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High Habitat Potential but Limited Connectivity for Brown Bears Throughout Europe

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ABSTRACT

Aim: Large carnivores worldwide have experienced substantial range contractions due to human activities, though several species are recolonising parts of their historical range. We aimed to assess current and potential European brown bear (*Ursus arctos arctos*) habitat as well as habitat connectivity on a continental scale.

Location: The extended biogeographical regions of Europe, spanning from Portugal to central Russia, longitudinally, and from Norway to Türkiye, latitudinally. Excluding inland seas; this area covers 11,151,636 km^2.

Methods: We assessed habitat suitability throughout the study area using an ensemble species distribution model with nine submodels, using data from 10 European bear populations and Türkiye. We used the resulting habitat suitability maps to conduct a least-cost path connectivity analysis and an omnidirectional circuit connectivity analysis.

Main Conclusions: Habitat suitability was strongly associated with low percentages of agricultural cover, low percentages of human development, and proximity to forest. Of our entire study area, 37% (4.09 million km^2) is occupied or potentially suitable for bears. Connectivity analyses identified corridors that could facilitate movement among southern European bear populations, though agricultural land and human development limit connectivity between northern and southern European bear populations. Previous research estimated bears occupied 0.5 million km^2 across the European Union, while our results estimate 1.82 million km^2 of this part of our study area is potentially suitable for bears, though connectivity is limited. Our results inform conservation strategies and policy development for the future of brown bears in Europe, emphasising the need for transboundary conservation efforts.

For affiliations refer to page 10.

1 | Introduction

Large carnivore ranges have contracted substantially worldwide, driven primarily by human persecution, habitat loss, and habitat fragmentation (Ripple et al. 2014). In Europe and North America, these range contractions have paralleled expanding human populations and land use intensification since the 1700s (Ripple et al. 2014; Zedrosser et al. 2011). Several species have recently reoccupied parts of their former ranges on both continents (Ripple et al. 2014; Chapron et al. 2014), resulting from increased legal protection due to recognition of the ecological importance of large carnivores and increased public support for their conservation (Ripple et al. 2014; Chapron et al. 2014). The recent expansion of large carnivores in Europe has been associated with increased forest cover and abandonment of rural areas (Cimatti et al. 2021).

Despite the predominance of humans and their activities across terrestrial landscapes, unoccupied large carnivore habitat remains throughout Europe (Milanesi et al. 2017; Wolf and Ripple 2018). Recolonisation of unoccupied habitat requires connectivity with the current range, while habitat fragmentation can limit recolonisation and inhibit processes including gene flow and range shifts in response to environmental change (Boitani et al. 2015). Because large carnivores are vulnerable to habitat fragmentation due to their large home ranges and low population densities (Crooks et al. 2011), large carnivore populations require extensive contiguous habitat, though smaller areas can serve as stepping stones between established range and unoccupied habitat (Recio et al. 2021).

European brown bears (*Ursus arctos arctos*) are an excellent example of a large carnivore facing challenges. The species occurred throughout most of Europe at the beginning of the Holocene (about 12,000 years ago) but experienced range contractions caused by climate change (Albrecht et al. 2017) and, more recently, anthropogenic habitat loss and persecution (Zedrosser et al. 2011). Although currently absent from much of their former range, an estimated 20,500 European brown bears occur throughout the European Union (EU) and the countries that geographically lie within it (Cimatti et al. 2021; Milanesi et al. 2017), primarily in areas with extensive natural land cover and low human landscape disturbance (McLellan et al. 2017; Kaczensky et al. 2024). There, brown bears occur across 10 populations that appear stable or increasing, though some have precariously small distributions and population sizes (Swenson et al. 2020). Connectivity within and among brown bear populations is considered critical to their conservation (Boitani et al. 2015).

Brown bears are globally listed as Least Concern by the International Union for Conservation of Nature (IUCN); however, six of the 10 European populations are considered threatened (McLellan et al. 2017). European brown bears are relatively well-studied (Swenson et al. 2020; Davison et al. 2011) and there have been several assessments of habitat availability (Cimatti et al. 2021; Scharf and Fernández 2018), but habitat availability and connectivity potential on a continental scale have not been assessed. Further, while most brown bears in Europe currently occur outside of protected areas (Chapron et al. 2014), the extent to which unoccupied but potential bear habitat is protected is unknown.

We used species distribution modelling employing data from 10 European brown bear populations and Türkiye to estimate areas suitable for bears throughout geographical Europe, expecting occupied and potential habitat to occur in areas with low human development, high proportions of natural land cover as opposed to agricultural land cover, and low distances to forest. We then estimated habitat connectivity throughout geographical Europe, Georgia, Azerbaijan, Armenia, and Türkiye, as well as parts of Kazakhstan, to identify habitat corridors that could connect currently occupied bear range with potential habitat. Our goal was to investigate whether large tracts of potential habitat remain across the broader region, and to assess continental-scale connectivity among currently occupied habitat and areas suitable for recolonisation. We also aimed to assess the proportions of currently occupied and potential bear habitat under protected status. This information is critical for understanding recolonisation potential and guiding conservation planning on a continental scale.

2 | Materials and Methods

2.1 | Study Area

Our study area included the extended Biogeographical Regions of Europe, as adopted by the European Environment Agency (Roekaerts 2002), with the addition of Armenia and parts of Kazakhstan, Georgia, and Azerbaijan (hereafter 'biogeographical Europe') to assess habitat suitability and connectivity across a contiguous landmass. Major islands separated from mainland biogeographical Europe (e.g., United Kingdom, Cyprus, etc.) were also included as they could be of interest in regard to their potential for future human-assisted introduction. This area (Figure 1), excluding inland seas, comprises 11,151,636 km^2 of which 46% is forest cover, 24% is non-forest natural land cover, and 24% is agricultural land (Buchhorn et al. 2020). About 3% is freshwater, 2% urban developed land, and < 1% is sparse vegetation (ice or snow cover, lichen and moss, barren land). Previous brown bear habitat assessments considered a smaller area coinciding with the eastern border of the current EU, delineated by the eastern borders of Finland, the Baltic states, Poland, Romania, Bulgaria, and Greece (Chapron et al. 2014; Scharf and Fernández 2018). When comparing our results to this previous research, we refer to this area as the 'extended EU' (Figure 2) as it refers to the spatial extent of the EU but includes countries that are not member states (e.g., Norway, Switzerland).

2.2 | Data Collection

We used brown bear data collected during 2000–2018 from various research projects and monitoring programs. Data were previously compiled as part of the BearConnect initiative (https://bearconnect.org), and sourced from research groups, government agencies, and non-governmental organisations. We used a dataset of bear occurrences including all 10 European bear populations (Table A1: Appendix A) and Türkiye using GPS telemetry locations and various other types of occurrences (i.e., VHF telemetry, genetic samples, footprints, remote camera images and videos, sightings, damages, dead and captured bears, scats, hair, and other signs of

