terrain Ruggedness

We calculated the terrain ruggedness index (TRI, Riley, DeGloria, and Elliot 1999), a measure of topographic heterogeneity, using the Elevation map of Europe from the European Environmental Agency (https://www.eea.europa.eu/) at a 1 km resolution. TRI ranges from level terrain (values of 0–80), nearly level (81–116), slightly rugged (117–161), intermediately rugged (162–239), moderately rugged (240–497), and to highly rugged terrain (> 498). TRI values derived from the 25 m DEM were too fine to capture differences in large-scale terrain undulations

among populations. Additionally, interpretation of TRI values is based on maps calculated from digital elevation models at 1 km resolution (Riley, DeGloria, and Elliot 1999). We calculated the median TRI of all values falling within a home range.

2.3.7 | Additional Covariates Explored in the Appendix

2.3.7.1 | Artificial Feeding. For each country, we extracted information about the use of artificial feeding (binary: yes/no) as a management tool from Bautista et al. (2017). Artificial feeding can constrain animal movement (Selva et al. 2017), however, no comprehensive data are available for Europe on when, where, and how much food is supplied to wildlife. Therefore, we contrasted bear space use in countries where artificial feeding is or is not allowed (Table S1, Appendix S4).

2.3.7.2 | Age Class. Age class is known to affect bear space use as young dispersing bears, in particular males, often roam over larger areas (Dahle and Swenson 2003). While we excluded bear tracks showing directed dispersal, young bears can also show home range shifts over time. Bear age was not recorded for all bears in a standardized way. Therefore, we categorized a subset of bears for which we had some age information (Table S6) as either subadult (1–4 years of age) or adult (> 4 years of age), and tested whether subadult males or females would occupy larger home ranges or move over longer distances (Appendix S5).

2.4 | Statistical Analyses

We fitted full Bayesian linear mixed effects models for each of the log-transformed space use metrics (Table S4): home range size, the 90th percentile of 10-day displacement distances, and median 1-day displacement distances. We accounted for the main effects of vegetation productivity, vegetation predictability, temperature seasonality, the proportion of forest cover, the proportion of early successional forest after a disturbance, HFI, the proportion of protected and roadless areas, terrain ruggedness, and sex. We further incorporated random intercepts for population and individual identity. We tested whether a non-linear term (second-order polynomial or threshold model) would represent the relationship between space use and HFI, vegetation productivity, vegetation predictability, and forest disturbance better (Table S4). Non-linear terms did not explain more variance than linear terms, except for forest disturbance. We therefore retained a non-linear relationship (second-order polynomial) in the main model. We also tested for sex-specific responses to the most relevant environmental gradients (see Appendix S6). Our models did not suffer from multicollinearity, as indicated by a variance inflation factor < 3 for all comparisons (see also Figure S1). All models were fitted with a Gaussian family with the R package *brms* (Bürkner 2017), running four chains over 4000 iterations with a warmup of 2000 and a thinning interval of 2. The model inference was based on 4000 posterior samples and had satisfactory convergence diagnostics with $R < 1.01$ and effective sample sizes > 1000. Posterior predictive checks recreated the underlying Gaussian distribution well and did not show signs of heteroscedasticity. We report the median as a measure of centrality and 89% credible intervals, calculated as equal tail intervals, as a

measure of uncertainty (Kruschke 2014; McElreath 2020). Data and code to reproduce the analysis are available via the Open Science Framework (Hertel 2024).

3 | Results

Intraspecific variation of brown bear space use in Europe was evident on all spatiotemporal scales. Home range sizes varied from 74 to 269 km² (first and third quartile, median = 131 km²; Figure 2b), 10-day long-distance displacements from 11 to 26 km (median = 15.5 km; Figure 2c), and daily displacements from 2.5 to 5.4 km (median = 3.8 km; Figure 2d). The smallest estimates were recorded in the Carpathian and Dinaric Pindos populations, and the largest in the Karelian population (Figure 2). Males occupied larger home ranges and moved more in all populations, except for the Eastern Balkan (Figure 2; Table S2). The three space use metrics were positively correlated (Figure S2). Across populations, European brown bears occupied a wide range of environments (Figure 1). For example, bears in the Karelian and Scandinavian populations experienced the lowest vegetation productivity, highest temperature seasonality, occupied home ranges with the highest proportions of early successional forest cover, and experienced the lowest HFI (Figure 1; Table S3).

