RESEARCH ARTICLE

Widespread habitat for Europe's largest herbivores, but poor connectivity limits recolonization

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Abstract

Aim: Several large-mammal species in Europe have recovered and recolonized parts of their historical ranges. Knowing where suitable habitat exists, and thus where range expansions are possible, is important for proactively promoting coexistence between people and large mammals in shared landscapes. We aimed to assess the opportunities and limitations for range expansions of Europe's two largest herbivores, the European bison (*Bison bonasus*) and moose (*Alces alces*).

Location: Central Europe.

Methods: We used large occurrence datasets from multiple populations and species distribution models to map environmentally suitable habitats for European bison and moose across Central Europe, and to assess human pressure inside the potential habitat. We then used circuit theory modeling to identify potential recolonization corridors.

Results: We found widespread suitable habitats for both European bison ($>120,000\,km^2$) and moose ($>244,000\,km^2$), suggesting substantial potential for range expansions. However, much habitat was associated with high human pressure (37% and 43% for European bison and moose, respectively), particularly in the west of Central Europe. We identified a strong east–west gradient of decreasing connectivity, with major barriers likely limiting natural recolonization in many areas.

Main conclusions: We identify major potential for restoring large herbivores and their functional roles in Europe's landscapes. However, we also highlight considerable challenges for conservation planning and wildlife management, including areas where recolonization likely leads to human–wildlife conflict and where barriers to movement prevent natural range expansion. Conservation measures restoring broad-scale connectivity are needed in order to allow European bison and moose to recolonize their historical ranges. Finally, our analyses and maps indicate suitable but isolated habitat patches that are unlikely to be colonized but are candidate locations for reintroductions to establish reservoir populations. More generally, our work emphasizes that transboundary cooperation is needed for restoring large herbivores and their ecological roles, and to foster coexistence with people in Europe's landscapes.

KEYWORDS

Alces alces, Bison bonasus, ecological restoration, megafauna, niche modeling, potential habitat, range expansion, rewilding, wildlife crossings

1 | INTRODUCTION

Anthropogenic impacts are driving an ongoing wave of defaunation, encompassing local and global extinctions and proliferating declines in abundance (Dirzo et al., 2014; Young et al., 2016). Large mammals are particularly vulnerable, due to traits such as extensive spatial requirements, migratory behavior, slow reproductive rates and low population densities (Cardillo et al., 2005). While large carnivores are frequently in the spotlight as threatened keystone species, large herbivores and their important ecological functions often receive less attention (but see Linnell et al., 2020; Ripple et al., 2015). However, large herbivores are the primary food source for predators and scavengers (Ripple et al., 2015), and shape wildfire regimes (Rouet-Leduc et al., 2021), landscape mosaics (Kowalczyk et al., 2021), vegetation dynamics (Sandom et al., 2014) and nutrient cycling (le Roux et al., 2020). As a result, restoring large herbivores is a key component of ecological restoration and rewilding (Perino et al., 2019). Despite their importance, most large herbivores on the globe are facing dramatic declines in their abundance and distribution due to

rising human pressure, making their protection and restoration priorities (Ripple et al., 2015).

Restoring large herbivores is possible even from the brink of extinction, as powerfully exemplified by the European bison (or wisent, *Bison bonasus*), which was restored from a captive population of only 54 individuals in the 1920s to almost 7000 free-ranging individuals in 2020 (Pucek et al., 2004; Raczyński, 2021). Several factors can contribute to halting and reversing declining population trends, including systematic breeding and reintroduction programs, such as in the case of the European bison. Similarly, better protection through stricter hunting regulations and law enforcement are crucially important and have, for example, been a major factor in the recent range expansion of large carnivores across Europe (Boitani & Linnell, 2015). Finally, structural changes in agriculture, outmigration from rural areas and abandonment of land provide more space for large herbivores in many areas, trends that are likely to continue in many rural regions (Ceaușu et al., 2015).