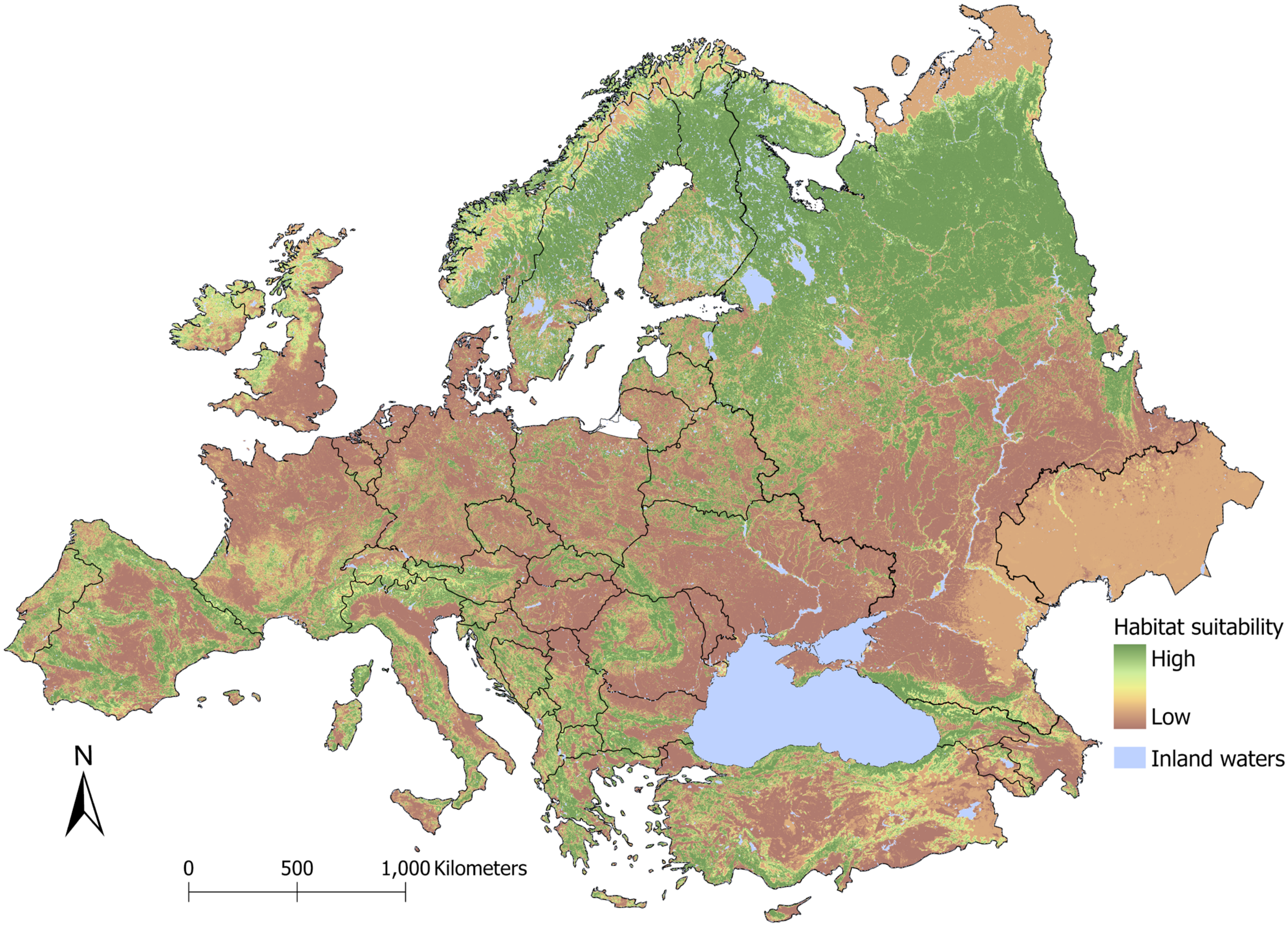

FIGURE 1 | Continuous habitat suitability map based on an ensemble species distribution model for brown bears (*Ursus arctos arctos*) in the study area representing biogeographical Europe.

activity such as animal kills, dens and daybeds, markings, and feeding remains). A small number of occurrences did not have this level of specification regarding data type and were included in the main dataset as 'other signs of presence'. All records of bear occurrences were collected under appropriate ethical approvals and permits, and all occurrences were verified by experts of the respective research groups and agencies according to respective national standards.

2.3 | Data Processing

We filtered presence data to one bear occurrence per 1 km^2 to reduce temporal and spatial autocorrelation (van den Bosch et al. 2022). We generated one pseudo-absence point per presence point, ensuring no points occurred in cells classified as permanent water. We generated pseudo-absences ≥ 20 km from presence points to reduce false negatives and improve model sensitivity (Barbet-Massin et al. 2012). We limited the selection of pseudo-absences to a convex hull of all presence points (Appendix B), excluding countries with bear populations for which we had no occurrence data (i.e., Russia, Kazakhstan, Georgia, Azerbaijan, and Armenia). Sampling pseudo-absences across the entire study area would imply that regions lacking occurrence records are environmentally unsuitable, though the absence of bears in many areas is due to historical persecution and ecological unsuitability should not be assumed. We opted for broad sampling of pseudo-absences including areas far from the current range (e.g., Germany) to avoid underestimating the full potential distribution of the species and the potential for future natural or human-assisted recolonisation.

2.4 | Ensemble Modelling

We used five variables to model bear habitat, based on the hypothesis that bear habitat suitability is positively related to natural land cover and negatively related to high levels of human landscape disturbance (Chapron et al. 2014; Cimatti et al. 2021): percentages of forest, non-forest natural, agricultural, developed land cover, and distance to forest. We used the Copernicus Global Land Service (100-m resolution; Buchhorn et al. 2020) to derive percentages of forest cover (all forest classes), agricultural cover (class 'cropland'), developed cover (including buildings, roads, and other built infrastructure.; class 'built-up'), and non-forest natural cover (classes 'shrubland', 'herbaceous vegetation', and 'herbaceous wetland'). Cells classified as permanent water were excluded from all analyses, as brown bears frequently swim but the suitability of waterbodies for bears varies greatly with their size and seasonality (Garshelis 2009). We derived distance to forest (m) by calculating the Euclidean distance from each raster cell to the nearest cell classified as forested cover.

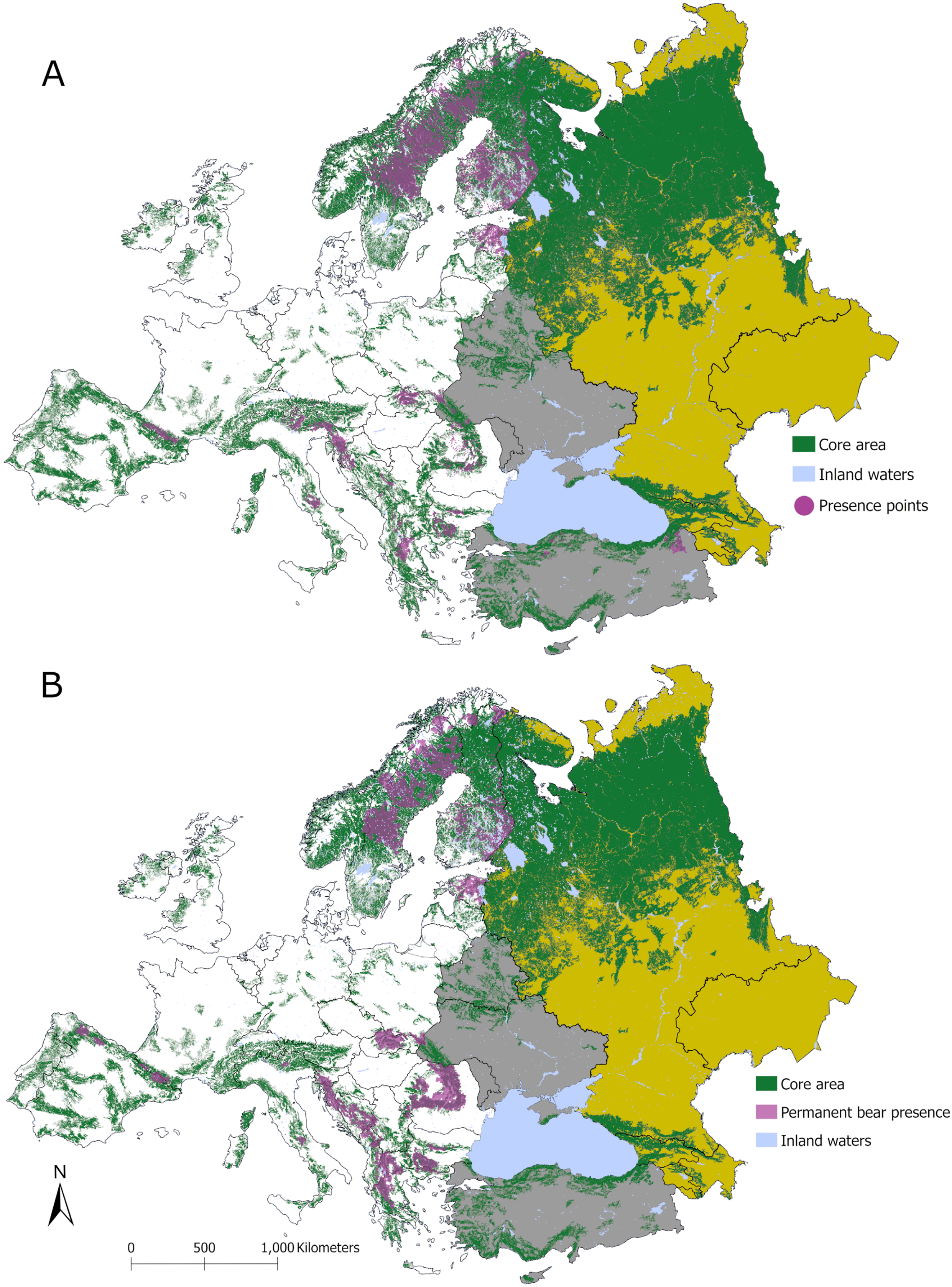

FIGURE 2 | Legend on next page.