3.1 | Drivers of Space Use Patterns

Intraspecific variation in brown bear space use patterns was explained by sex, proxies of resource availability, and human pressure. Vegetation productivity, the proportion of disturbed forest in early successional stages, HFI, and sex had a consistent and strong effect on brown bear space use across all three spatiotemporal scales. All models explained a good amount of variance in the data but generally fixed covariates performed best at explaining intraspecific variation in movement over longer time scales, that is, on the home range (marginal $R^2 = 0.52$) and 10-day scale (marginal $R^2 = 0.49$), compared to the daily scale (marginal $R^2 = 0.36$).

In line with our first prediction, three proxies of resource availability—vegetation productivity, vegetation predictability, and the proportion of disturbed forest in early successional stages—were negatively correlated with bear space use, while temperature seasonality had a positive effect (Figure 3a-d). Bear home ranges were four times larger in areas with low vegetation productivity (Figure 4a), low vegetation predictability (Figure S3a), and high seasonality (Figure S3b). Predicted 10-day displacements were twice as far in less productive (21 km vs. 10 km, Figure 4d), less predictable (23 km vs. 12 km, Figure S3c), and more seasonal environments (12 km vs. 25 km, Figure S3d). Likewise, routine daily movements were also longer (4.2 km vs. 1.5 km, Figure 4g) in areas with low vegetation productivity; however, effects of vegetation predictability and seasonality were not supported at the 1-day scale. Across continuous time scales (1- to 10-day displacement distances), vegetation productivity was an influential predictor of bear movements, while vegetation predictability only affected bear movements at long temporal scales (Appendix S1). Temperature seasonality affected long distance displacements at all time scales (1–10 days) but not routine median displacements (Appendix S1).
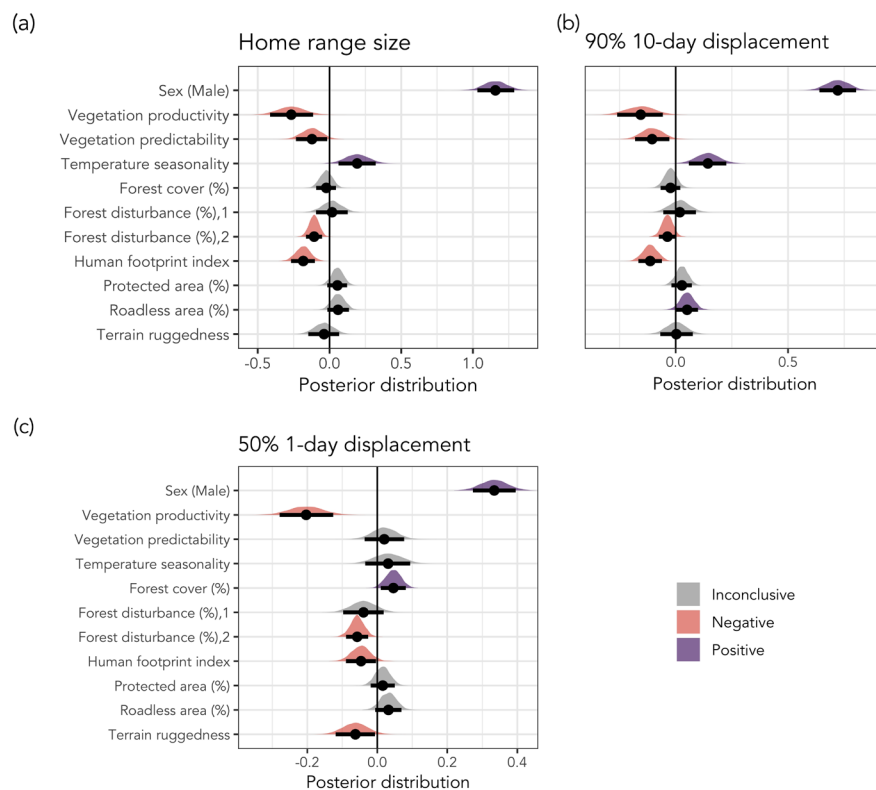
FIGURE 3 | Posterior distributions of covariate coefficients on home range size (a), 10-day long distance displacements (b), and 1-day routine displacements (c) of brown bears across Europe. Black dots and credible intervals indicate the mean and 89% equal tail intervals of the posterior distribution. Significance was inferred based on 89% equal tail intervals not overlapping 0. Across spatiotemporal scales, we found consistent effects of sex, vegetation productivity, human footprint index, and the proportion of forest disturbances on bear space use. See also Table S5 for all model coefficients.