Europe is a particularly interesting region as many large mammals have suffered major range losses in the past but are now

recolonizing parts of their historical ranges (Chapron et al., 2014; Deinet et al., 2013). Yet, most European regions still harbor only few or none of the largest herbivores, and a better understanding of recolonization opportunities and limitations in these landscapes is crucial (Linnell et al., 2020). Specifically, given Europe's strongly modified landscapes, it remains unclear where the remaining potential habitat is located and whether natural recolonization is likely, or alternatively, reintroductions would be needed.

Furthermore, where large herbivores return, conflicts with people are likely (e.g. damages to crops and forestry, vehicle collisions) and might reduce the social acceptance toward the species (Klich et al., 2021; König et al., 2020). Understanding where conflicts are more or less likely to occur is thus important for proactive conservation planning and wildlife management. However, most habitat suitability assessments typically combine predictor variables characterizing environmental conditions (e.g. land cover, vegetation types) and human pressure (e.g. settlements, roads), making it hard to distinguish unsuitable environments from areas that are environmentally suitable but with high human pressure and thus high conflict potential. Assessing both dimensions of habitat suitability separately (Naves et al., 2003) allows for disentangling them, helping to mitigate and manage potential conflicts in a forward-looking manner, in order to foster coexistence between people and large herbivores in shared landscapes (König et al., 2021).

Identifying suitable habitats can help to understand range expansion potential, yet assessing the reachability of unoccupied habitats for animals is equally important. This, in turn, critically depends on how unoccupied patches are connected to extant populations and how permeable potential dispersal corridors are (Kramer-Schadt et al., 2004). The recent recoveries of large mammals in Europe have followed a predominantly westward expansion, which is exemplified by recolonization dynamics observed for wolves (Jarausch et al., 2021); a westward expansion of moose within Poland (Zalewski et al., 2018), and increasing numbers of moose sightings in eastern Germany (Schönfeld, 2009); or the first European bison in several hundred years crossing the Oder river from Poland to Germany (NYT, 2017). Knowledge about potential dispersal corridors is key to understand where such westward expansion is most likely to happen and where barriers limit recolonization or steer animals into suboptimal, potential sink habitats (Kramer-Schadt et al., 2004; Ziółkowska et al., 2016). However, corridor assessments for large mammals in Europe have been confined to small areas (Bruinderink et al., 2003; Romportl et al., 2013) or focused only on carnivores (Huck et al., 2010; Schadt et al., 2002). Broad-scale, up-to-date assessments of dispersal corridors and landscape connectivity for large herbivores are currently missing.

Our goal here was to assess opportunities and limitations for range expansions of Europe's two largest herbivores, the European bison and moose in Central Europe. Specifically, we asked three research questions:

1. Where are environmentally suitable habitats for European bison and moose across Central Europe?
2. What is the level of human pressure within environmentally suitable habitats?
3. Where does landscape connectivity allow for a westward expansion of European bison and moose, and where are barriers toward such an expansion?