FIGURE 2 | Core habitat area (i.e., habitat patch > 743 km^2) from a brown bear (*Ursus arctos arctos*) species distribution model for biogeographical Europe. Map A shows presence points used in the species distribution model. Map B shows permanent bear presence based on Chapron et al. (2014) and is limited to the extended European Union (the area with white background). Additional countries included in our species distribution model also contained presence and pseudo-absence points (light grey) and the resulting model was projected across biogeographical Europe including areas with no presence or pseudo-absence points (yellow).

To reflect ecological relevance and facilitate interpretation, we constrained this variable to ≤ 5000 m, assuming that distances beyond this threshold are unlikely to influence habitat selection differently.

We excluded physical landscape attributes (e.g., slope, elevation) after preliminary analyses as after historical range contractions, bears are more common in areas with medium to high elevations or slope, resulting in the species distribution model estimating a negative relationship between habitat suitability and the lowest elevations or mildest slopes. However, the positive association between bear habitat and high elevations and slopes is likely a historical artefact, as these are areas where bears remained after widespread historical persecution due to low human accessibility (Cimatti et al. 2021). Similarly, we acknowledge the limitation of our assumption that factors influencing brown bear habitat suitability are identical across the study area, given the distinct conditions in which European bear populations occur (Swenson et al. 2020). For example, bear habitat in southern Europe primarily consists of broadleaf forests, while bears in Scandinavia occur in conifer-dominated forests. We addressed this limitation by using general landscape variables such as forest and non-forest land covers, rather than specific forest types.

We resampled variables to a 1-km^2 resolution to reduce spatial mismatch between species occurrence data and environmental variables (Barbet-Massin et al. 2012). We used pairwise correlations to assess collinearity of variables. For variables with pairwise correlation > 0.70, we compared model performance metrics from full ensemble runs that each excluded one of the correlated variables, retaining the model with a higher true-skill statistic (see below) (Guisan et al. 2017). This stepwise variable exclusion was repeated until pairwise correlations were < 0.70. We developed an ensemble model with nine submodels: random forest (RF), generalised linear model (GLM), generalised additive model (GAM), generalised boosted model (GBM), flexible discriminant analysis (FDA), multivariate adaptive regression splines (MARS), classification tree analysis (CTA), artificial neural network (ANN), and maximum entropy (MaxEnt). We created the model using the biomod2 package (Thuiller et al. 2009) in program R 4.2.2 (R Core Team 2023), performing three replicates of random 70% calibration and 30% evaluation data splits to assess model performance through cross-validation, fitting ensembles of nine submodels in each replicate. We used area under the curve (AUC), true skill statistic (TSS; Allouche et al. 2006), and associated sensitivity and specificity scores as evaluation metrics (Thuiller et al. 2009). We considered AUC scores > 0.9 as “excellent”, 0.9 ≥ x > 0.8 as “good”, and 0.8 ≥ x > 0.7 as “fair” (Araújo et al. 2005). For TSS scores, values < 0.4 and 1 indicate poor and perfect model discrimination, respectively (Beaumont et al. 2016). We included submodels with a TSS > 0.5 into the ensemble model, weighted by their respective TSS evaluation scores, then projected the model to the entire study area (Barbet-Massin et al. 2012). We classified habitat by transforming the landscape suitability map to binary format using an optimised probability threshold with maximised TSS in Biomod2 (Thuiller et al. 2009). We used AUC for descriptive evaluations of model performance but not for model selection or weighting.

2.5 | Connectivity Analysis

Habitat patches separated ≤ 1 km were merged, after which we defined core areas as contiguous habitat patches ≥ 743 km^2, representing the average annual home range for adult male brown bears across populations in the extended EU (Dahle and Swenson 2003; Preatoni et al. 2005; Kanellopoulos et al. 2006; Mertzanis et al. 2011; Pop et al. 2018; Olejarz 2020; Todorov et al. 2020). We then created a raster representing resistance to movement, the inverse of the continuous habitat suitability map.

We used Omniscape software to calculate omnidirectional connectivity (Landau et al. 2021) at the landscape level. This method implements a sliding-window form of circuit theory to map omnidirectional current flow across the resistance surface raster, whereby the resulting map reflects the relative likelihood of movement through a cell assuming random walks originating from all directions (Landau et al. 2021). We clipped the omnidirectional connectivity map to the study area excluding core areas, so the resulting map represents connectivity for bears moving randomly among core areas. We complemented this by calculating least-cost path (LCP) connectivity between core areas using the LinkageMapper toolbox in ArcGIS (McRae and Kavanagh 2011). The analysis connected each core to its six nearest neighbours based on Euclidean distance, limiting linkages to ecologically plausible dispersal routes. We excluded paths < 5 km as they were unfeasible to visualise or discuss on a near-continental scale. We compared the connectivity potential of LCPs using cost-weighted distance (CWD); the combined movement resistance of all cells an LCP intersects with.

2.6 | Protected Area Status

We used the World Database on Protected Areas (UNEP-WCMC and IUCN 2025) to assess the protection status of all core areas estimated by our model, including currently occupied and potential bear habitat. For each country we calculated the percentage of protected core area.

3 | Results

Our final dataset comprised 42,536 presence points and 42,536 pseudo-absence points across most of biogeographical Europe

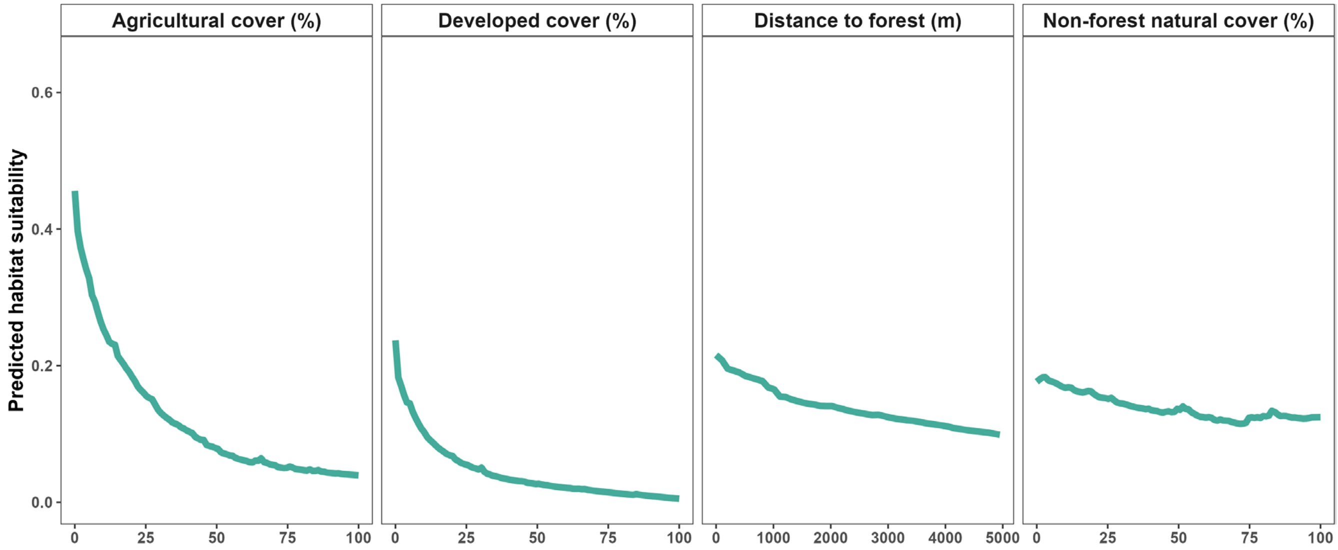

FIGURE 3 | Relationship between variables of an ensemble model to predict brown bear (*Ursus arctos arctos*) habitat suitability across biogeographical Europe. Relationships between nine submodels and environmental variables were averaged then weighted by the relative contribution of each submodel to the ensemble model.