Disturbed forest in early successional stages covered between 0% and 21% of bear home ranges [median = 5%, SD = 4%, Table S3]. When home ranges encompassed > 5% of proportion of forests in early successional stages, bears occupied smaller home ranges (Figure 4b, predicted size at 5% = 140 km² vs. at 15% = 79 km²) and moved over shorter 10-day and daily distances (Figure 4e & 4h, predicted distance at 5% = 17 km/3.3 km vs. at 15% = 15 km/2.2 km, respectively). A high proportion of disturbed forest was influential and led to reduced movements across continuous temporal scales (Appendix S1). General forest cover only affected 1-day displacements (Figure 3, Appendix S1), with bears moving longer distances in areas with more forest cover (predicted distance at 13% forest cover = 2.6 km vs. 100% forest cover = 3.5 km).

The Human Footprint Index strongly shaped intraspecific variation in brown bear space use (Figure 3a–c), supporting our second hypothesis. Bears occupied home ranges with a median HFI between 0 and 32 (median = 2.5, Table S3), that is, from natural to highly modified environments, wherein human footprint consistently shaped bear space use across all scales. In general, with increasing HFI, bears formed smaller home ranges and moved less (Figure 3a–c). This reduction was most apparent at larger spatiotemporal scales. For example, bears in areas with high HFI occupied home ranges a fifth the size of those in low HFI areas (predicted home range size at HFI 32 = 37 km² vs. at HFI 0 = 170 km², Figure 4c). Similarly, 10-day long-displacements in areas with low HFI were three times as long compared to highly

disturbed areas (predicted distance at HFI 32 = 8 km vs. at HFI 0 = 20 km, Figure 4f). At shorter time scales the effect was less strong but still apparent—predicted daily displacements in natural landscapes (HFI 0) were 3.5 km, while in highly modified landscapes (HFI 32) daily movements were reduced to 2.3 km (Figure 4i; Appendix S1).

We found weak and mixed support that area-based conservation measures affect brown bear space use in Europe (Figure 3). Most home ranges overlapped marginally with protected areas (median = 2.2% [range = 0%–100%], Table S3) and we found no effect of the proportion of protected areas on brown bear space use at the home range, 1-day and 10-day scale, though routine displacements over longer time scales (5–20 days) were longer in more protected areas (Appendix S1). Although, bear home ranges readily overlapped with roadless areas (median = 37% [range = 0%–100%]), we found that the proportion of roadless areas only affected 10-day displacement distances, with bears traveling longer distances in more roadless areas (predicted distance at 0% and 100% roadless areas: 16.5 km vs. 19 km, respectively). On a continuous timescale from 1 to 10 days, support was mixed and weak (Appendix S1).

Finally, terrain ruggedness affected bear space use at short temporal scales only, with shorter daily displacements in more rugged terrain. Sex-specific differences in bear space use were strong and evident across spatiotemporal scales (Figure 3). Across populations, males formed home ranges that were three
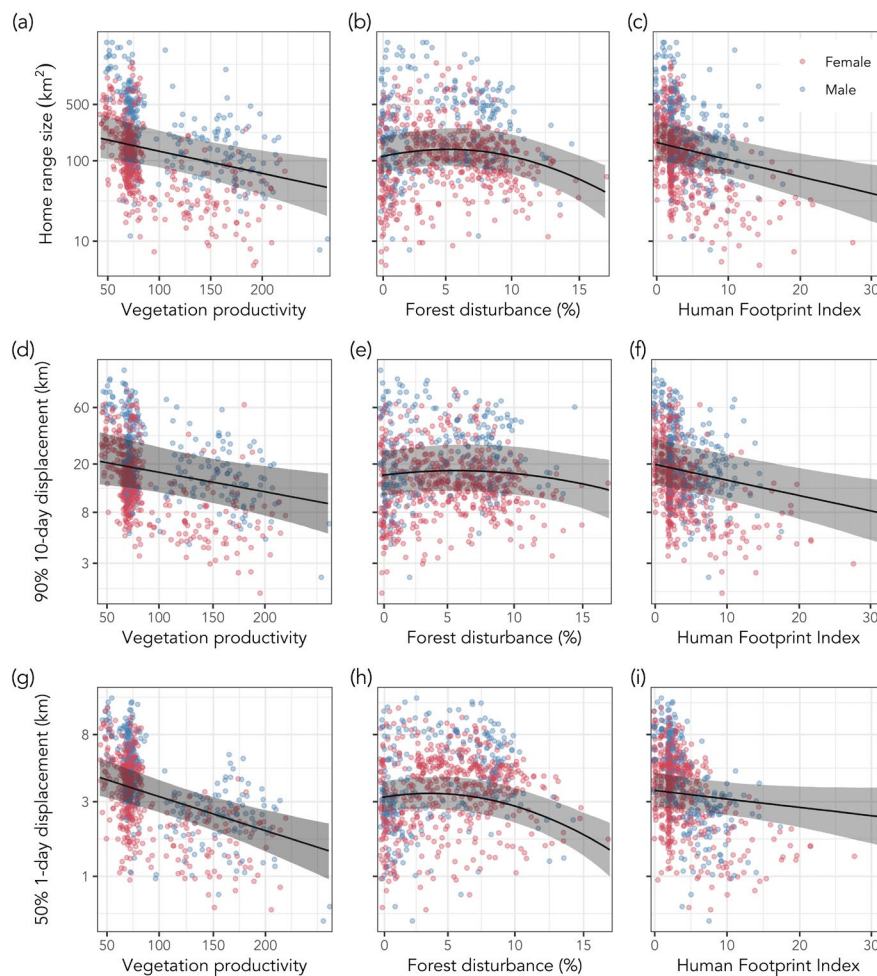
FIGURE 4 | Conditional effects (mean and 95% uncertainty interval) of vegetation productivity, the proportion of early successional forest, and human footprint index on home range size, long-distance displacements, and routine displacements of brown bears across Europe. Conditional effects were estimated by setting all other model covariates to their mean value and using females as reference category. These three covariates significantly affected space use across spatiotemporal scales. Space use decreased with increasing vegetation productivity (a, d, g), with an increasing proportion of recent forest disturbances (i.e., early successional forest) in a bear's home range (b, e, h), and with increasing median human footprint index in the home range (c, f, i). See also Figure S3 for effect sizes of vegetation predictability and temperature seasonality.