2 | METHODS

2.1 | Study area and target species

Our study area (Figure 1, approx. 925,000 km^2) focused on the broad region around the current western range boundaries of European bison and moose, encompassing Austria, Czechia, Denmark, Germany, Poland and Slovakia. The region is predominantly characterized by cropland (44% of the area), coniferous, broadleaved and mixed forests (17%, 8% and 7%, respectively) and grasslands (15%)
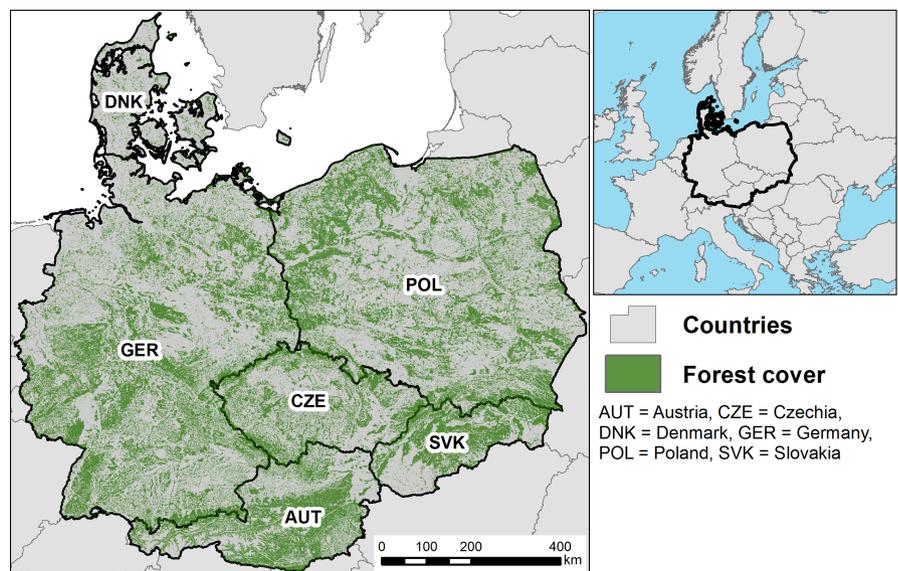

FIGURE 1 Our study area in Central Europe

(CORINE, 2018). Wetlands and water bodies make up 2% of the area, and 7% are human settlements and other artificial surfaces. Annual mean temperature ranges from −6.9°C in the highest elevations of the Alps to 11.6°C in western Germany, while annual precipitation ranges from about 400 mm to 2500 mm (Karger et al., 2017).

Throughout the mid- and late-Holocene, European bison (hereafter: E. bison) were widespread across Europe (Kuemmerle et al., 2012; Olech & Perzanowski, 2022). Habitat loss, overhunting and poaching gradually decimated their populations, and the species eventually became extirpated in the wild in the 1920s (Krasińska & Krasiński, 2013). Systematic breeding began soon after, and reintroduction programs starting in the 1950s enabled the return of E. bison (Krasińska & Krasiński, 2013), with today again almost 7000 free-ranging individuals across ten countries (Raczyński, 2021). Within our study area, Poland currently harbors E. bison populations in eight regions (Augustowska, Białowieska, Borecka, Knyszynska, Romincka and Janowskie forests, Bieszczady and Western Pomerania) with a total of >2000 individuals. There are additionally small free-ranging herds in the Slovakian Poloniny National Park and the German Rothaar Mountains (Schmitz et al., 2015). The Polish Western Pomeranian population—supported by translocations from other regions—has been the most dynamic recently, with considerable population growth (from 22 individuals in 2006 to 334 individuals in 2020) and westward expansion (Raczynski, 2007; Raczyński, 2021).

The distribution range of moose in the early and mid-Holocene included large parts of Western, Central and Eastern Europe, before many of these populations gradually became extinct due to a combination of factors including fragmentation of habitats and excessive hunting (Schmölcke & Zachos, 2005). Whereas today moose are abundant in Eastern and Northern Europe, their occurrence in Central Europe is limited (Jensen et al., 2020). However, since a nationwide moose hunting ban was imposed in Poland in 2001, populations have exhibited a remarkable demographic and spatial expansion (Raczyński & Ratkiewicz, 2011). The current total population in Poland is estimated at roughly 30,000 individuals (GUS, 2020), with moose densities highest in north-eastern Poland. Moose have been gradually recolonizing habitats across the country and are now expanding into western Poland and eastern Germany (Berndt et al., 2021; Zalewski et al., 2018). Moreover, an isolated moose population exists in the border triangle of Austria, Czechia and Germany (Janík et al., 2021).