(Figure B1: Appendix B). We removed the variable percentage of forest cover as it was negatively correlated with the percentage of agricultural cover ($r = -0.94$) and a model containing the percentage of agricultural cover yielded a marginally higher TSS than one with the percentage of forest cover. No variables retained in the final model were highly correlated ($r < 0.59$). All submodels had TSS scores >0.5, with limited variability in their respective sensitivity and specificity scores (Table C1: Appendix C) and general agreement in variable relationships to habitat suitability (Figure D1: Appendix D); thus all were retained for the ensemble model. The ensemble model had good performance with an AUC score of 0.87. The TSS score was 0.63, and sensitivity and specificity scores were 87 and 76, respectively. Habitat suitability was negatively related to the percentages of agricultural and developed cover (Figure 3). There was a moderately negative relationship with distance to forest, and an inconclusive relationship with the percentages of non-forest natural cover. Variable importance estimates indicated that the percentage of agricultural cover was the strongest predictor of core area location, followed by distance to forest cover, the percentage of developed cover, and the percentage of non-forest natural cover (Appendix C). Habitat suitability was lowest in parts of eastern biogeographical Europe, including much of Ukraine, southern Russia, and Kazakhstan, and parts of western Europe (e.g., northern France, Belgium, the Netherlands, Denmark; Figure 1). Habitat suitability was highest in Scandinavia, northwestern Russia, and parts of southern Europe and Türkiye. The model estimated 4.09 million km^2 (37% of biogeographical Europe) as occupied or potential bear habitat, of which 91.7% occurred in core areas (Table 1 and Figure 4). The largest core areas were across Scandinavia and western Russia (2.49 million km^2), the combined Alpine, Apennine, and Carpathian regions as well as parts of the Dinaric-Pindos and Eastern Balkan regions (0.42 million km^2), parts of the Iberian Peninsula (0.18 million km^2), and southern Russia, parts of Georgia, and northern Türkiye (0.17 million km^2). About 71,334 km^2 of core area, primarily in the United Kingdom and Ireland, were disjunct from the mainland.

There were 129 least-cost paths (LCPs) with lengths of 5–550 km (median = 53 km) connecting 121 core areas. Least-cost paths with lower CWDs (i.e., higher connectivity) were shorter and primarily connected smaller core areas within Germany, Poland, the Baltic states, and northern Ukraine (Figure E1: Appendix E). Lower connectivity occurred in longer LCPs connecting core areas in the northern part of the study area (e.g., Belarus) with core areas in the southern part (e.g., Georgia). Omnidirectional connectivity analysis suggested highest connectivity surrounding core areas in Scandinavia, the Baltic states, and western and central Europe (Figure 5).

The percentages of estimated core area within protected areas across countries were greater in western, central, and southern Europe compared to northern parts of the study area. The largest contiguous core area across Scandinavia and western Russia appears to be less protected than core areas in currently occupied and potential bear habitat in the Alpine, Apennine, Carpathian, Dinaric-Pindos and Eastern Balkan regions (Figure F1: Appendix F).

4 | Discussion

Our estimate of European brown bear habitat supported our expectations that bear habitat is positively associated with areas of low human development, low agricultural cover, and low distances to forest (Cimatti et al. 2021; Milanesi et al. 2017). We estimated about four million square kilometres of occupied and potential bear habitat exist across biogeographical Europe. Previous research (Chapron et al. 2014) estimated bears occupied 485,400 km^2 across part of biogeographical Europe, namely the extended European Union (EU; Figure 2), an area of 5 million km^2. Our results estimate 1.82 million km^2 (or 36%) of the extended EU is either occupied or potential bear habitat, suggesting brown bears currently occupy about 27% of bear habitat throughout this area. Beyond the EU, our model identified large

TABLE 1 | Estimated brown bear (*Ursus arctos arctos*) habitat by country with > 1500 km^2 of estimated habitat. An asterisk (*) indicates countries only partially included in the study area.

Country	Habitat (km^2)	Core area (km^2)	Protected core area (%)	Country	Habitat (km^2)	Core area (km^2)	Protected core area (%)
Russia*	1,864,272	1,798,249	10.1	Bosnia & Herzegovina	24,850	23,707	12.2
Sweden	310,763	305,710	14.5	Ireland	23,158	17,588	21.4
Finland	242,295	238,107	13.1	Croatia	21,085	16,265	46.9
Türkiye	205,696	180,521	NA	Estonia	19,633	17,775	32.8
Spain	192,812	177,742	47.1	Slovakia	17,524	16,059	65.1
Norway	187,070	177,210	10.9	Switzerland	15,991	15,367	17.4
France	117,271	93,823	59.5	Albania	14,256	14,017	26.1
Italy	103,610	94,034	37.3	North Macedonia	13,382	13,225	35.4
Ukraine	76,789	51,777	50.7	Czech Republic	13,581	5859	76.5
Romania	68,458	60,986	41.5	Lithuania	12,322	5401	49.5
Belarus	67,482	56,897	20.4	Azerbaijan	11,956	10,780	45.7
Greece	60,958	52,690	41.8	Hungary	8666	2602	67.5
Poland	59,328	34,267	77.8	Slovenia	8584	7621	62
Germany	54,193	27,486	72.9	Montenegro	7003	6883	25.6
United Kingdom	47,157	34,316	33.6	Armenia	5669	4414	43.1
Portugal	39,746	36,859	27.9	Belgium	3200	2198	45.5
Austria	37,518	33,797	38.4	Cyprus	2474	1993	93.9
Georgia	36,942	35,814	28	Kazakhstan*	3138	0	NA
Bulgaria	35,312	32,677	61.5	Denmark	1732	0	NA
Serbia	28,944	25,961	26.8	Netherlands	1585	0	NA
Latvia	25,494	21,694	25.4				

areas of habitat in western Russia, where bears are known to occur, though systematic data on occupied habitat remain limited (Chapron et al. 2014). Previous habitat estimates were based on upscaled local distribution models and appeared to underestimate habitat in areas where bears are permanently present, particularly in northern Europe (Scharf and Fernández 2018). Within the extended EU, most core areas are in Scandinavia, Spain, Italy, and France. Other countries, including Ukraine, Poland, and Germany, have relatively large amounts of potential bear habitat of which most are not part of core areas, that is, fragmented habitat patches unlikely to be recolonised naturally. If such fragmented habitats are naturally recolonised, they are likely not large enough to sustain a viable population. Habitat not within mainland Europe including the United Kingdom or Ireland could only be colonised with human assistance. Habitat fragmentation, primarily in the form of extensive agricultural land, limits habitat connectivity among core areas across biogeographical Europe, reducing potential for natural recolonisation.

The variables we used to model bear habitat primarily reflected human disturbance. European brown bear range encompasses diverse habitats, while bear diet varies from almost entirely plant-based to nearly exclusive carnivorism (Swenson et al. 2020). Due to this habitat and resource generalism, human landscape disturbance is considered the primary driver of brown bear habitat suitability (Cimatti et al. 2021) while also affecting space use (Hertel et al. 2025). Additionally, species that have only partially recolonised former range may not occupy their entire ecological niche, such that the current distribution is partially an artefact of historic persecution and does not represent the range of landscape attributes suitable for the species (van den Bosch et al. 2022). For example, large carnivores may have persisted in mountainous regions (Cimatti et al. 2021; Albrecht et al. 2017) because these areas offered protection from persecution, thus models representing partially recolonised carnivore ranges may erroneously suggest areas of low elevation or ruggedness as unsuitable. We attempted to address this by modelling only general