times the size of females (442 vs. 140 km²) and male long-term displacements covered twice the distance (36 km for males compared to 18 km for females). Males also moved over longer routine daily displacements; however, the difference was less pronounced (4.7 and 3.4 km, resp.). Despite the profound sex differences in space use, we found no evidence for sex-specific responses to environmental covariates (Appendix S6): male and female home range size and displacements decreased in a similar fashion with increasing vegetation productivity, proportion of early successional forest, and human footprint.

3.2 | Population-Level Differences in Space Use

For all three space use metrics, some variation remained that could not be explained by fixed covariates (Table S5). Between-population differences, that is, bears belonging to a given population behaving in a similar fashion and different from bears in other populations, accounted for 29%, 44%, and 21% of the remaining variance in home range size, 10-day long-distance displacements, and 1-day routine displacements, respectively. Additionally,

between-individual differences accounted for 46%, 26%, and 8% of the remaining variance. The total explained variance including fixed and random effects (conditional R^2) was 82% for home range size, 74% for 10-day displacement, and 55% for daily displacements (Table S5). Based on the posterior distribution of the random intercept for study population (Figure 5), that is, after accounting for environmental fixed covariates, we found between population differences and within population consistency in space use estimates, hinting at uncontrolled environmental or intrinsic variation between populations. Continental intercepts were on average 140 km² for home range size, 18 km for 10-day displacements, and 3.4 km for daily displacements. Bears in the Carpathian and Eastern Balkan populations showed limited space use compared to the continental intercept across all spatiotemporal scales: they occupied consistently smaller home ranges and moved over shorter distances (10-day around 14 km, 1-day < 3 km, Figure 5). Further, bears in the Scandinavian population occupied consistently smaller home ranges (100 km²) and showed limited long-distance displacements (13 km), as compared to the continental intercept, while bears in the Alpine occupied consistently larger home ranges (287 km²) than expected and showed more exploratory
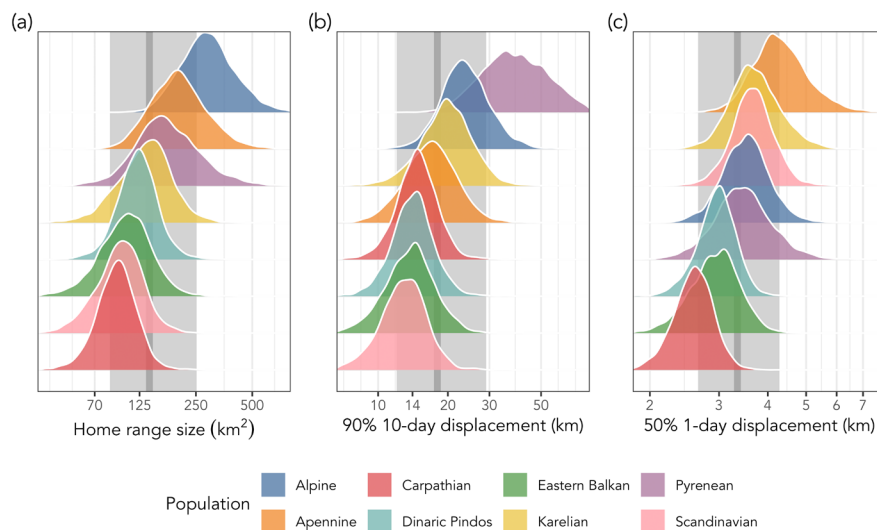
FIGURE 5 | Between-population differences after accounting for fixed covariates are shown as the posterior distribution of the random intercept for each study population of brown bears in Europe. Continental model intercepts (mean ± CI) are shown in gray and were on average 140 km² for home range size, 18 km for 10-day displacements, and 3.4 km for daily displacements. Point estimates for population random intercepts in (a) home range size ranged from 95 to 287 km², in (b) 10-day displacements ranged from 13 to 40 km, and (c) in 1-day displacements ranged from 2.6 to 4.3 km.