2.2 | Species occurrence data

We compiled large datasets of E. bison and moose occurrence locations from extant populations in-or-close to Central Europe. Our E. bison dataset included GPS-tracking data from all current free-ranging herds in the study area (except the recently reintroduced herds in the Romincka and Janowskie forests), as well as additionally confirmed occurrences collected directly in the field by wildlife experts and foresters (i.e. direct observations, tracks, dung, feeding marks). In total, our E. bison dataset contained >1.8 million individual occurrence records (Table S1). For moose, we integrated occurrence data from GPS tracking, camera traps and transect surveys, and confirmed sightings in the field (i.e. individuals, tracks, marks). In addition to data from Central Europe, we also included occurrence data from southern Sweden, where moose are abundant under environmental conditions similar to those in the northern parts of our study region. Our moose dataset comprised a total of >780,000 individual occurrence records (Table S1).

For modeling habitat suitability, we filtered the data to exclude sporadic occurrences (e.g. representing migratory or exploratory movements) as these might not reflect environmental conditions in core habitats (Killeen et al., 2014) (See S1 for details). To account for sampling bias (Kramer-Schadt et al., 2013), we first rarefied the occurrence datasets using a minimum distance of 500 m between records, in line with other assessments of large-mammal habitats and distributions (Bleyhl et al., 2015; Perzanowski et al., 2019) and second, spatially balanced records by drawing a random sample of maximum 1000 records (E. bison) and 500 records (moose) per population, thus aligning record numbers across populations. This resulted in 4297 (E. bison) and 2713 (moose) independent records that we used in our models. To create resistance surfaces for the connectivity assessment (RQ 3), we additionally included all sporadic occurrences, yielding 5804 (E. bison) and 3701 (moose) records.

2.3 | Predictor variables

We used a total of 14 predictor variables to characterize habitat conditions for E. bison and moose (Table 1). Predictors described, on the one hand, the natural environment (i.e. landscape composition and structure) and, on the other hand, anthropogenic impact as a proxy for human pressure. We generated all predictors at a spatial resolution of 100 m: To account for variation in the spatial scale at which different variables influence the habitat selection of animals, we considered predictors at the local (100 m) and home range (Figure S1) scales (Mateo Sánchez et al., 2014) (See S2 for details about predictors). We tested all predictors for collinearity and, in case of variable pairs with Pearson's $|r| > 0.7$, retained the variable yielding higher model performance (Dormann et al., 2013).

2.4 | Mapping habitat suitability and human pressure within potential habitat

To map potential habitats for E. bison and moose, we used an ensemble of two species distribution models (SDM): Maximum entropy modeling (*Maxent*) and Boosted Regression Trees (*BRT*), which have been demonstrated to perform well (Valavi et al., 2021). We sampled background points using kernel density maps of our occurrence records as sampling probability surfaces, to account for the remaining spatial bias in our data (Phillips et al., 2009). For Maxent models, we sampled a large number of background points (ratio 5:1 to the number of occurrences), while using a subset of these (ratio

TABLE 1 Predictor variables used in the habitat suitability models

| | Predictor variable | | Related habitat features | Expected influence | | Data source [resolution] |
	Home range scale	Local scale		E.Bison*	Moose	
Habitat composition	Share of core forest		Resources, shelter	+	+	Copernicus [20 m]
	Share of edge forest		Resources	+	+	Copernicus [20 m]
	Share of grasslands		Resources	∩	∩	Pflugmacher et al. (2018) [30 m]
	Share of cropland		Resources	+/−	+/−	Pflugmacher et al. (2018) [30 m]
	Share of wet forests and grasslands		Resources, thermal shelter	**	+	Pflugmacher et al., (2018) [30 m] and Copernicus [20 m]
Habitat structure		Distance to nearest core forest pixel	Resources, shelter	−	−	Copernicus [20 m]
		Median tasseled cap greenness (vegetation productivity)	Resources	+	+	Landsat [30 m]
		Interdecile range of tasseled cap greenness (phenology)	Resources	+/−	+/−	Landsat [30 m]
		Median tasseled cap wetness (vegetation type/ structure)	Resources, shelter	+/−	+/−	Landsat [30 m]
Topo		Mean slope	Movement, exposure	−	−	SRTM [30 m]
Human pressure	Mean population density		Human disturbance	−	−	JRC [250 m]
	Mean road density		Human disturbance	−	−	OSM [vector]
		Distance to nearest major road	Human disturbance	+	+	OSM [vector]
		Distance to nearest settlement	Human disturbance	+	+	CORINE [100 m]

Note: *European bison **only used in the moose models.