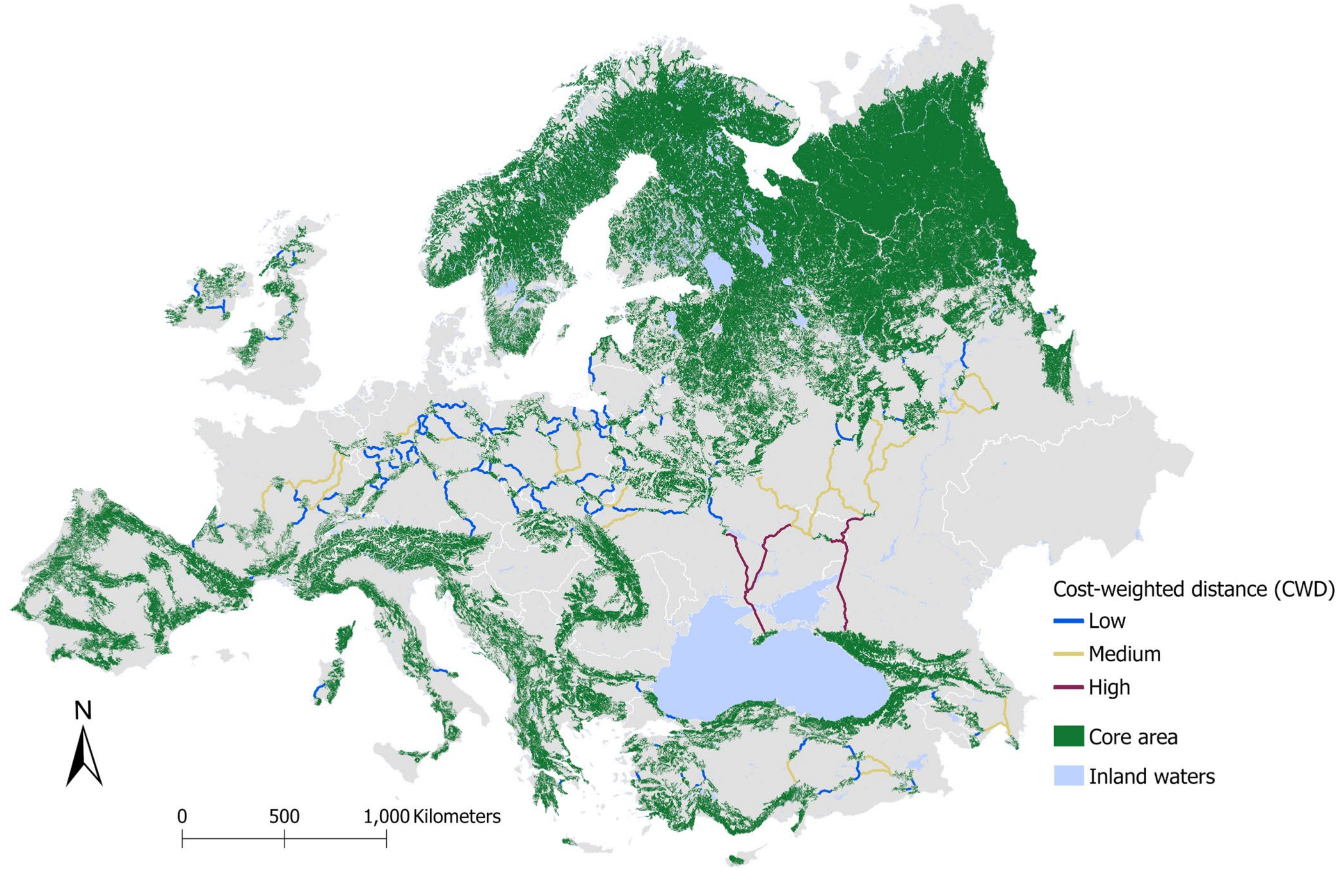

FIGURE 4 | Core habitat areas (i.e., habitat patch > 743km^2) for brown bears (*Ursus arctos arctos*) throughout biogeographical Europe. Least-cost paths (LCPs) are categorised using three Jenks natural breaks of their cost-weighted distances, which is the distance of a least-cost path accounting for its resistance to bear movement.

land cover variables, rather than specific physical landscape attributes such as elevation.

Most potential bear habitat in the extended EU occurs within regions currently supporting bear populations (i.e., Scandinavia, the Iberian Peninsula, the Alps, and the Mediterranean region, primarily in Italy and Greece), though except for the Scandinavian bear population, each of these populations is classified as threatened (McLellan et al. 2017). These threatened populations could benefit from increased connectivity within and among populations (Boitani et al. 2015; Recio et al. 2021), and our results suggest relatively high connectivity potential among several of these populations, in line with prior research and empirical evidence of GPS-collared individuals dispersing among populations (Bartoń et al. 2019). For example, Scandinavian bear populations are connected to the population in western Russia through the Finnish-Karelian population (Kopatz et al. 2021). Connectivity between bear populations in northern and southern biogeographical Europe seems unlikely due to large-scale habitat fragmentation. The Carpathian and Baltic bear populations are separated by about 1000km of unsuitable area, including areas of extensive agriculture in central Europe. Corridors with higher connectivity in western Europe could connect southern and northern bear populations, but these corridors generally connect small, unoccupied core areas; almost 25% of corridors with higher connectivity intersect Germany, which has no permanent bear presence. Notably, we analysed connectivity on a continental scale which does not account for smaller-scale barriers such as high-traffic roads and fencing, such as the recently established border fence between Poland and Belarus (Bhardwaj and Selva 2025). Our analysis represents large-scale potential connectivity for bears rather than effective connectivity, and many corridors such as those identified in Germany may contain physical barriers such as highways that restrict movements.

Our analysis of the protection status of bear habitat reveals a spatial mismatch between bear habitat extent and legal protection. Many countries in central, southern, and western Europe have relatively high percentages of protected habitat, often in regions where bears are absent or populations are threatened. Conversely, occupied and potential habitat in northern Europe and western Russia, which represents the largest contiguous area of habitat, appears to have lower proportions of protected habitat. This discrepancy may reflect differences in land use pressure, policy priorities, or the legacy of existing protected area networks. However, most bears in our study area persist in non-protected areas, and the current extent of protected areas is insufficient to sustain existing large carnivore populations, highlighting the importance of conserving bears in unprotected areas (Chapron et al. 2014; Santini et al. 2016; Terraube et al. 2020). These regions, including large, forested areas in Scandinavia and Russia, currently provide habitat for bears though their unprotected status means they may