long-distance displacements (24 km, Figure 5). Estimates for the Pyrenean population should be treated with caution because of the limited availability of movement data, stemming from only three individuals included in our final dataset that were reintroduced and tracked post-release (Table S2). Notably, these results do not correspond to populations showing overall more expansive or more limited space use (for this refer to Figure 2 and Table S2) but rather highlight that some populations have consistently higher or lower space use than expected, given the controlled intrinsic and environmental factors moderating space use.

3.3 | Artificial Feeding

Nine out of 14 countries included in our study generally provided artificial food to bears (Table S1), representing 211 of 758 annual bear tracks from the Carpathian, Dinaric Pindos, Eastern Balkan and Karelian populations. Given that we had no information on the amount, spatial, or temporal distribution of artificial feeding at the individual home range level we could not conclusively test the effect of artificial feeding on brown bear space use with our dataset. Yet, the raw data suggested smaller home ranges and shorter daily movements for bears in populations where artificial feeding is common, as compared to bears in populations where artificial feeding is not common (Appendix S3).

4 | Discussion

We found that brown bear space use patterns across the European continent were jointly governed by resource availability and human pressure while the effects of area-based conservation measures were not supported. Specifically, bears occupied smaller home ranges and moved less in areas of higher vegetation productivity and predictability or where recently disturbed, early successional forests provide abundant food (supporting our first hypothesis). Increasing human footprint restricted bear space use while

increasing proportions of forest cover promoted movement (supporting our second hypothesis), which corroborates earlier findings of reduced mammalian movements in areas with high human pressures at global scales (Doherty, Hays, and Driscoll 2021; Main et al. 2020; Mumme et al. 2023; Tucker et al. 2018). Our findings suggest that human footprint hinders landscape permeability for brown bears on a continental scale. Contradicting to these findings and to our third hypothesis, the amount of roadless area in bear home ranges did not promote space use, potentially because of the high fragmentation and the small size of roadless areas in Europe (Ibisch et al. 2016). Alternatively, bears might show restricted space use in areas with a high human footprint because these areas provide abundant food through artificial feeding, croplands, orchards, beehives, or garbage (Bautista et al. 2021). Human pressures, including human footprint, forest disturbance, access to artificial food, and recreational activities in protected areas are ubiquitous across Europe. Here we provide the first comprehensive overview on how anthropogenic effects govern the spatial behavior of a recolonizing large mammal, the brown bear, across Europe's highly fragmented and human-dominated landscape.

4.1 | Resource Availability Shapes Space Use: The Role of Vegetation Productivity and Predictability, Seasonality, Forestry, and Artificial Feeding

Brown bear populations in south-eastern Europe overall occupied the smallest home ranges and moved over shortest distances, while populations in Fennoscandia occupied the largest ranges. This marked intraspecific variability seems to be the outcome of different cost-to-benefit ratios of moving and acquiring resources at varying levels of human pressure and resource availability along the species' distribution range. In line with previous studies (Mcloughlin, Ferguson, and Messier 2000), a gradient of natural variation in plant food availability drove intraspecific variation in space use. Home ranges were smaller and movement distances shorter in areas of higher vegetation

productivity and predictability, well known proxies of forage availability. Food resources are more limited at the northern latitudes due to the gradual decline in the length of the growing season and greater temperature seasonality, and consequently, animals need to move over larger areas to find sufficient food resources (Mcloughlin, Ferguson, and Messier 2000; Morellet et al. 2013). Indeed, bears living at the northern edge of the distribution range under higher temperature seasonality compensated for the generally lower vegetation productivity and spatiotemporal unpredictability of food resources by foraging over larger areas and by travelling over longer long-distance displacements, possibly in an attempt to track seasonal foods. We found no support that vegetation predictability and seasonality affected routine 1-day displacement distances, likely because, on a daily basis, bears adapt foraging strategies to immediate environmental cues and not to long-term spatiotemporal predictability of vegetation.