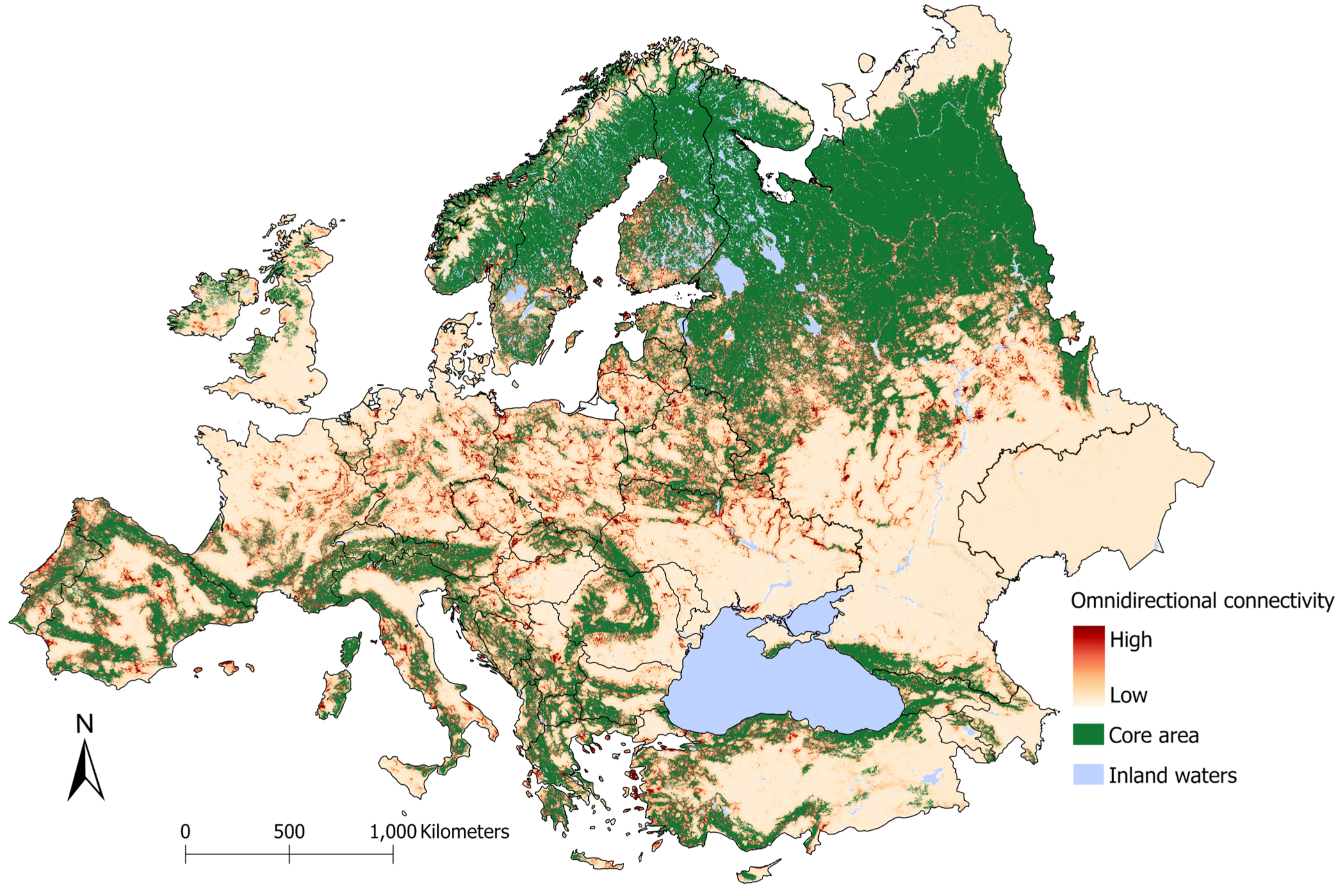

FIGURE 5 | Omnidirectional habitat connectivity for brown bears (*Ursus arctos arctos*) and core areas (i.e., habitat patch > 743km^2) throughout biogeographical Europe.

be vulnerable to habitat degradation. The higher percentages of protected potential habitat in some southern and central countries may present opportunities for population recovery and range expansion if large-scale habitat connectivity can be improved.

The large spatial scale of our analysis necessarily limits its fine-scale accuracy, as we used general variables applicable across the study area that cannot account for population-specific variation in environmental conditions (e.g., variability in predominant forest types across the study area) or variation in biotic interactions that may influence habitat suitability (Lucas et al. 2025). Similarly, while the relationship between human development and bear habitat suitability is generally negative, low-intensity development may in some cases provide resource opportunities such as apiaries, orchards, and agricultural crops, though with high potential for human–bear conflict (Penteriani and Melletti 2020). Further, we estimated the minimum area needed for bear habitat to potentially contribute to recolonisation by averaging home range sizes across populations for which home range data were available, which is plausible but unvalidated. Similarly, the minimum area of habitat required for a viable bear population likely varies widely across our study area, reflecting differences in bear densities resulting from variability in resource availability. The large variability in home range sizes among populations [e.g., male bears in Scandinavia have home ranges four to five times larger than those in the Carpathian population (Dahle and Swenson 2003; Pop et al. 2018)] underscores this point. Nevertheless, areas too small for a viable population may still serve as stepping stones to larger areas of habitat (Recio et al. 2021). Estimates of recolonisation potential that incorporate region-specific environmental variables and account for local home range size and minimum area required to support a viable population are needed. Incorporating data on dispersal, mortality, reproduction, and minimum viable population sizes would improve the accuracy of future models and help evaluate the functional connectivity of potential corridors, as well as the viability of potential new populations.

We used land cover data collected in 2018, not accounting for potential changes in habitat suitability due to land cover changes during the period of data collection (2000–2018). However, percentage agricultural cover was the primary determinant of habitat suitability in our analysis and changed only ±0.25% during this period across 39 countries considered by the European Environment Agency (European Environment Agency 2023), which we consider unlikely to strongly affect our results. Species distribution models and resulting connectivity models for recolonising species have limited temporal validity, as species-habitat relationships of recolonising species are dynamic: recolonising large carnivores may initially occur only in remote areas but increasingly occupy areas with higher human disturbance (van den Bosch et al. 2024). A linear relationship between habitat suitability and connectivity does not account for dispersing animals using lower-quality habitat. However, transforming these relationships is only appropriate when differences between habitat use of dispersing and resident animals are quantified (van den Bosch et al. 2023), which was not possible because the use of non-GPS occurrences inhibits identification of individual bears. Further, assessing recolonisation potential ideally incorporates indicators of human tolerance (Bruskotter and Wilson 2014), but such data are not available on a pan-European scale. Finally, the protected area database we used did not have data for Türkiye, and may be incomplete for other countries, particularly those outside of the EU, and we lacked information on the extent and effectiveness of protection across the diverse national protection levels represented in our dataset (UNEP-WCMC and IUCN 2025).

Like other large carnivore species recognised to have important ecosystem roles (Ripple et al. 2014), brown bears are a priority species under the EU Biodiversity Strategy 2030 and the EU Habitats Directive (European Commission 2020). Nevertheless, most European bear populations within the extended EU are currently considered threatened (McLellan et al. 2017) and largely occur in non-protected areas (Chapron et al. 2014). Conserving these populations will require transboundary research, management, and policy initiatives, including consistent legal protection across national borders for dispersing individuals (Bartoń et al. 2019), as eight of the 10 European populations occur across multiple countries (Penteriani et al. 2018). Transboundary initiatives could simultaneously support bear recovery in unoccupied habitat (Recio et al. 2021). Because the persistence and potential expansion of bear populations depend on human tolerance (Lamb et al. 2020), conservation and management initiatives should emphasise human-bear coexistence. This study provides a baseline of areas where natural recolonisation may be possible, thus where the promotion of coexistence is most pertinent, while also identifying potential bear habitat unlikely to be naturally recolonised, and where human assistance would be required if recolonisation is desired (Wolf and Ripple 2018).

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M.B.: conceptualisation, methodology, validation, formal analysis, data curation, writing – original draft, writing – review and editing, visualisation. **M.D.B.**, **A.Z.**, **N.S.**, **N.B.**, **L.M.:** conceptualisation, data curation, project administration, funding acquisition, writing – review and editing. **J.R.**, **G.S.**, **A.G.**, **S.C.F.**, **A.G.H.**, **A.P.**, **H.A.**, **A.B.**, **N.B.**, **H.B.**, **M.C.**, **D.Ć.**, **P.C.**, **C.D.**, **A.D.**, **A.E.**, **A.F.**, **M.F.**, **S.F.**, **S.F.**, **L.F.**, **M.H.**, **C.G.**, **S.B.H.**, **B.H.**, **D.H.**, **O.H.**, **G.I.**, **O.I.**, **K.J.**, **A.A.K.**, **J.K.**, **I.K.**, **A.K.**, **D.K.**, **J.V.L.-B.**, **P.M.**, **Y.M.**, **A.M.-J.**, **P.M.**, **A.M.**, **J.N.**, **S.O.**, **D.Ö.**, **S.P.**, **J.P.**, **L.P.**, **M.P.**, **A.P.**, **S.P.**, **V.P.**, **M.I.P.**, **M.P.**, **P.Q.**, **G.R.**, **S.R.**, **E.R.**, **U.S.**, **A.S.**, **A.S.**, **C.S.**, **A.S.**, **T.S.**, **M.S.**, **A.S.**, **A.S.**, **K.T.**, **A.T.**, **I.T.**, **T.T.**, **F.Z.**, **D.Z.**, **T.Z.-K.:** resources, project administration, funding acquisition, writing – review and editing. **J.L.B.:** conceptualisation, project administration, writing – review and editing, supervision.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Raw species presence data are not publicly available as the subject species (European brown bear) is subject to poaching in the study area and listed under Annex IV of the EU Habitats Directive (Council Directive 92/43/EEC), which designates it as a species of community interest in need of strict protection. Article 12 of the directive prohibits deliberate disturbance, capture, or killing of individuals in the wild and includes protections for breeding sites and resting places. Presence data censored to a 10-km resolution are available from the Dryad repository, as is the code used to create the ensemble model, through https://doi.org/10.5061/dryad.83bk3jb48.

Peer Review

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Appendix A

TABLE A1 | Number of presence locations retained for the final model derived from GPS-telemetry data and other data types for occurrences (genetic samples, camera traps, etc.), respectively. Data were collected during 2000–2018 from 10 European brown bear (*Ursus arctos arctos*) populations and the Turkish population. Points labelled 'Outside permanent EU range' refer to locations within the EU but outside permanent EU population ranges cf. Chapron et al. 2014 (n = 10,182), which may fall within current permanent EU population ranges or in sporadic-use areas. The category also includes occurrences from the Turkish population of bears (n = 1826).

Bear presences by population (n = 43,753)	GPS telemetry locations (n = 18,010)	Other occurrences (n = 25,743)
Scandinavian	6764	8778
Dinaric-Pindos	2433	1634
Karelian	1839	3419
Carpathian	1617	1227
Eastern Balkans	341	601
Apennine	282	401
Pyrenean	127	612
Alpine	0	250
Baltic	0	1377
Cantabrian	0	43
Outside permanent EU range	4607	7401

Appendix B

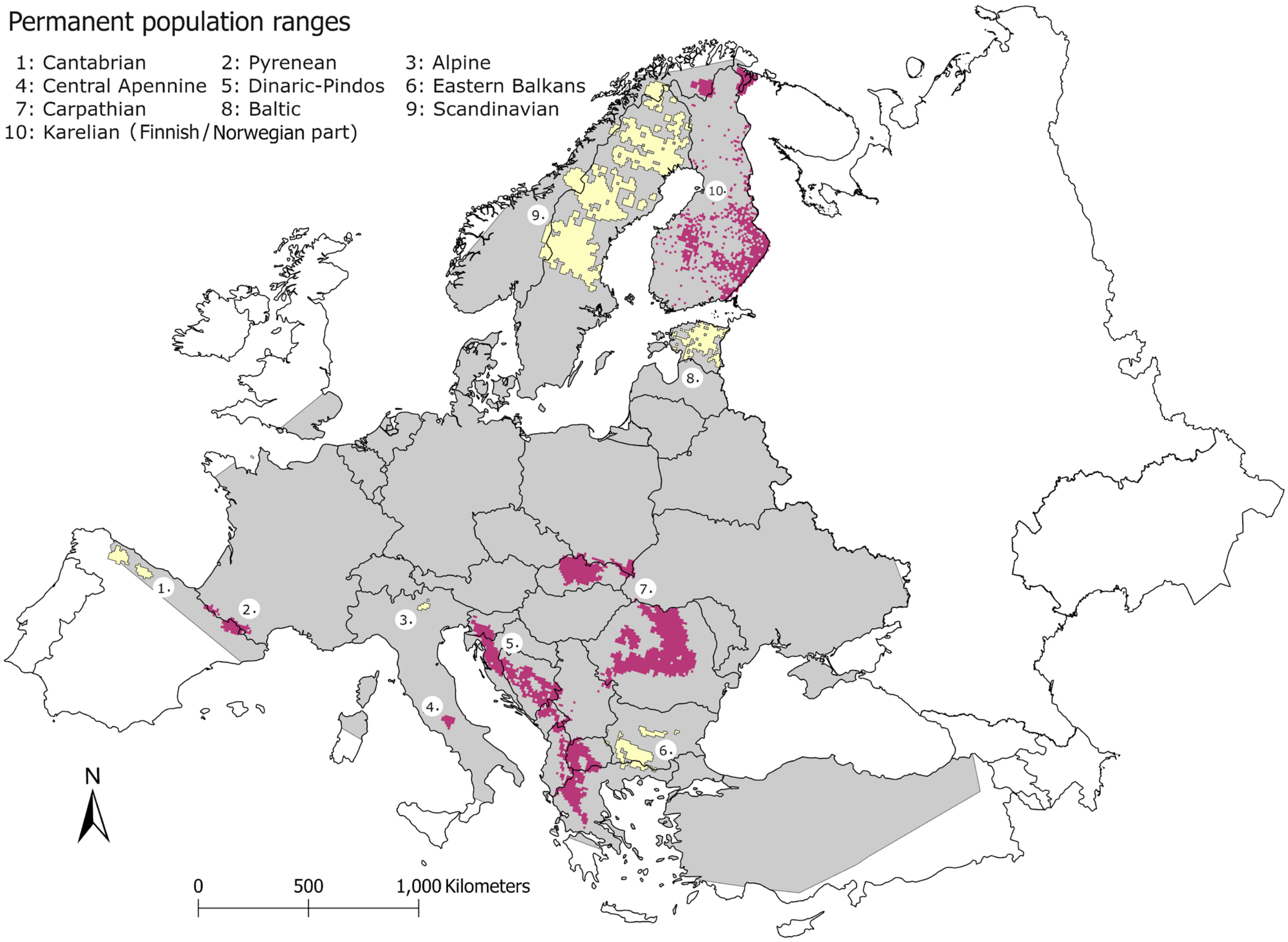

FIGURE B1 | All 10 contemporary permanent brown bear (*Ursus arctos*) populations in Europe after Chapron et al. (2014). The grey background is the minimum convex hull which contains all presence and pseudo-absence points used to model bear habitat suitability. Yellow and pink colours were used to visually distinguish neighbouring population ranges.

Appendix C

TABLE C1 | Left: Sensitivity and specificity scores of nine submodels that contributed to the ensemble model, listed in order of relative contribution to the ensemble model: random forest (RF), generalised boosted model (GBM), classification tree analysis (CTA), maximum entropy (MaxEnt), artificial neural network (ANN), generalised additive model (GAM), multivariate adaptive regression splines (MARS), generalised linear model (GLM), flexible discriminant analysis (FDA). Right: Four variables used in the ensemble model, ordered by their estimate of variable importance.

Submodel	Sensitivity	Specificity	Variable	Importance
RF	94.3	72.5	Percentage of agricultural cover	0.63
GBM	86.5	76.3	Distance to forest	0.15
CTA	85.3	77.1	Percentages of developed cover	0.10
MAXENT	87.6	74.8	Percentages of non-forest natural cover	0.02
ANN	86.0	76.5		
GAM	86.5	75.8		
MARS	87.7	74.3		
GLM	88.7	73.1		
FDA	87.0	73.9		

Appendix D

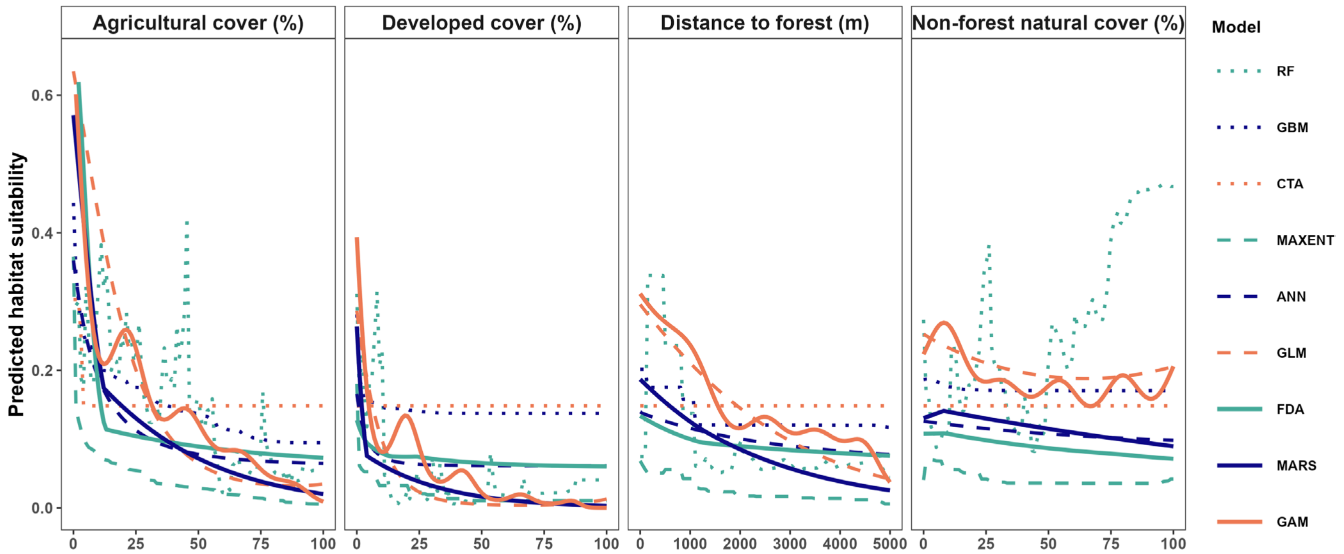

FIGURE D1 | Variable responses in an ensemble model to predict brown bear (*Ursus arctos arctos*) habitat suitability across biogeographical Europe. Submodels are listed in order of relative contribution to the ensemble model: random forest (RF), generalised boosted model (GBM), classification tree analysis (CTA), maximum entropy (MaxEnt), artificial neural network (ANN), generalised additive model (GAM), multivariate adaptive regression splines (MARS), generalised linear model (GLM), flexible discriminant analysis (FDA).