Additionally, we found that the proportion of recently disturbed forest patches led to a reduction in movement and smaller home ranges. Such early successional forests often offer clustered and abundant food resources, such as ants or berries, and bears may be able to satisfy caloric needs over smaller areas and with shorter movement distances. While we could not quantify whether these disturbances were anthropogenic (i.e., forestry) or natural (i.e., bark beetle and wind falls) disturbances (Senf and Seidl 2021), it has been estimated that 95% of all forest disturbances in Europe are due to forestry (Curtis et al. 2018). It is noteworthy that our inference on how recent forest disturbances affect bear space use comes primarily from the boreal needleleaf forests in the Scandinavian and Karelian population, and the broadleaf forests in the Carpathian population, as the proportions of recent forest disturbances were small in all other populations (Figure 1, Table S3). This aligns with Sweden and Finland being the biggest timber producing industries in Europe, where ~2% of forest area is harvested every year (Ceccherini et al. 2020). While several studies have evaluated the relationship between forest clearings, food abundance, and bear space use within populations (Frank et al. 2015; Larsen et al. 2019; Nielsen et al. 2004), we here provide the first generalizable evidence that forest disturbance may affect species movements across larger spatial scales and biomes. Future research should evaluate whether more generalizable patterns regarding, for example, successional forest patch size or distribution, on animal space use emerge.

We expected that space use would additionally be linked to the exploitation of anthropogenic food resources in human-dominated landscapes, such as agricultural fields or artificial feeding sites, as animals need to travel less to find food (Doherty, Hays, and Driscoll 2021). While agricultural fields are accounted for in the human footprint index and indeed bears moved less in areas of higher human pressure, the use of readily available artificial or diversionary feeding sites by brown bears is likely more common. Although a reduction in home ranges and movement distances associated with artificial feeding has been previously shown in brown bears and other mammal species (De Angelis et al. 2021; Jerina 2012; Selva et al. 2017), we were not able to test for it at the continental scale. Our inference was limited by the fact that we only had country-level binary information on whether artificial feeding was used or not as a

management tool, which is too coarse to test for causal links between artificial feeding and space use at the individual home range level. While artificial feeding may be a used management tool in a country, whether a feeding station is available at the individual home range level and whether the amount of food is comparable across stations and countries is unknown (Appendix S4). We still assume that artificial feeding drives differences in space use, as bear populations where artificial feeding is a most prevalent management tool, particularly the Carpathian, Dinaric Pindos and Eastern Balkan populations (Bautista et al. 2017; Selva et al. 2017), consistently occupied smaller home ranges and moved less than expected after controlling for environmental covariates.

In summary, the link between bear space use and food availability was strong and supported through multiple pathways, that is, vegetation productivity and predictability, temperature seasonality, forest disturbance, and potentially access to artificial feeding sites. Climate change is predicted to alter vegetation and fruit-based food availability across the latitudinal gradient of Europe. For example, in Spain warming temperatures have been linked to shifts in brown bear diet away from boreal and temperate food items (Penteriani et al. 2019). Beechnut mast production, an important food source for brown bears in central and eastern Europe, has been shown to be suppressed in particularly hot and dry summers (Nussbaumer et al. 2020). And in Fennoscandia, winter warming events, which melt the protective snow cover, followed by freezing temperatures have been suggested to reduce berry crops, in particular on early successional forest stands that are lacking a protective canopy cover (Hertel et al. 2018). Because we assume that bears can forage effectively on berries on freshly disturbed forest stands, to the degree that they can reduce movements and range size, and because harvest rotations are intensifying in Fennoscandia, we also assume that ultimately climate induced shifts in food availability and abundance on disturbed forest stands may result in changes of brown bear space use patterns.

4.2 | Human Footprint Restricts Space Use

Brown bears in Europe occupied home ranges with a median human footprint ranging from 0 to 32, which aligns with the human footprint range occupied by other large mammals (Mumme et al. 2023; Tucker et al. 2018). Bears in central and southern Europe were exposed to higher levels of human pressures than bears in Fennoscandia (Figure 1), with bears in the Italian Alps occupying home ranges with the highest human footprint (Passoni, Coulson, and Cagnacci 2024). Across Europe, bears moved less and occupied smaller home ranges in areas with a higher human footprint. This reduction suggests that some of the human pressures included in the human footprint index, for example, human settlements or high-traffic roads (Selva et al. 2011), can act as barriers to bear movements at large spatiotemporal scales. Our study is the first to provide generalizable evidence from multiple populations that brown bear space use is affected by human pressures across biomes and environmental conditions. Landscapes with high human footprint may also provide clustered, high-caloric food, for example, in agricultural fields or garbage dumps, again modifying space use in human-dominated landscapes via resource availability

(Doherty, Hays, and Driscoll 2021). In line with these findings, a higher proportion of forest cover in a bear's home range resulted in longer routine daily movements, suggesting that more contiguous forest cover with fewer edges promote less restricted bear movements (Cimatti et al. 2021).