Appendix E

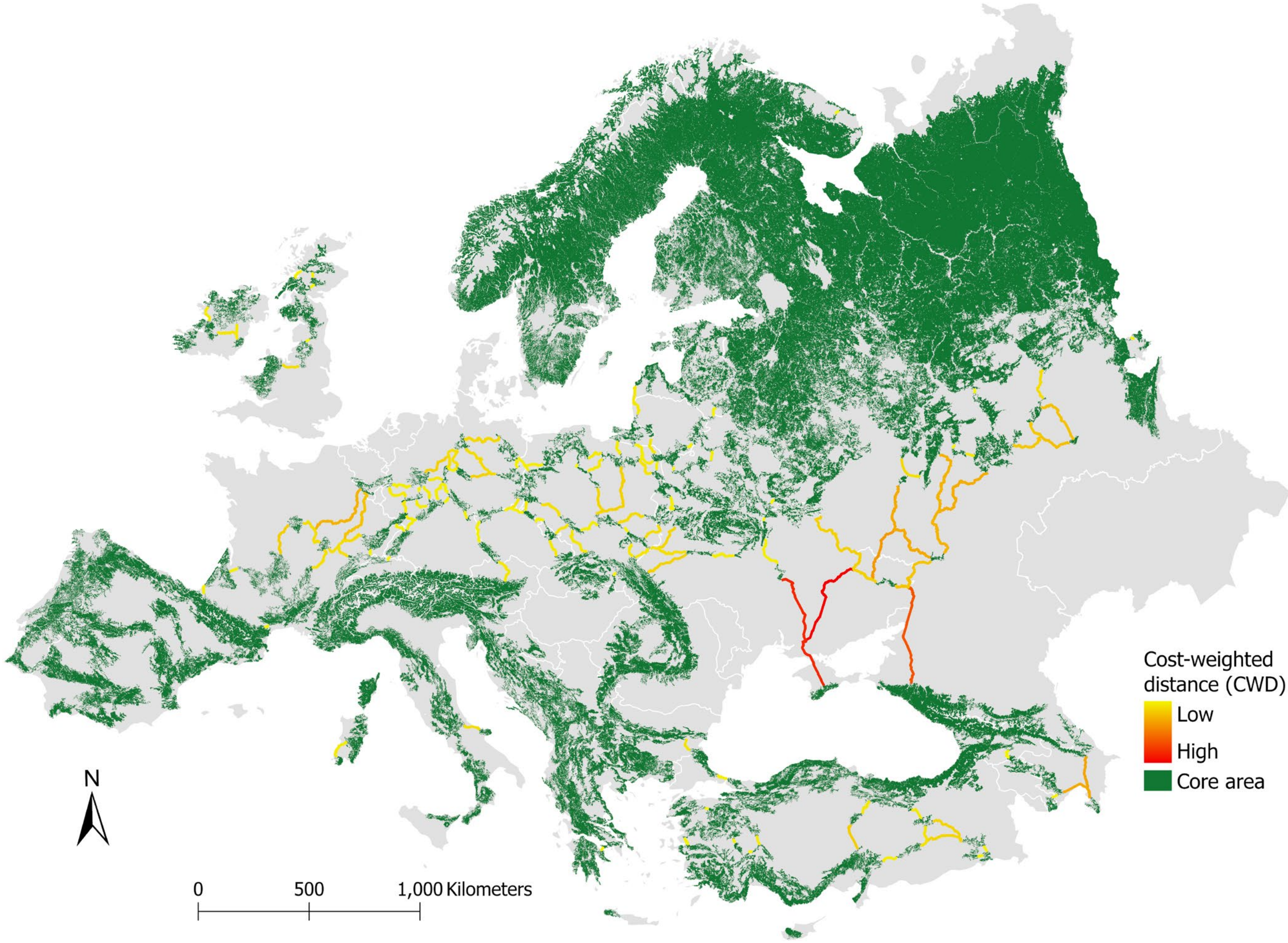

FIGURE E1 | Core habitat areas (i.e., habitat patch > 743 km^2) for brown bears (*Ursus arctos arctos*) throughout biogeographical Europe. Least-cost paths (LCPs) are visualised using a continuous gradient of their cost-weighted distances, which is the distance of a least-cost path accounting for its resistance to bear movement.

Appendix F

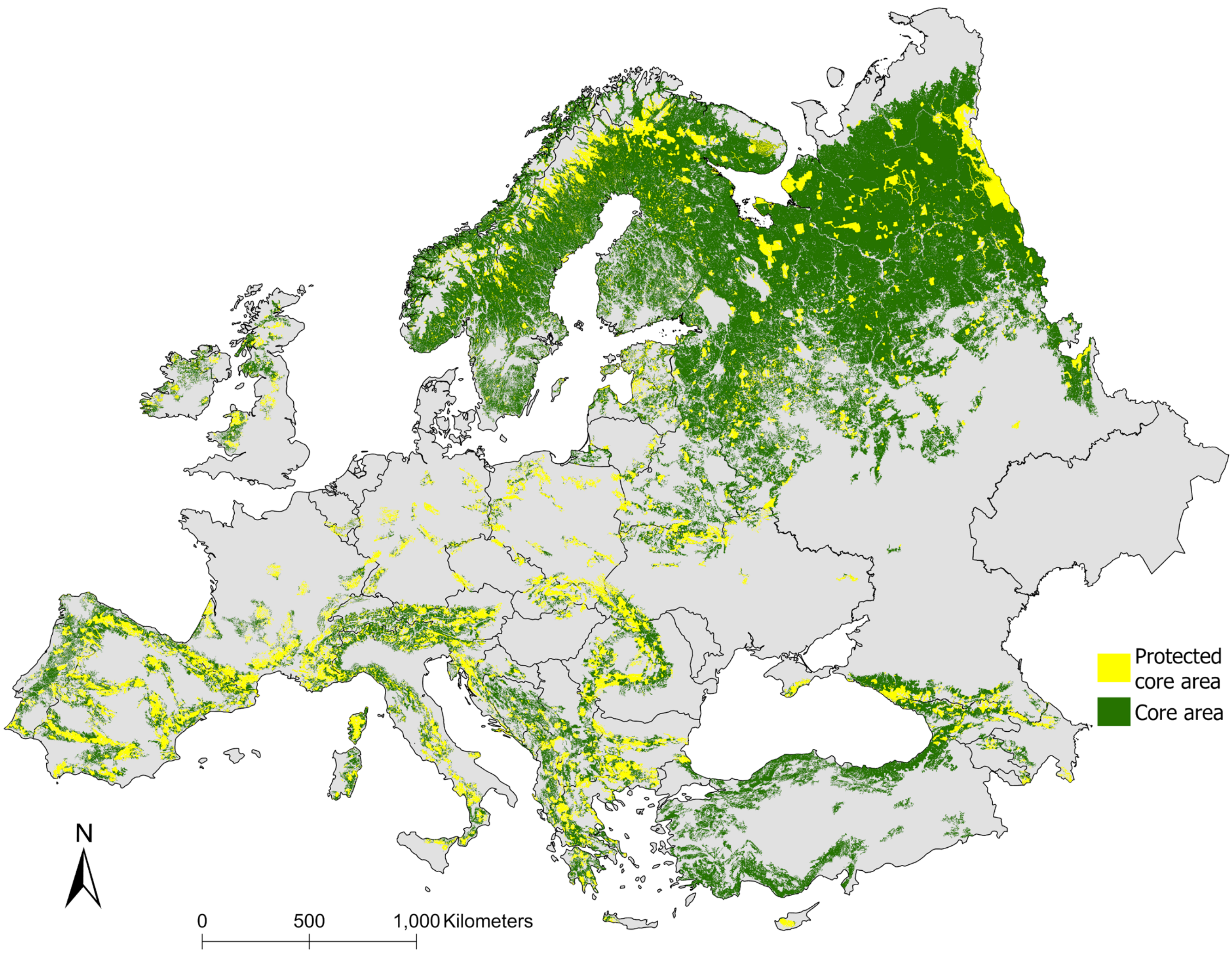

FIGURE F1 | Core habitat areas (i.e., habitat patch > 743 km^2) for brown bears (*Ursus arctos arctos*) throughout biogeographical Europe, overlaid with core areas with protected status according to the World Database of Protected Areas (WDPA).