4.3 | Inconclusive Effect of Area-Based Conservation Measures

Brown bear space use in Europe was largely unaffected by area-based conservation measures, that is, the proportion of protected and roadless areas within a bears' home range. The only detectable effect was that long-distance displacements were longer in areas with higher overlap with roadless areas. However, the median proportion of IUCN strictly protected areas, particularly strict nature reserves (Type Ia), wilderness areas (Type Ib), and national parks (Type II) within a home range was only 2%, and bears in the Italian Apennines were the only ones overlapping primarily with a protected area. Given the lack of overlap of bear home ranges with protected areas, we could not conclusively test the effect of protected areas on bear movement behavior. However, we suggest that protected areas in Europe are too small and poorly connected to encompass the spatial needs of highly mobile species, such as the brown bear, and to impact their movement behavior. In our analysis, we did not account for less-strictly protected lands as well as not formally protected areas with restricted human access (e.g., IUCN Types III–VI, Natura 2000 sites, military training areas) which also may serve as corridors or stepping stone habitats for wildlife. For example, military training areas have facilitated the recolonization of wolves in Germany (Reinhardt et al. 2019). More research is needed to better understand how current conservation strategies affect spatial behaviors of species with large spatial needs in highly humanized landscapes.

Finally, we were not able to account for differences in population density on space use because currently bear population density could only be estimated at a course country scale (Table S1) which did not align with home range level differences in density. Previous studies have suggested that population density affects bear-ranging behavior (Mcloughlin, Ferguson, and Messier 2000), but given that higher local population densities are likely supported by higher resource availability, we believe that bear space use in Europe is restricted by food availability and not population density per se.

4.4 | Potential Consequences of Altered Space Use for Connectivity and Ecosystem Functioning

While the return of large carnivores in Europe can be considered a conservation success, it also highlights that large carnivore species must have strong behavioral adaptability in order to coexist with humans (Gaynor et al. 2019; Gaynor et al. 2018; Lamb et al. 2020). These behavioral adaptations can come at a survival cost for individuals living in human-dominated landscapes (Cosgrove, McWhorter, and Maron 2018; Lamb et al. 2016; Oriol-Cotterill et al. 2015). For example, bears moving into landscapes with high human pressure, including

roads and railroads, but with high food availability, faced an elevated mortality risk such that these areas served as local ecological sinks driving population decline (Lamb et al. 2016). In addition, our observed disruption in long-distance 10-day displacements in particular may have implications for population expansion and demographic connectivity, potentially impeding dispersal or mate-searching behavior (Bartoń et al. 2019), and thereby promoting genetic isolation (Bischof, Steyaert, and Kindberg 2017; Epps et al. 2005). Especially for small and isolated populations (e.g., in southern Europe), decreasing genetic diversity, inbreeding, and inbreeding depression have been found, which can compromise population viability (Benazzo et al. 2017; De Barba et al. 2010; Palazón et al. 2012). For the small bear populations in the Italian Apennine and the French-Spanish Pyrenees, which have long been isolated and have no prospect for connectivity with other populations, actions tailored at supporting movements and range expansion are critical to promote population growth for their recovery (Kervellec et al. 2023; Maiorano et al. 2019). Where populations are in close proximity but barriers such as high traffic roads and settlements restrict movement, such as between the Dinaric Pindos and Carpathian populations in Serbia, or the Alpine and Dinaric Pindos populations in the Alps, corridors mitigating human pressures may aid in establishing inter-population connectivity (Bogdanović et al. 2023; Peters et al. 2015). The special protection of long-distance dispersers in particular, and of wide-ranging movement, in general, has also been suggested as a conservation measure to support population connectivity, particularly needed in highly-modified landscapes like Europe (Bartoń et al. 2019). However, recovering bear populations harbor the potential for increased human-wildlife conflict (Bautista et al. 2017). This is particularly true in expansion areas where bears have been formerly extirpated and people have forgotten the knowledge and tools, for example, about personal safety or livestock protection, to share space with bears (Passoni, Coulson, and Cagnacci 2024; Tosi et al. 2015).

Bears play an important role in the functioning of terrestrial and aquatic ecosystems and as connectivity umbrella species (Diserens et al. 2020; Dutta et al. 2023; Helfield and Naiman 2006), therefore, the human-induced reduction of their movements could have cascading impacts on many ecosystem processes and functions (Cosgrove, McWhorter, and Maron 2018; Doherty, Hays, and Driscoll 2021). As mobile omnivores (frugivores to a great extent), that travel between habitats and ecosystems with varying levels of human footprint, they may be instrumental in shaping trophic interactions and rewiring food webs (Bartley et al. 2019; Grinath, Inouye, and Underwood 2015; Ripple et al. 2014). Bears appear to be effective as connectivity umbrellas for several other coexisting mammals in Fennoscandia and in eastern Europe (Dutta et al. 2023), emphasizing the value of the species in anthropized regions. Although the functional role of bears in European ecosystems with higher human footprint can be questioned, studies have shown that, when the appropriate management measures are taken, their role as seed dispersers can be preserved, even in areas with high human pressure (García-Rodríguez, Selva, Zwijacz-Kozica, et al. 2021). However, management practices such as artificial feeding are likely to disrupt seed dispersal processes and predation effects

on ungulate populations (Kuijper et al. 2016). To our knowledge, the only region in Europe where any measurable top-down regulatory effects by brown bears on ungulates have been demonstrated is Scandinavia (Støen et al. 2022; Tallian et al. 2021), where both vegetation productivity and human footprint are generally low, and space use and mobility are higher than in central or southern Europe. Such evidence suggests potentially profound ecosystem-wide consequences from reduced space use, in central and southern Europe's human-dominated landscapes. Further research is needed on how space use affects the role bears play in their ecosystem. The implementation of effective measures to preserve animal movements in areas with a high human footprint will be key for the connectivity of recovering brown bear populations in Europe.

5 | Conclusion

The observed intraspecific variability in brown bear space use was driven by the different conditions in resource availability and human footprint across the brown bear distribution range in Europe. Bear space use was reduced in areas of increased vegetation productivity and predictability, in less seasonal environments, in areas with more forest disturbances, and higher human footprint. These results support the mounting evidence that point to a global restructuring of animal movement caused by the intensification of human activities (Doherty, Hays, and Driscoll 2021; Main et al. 2020; Mumme et al. 2023; Tucker et al. 2018). With the current expansion of large carnivores in the highly fragmented European landscape, it will be of key importance to reduce the negative impacts of humans on animal movement to ensure the successful future conservation of these populations and the functioning and resilience of the ecosystems they inhabit.

Author Contributions

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data and R code that support the findings of this study are openly available in the OpenScience Framework at https://doi.org/10.17605/OSF.IO/XH39F. This specimen represents an endangered or threatened species. The specific locality has been removed from the online record to protect this species from over-collection. These data may be supplied to researchers on request. The total vegetation productivity 2017–2023 layers were obtained from European Union's Copernicus Land Monitoring Service information at https://doi.org/10.2909/977e4bb8-407f-48ec-b4c4-403bca5a6a3b, https://land.copernicus.eu/en/products/vegetation/high-resolution-total-productivity#download. MODIS NDVI maps were obtained from the Land Processes Distributed Active Archive Center at https://doi.org/10.5067/MODIS/MOD13A3.006. The Human Footprint Index V3 (effective 2009) were obtained from Dryad at https://doi.org/10.5061/dryad.052q5. Temperature seasonality was obtained from the WORLDCLIM bioclimatic variables dataset at https://osf.io/t2jfz/. Forest cover and disturbance were obtained from Zenodo at https://doi.org/10.5281/zenodo.3924381. Digital Elevation Models were obtained from https://www.gpxz.io/blog/eudem (25m resolution) and the European Environmental Agency at https://www.eea.europa.eu/ds_resolveuid/d9cd252baa831ac4469ae055dbd8a8c1 (1km resolution). Protected areas were obtained from the World Database on Protected Areas at https://www.protectedplanet.net/. Roadless areas were obtained from http://www.roadless.online/. This study used the R packages amt (https://doi.org/10.32614/CRAN.package.amt), adehabitat (https://doi.org/10.32614/CRAN.package.adehabitatHR), hydrostats (https://doi.org/10.32614/CRAN.package.hydrostats), tlocoh (http://tlocoh.r-forge.r-project.org), brms (https://doi.org/10.32614/CRAN.package.brms), terra (https://doi.org/10.32614/CRAN.package.terra), raster (https://doi.org/10.32614/CRAN.package.raster), sf (https://doi.org/10.32614/CRAN.package.sf), sp (https://doi.org/10.32614/CRAN.package.sp) and tidyverse (https://doi.org/10.32614/CRAN.package.tidyverse).

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Supporting Information

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