1:1) in the BRTs (Barbet-Massin et al., 2012). We systematically tested different model parameterizations (see S3) and evaluated model performance using two metrics: the Continuous Boyce Index (CBI) (Hirzel et al., 2006) and the mean area under the curve (AUC) (Pearce & Ferrier, 2000). We validated all models using two types of cross-validation: internal validation, in which 10% of the occurrence and background data from each population were randomly sampled as test data in each fold (i.e. 10-fold stratified cross-validation); and external validation, withholding the data from one population at a time as test data. This external validation thus represented an assessment of model transferability. Since our goal was to generate transferable models capable of predicting currently unoccupied suitable habitats, we selected final models based on the external CBI (Cianfrani et al., 2010; Table S2). To create ensemble predictions of Maxent and BRT models, we calculated the weighted (by

external CBI) mean habitat suitability value per grid cell (Araújo & New, 2007).

We ran separate SDMs based on predictors describing (1) the natural environment and (2) human pressure (Naves et al., 2003). After creating ensemble predictions (Figure S6), we first converted the environmental habitat suitability maps into binary habitat/non-habitat maps using the threshold maximizing the sum of sensitivity and specificity (max$_{SSS}$) (Liu et al., 2013). Second, we used the human pressure models to divide environmentally suitable habitat into three human pressure levels: as upper threshold, indicating areas with low human pressure, we again used the max$_{SSS}$ threshold; as lower threshold, indicating strong human pressure, we used the 10th percentile of values predicted by the human pressure models at occurrence locations. Additionally, we classified all environmentally suitable habitats inside areas of the Natura 2000 network as

potential habitats with low human pressure, given that E. bison is strictly protected under the EU Habitats Directive, and assuming that the return of large herbivores will be supported in these protected areas.

2.5 | Connectivity assessment

We created resistance surfaces representing the local cost of movement through the landscape for each species based on a separate set of SDMs (Beier et al., 2008) including all sporadic occurrence records, thus also reflecting the ability of animals to move through suboptimal habitat (Killeen et al., 2014). We resampled all predictors to 1-km resolution for the connectivity analyses and used all variables with relevance for movement at that scale (i.e. dropping the fine-scale Landsat-based habitat metrics). We followed the same model selection and ensemble prediction approach as for the habitat suitability models and then rescaled habitat suitability to range between 1 and 100, inverting these values to represent cell-level resistances (Zeller et al., 2012). We additionally incorporated human settlements as total barriers (*NA* in resistance surface) and highways (OSM road classes *motorway* and *trunk*) as partial barriers (assigning a resistance value of 200). Moreover, we manually digitized green bridges over highways, as well as clearly visible larger underpasses under highways, using very high-resolution satellite imagery in GoogleEarth, assigning a lower resistance value (25) to cells with such structures.

We then used circuit theory modeling (Dickson et al., 2019; McRae & Shah, 2009) to carry out two complementary analyses. First, we assessed connectivity across the entire landscape. We generated a buffer around the study area (50% of the study area extent), randomly assigning cell values therein based on the quartile distribution of values in our resistance surfaces (Koen et al., 2014). We then randomly placed 60 nodes around the perimeter of the buffer to ensure the independence of results from the node placement (Koen et al., 2014). The resulting cumulative current density maps indicate the probability of use, per cell, by a moving individual (as random walker), thus representing an estimate of landscape connectivity (Koen et al., 2014). Sensitivity tests of models with a 60% buffer and with 70 nodes yielded highly similar results. Second, we simulated directed westward movement to assess potential corridors for the prevailing east-to-west expansion of E. bison and moose. For moose, we randomly placed 1000 source nodes along the eastern and north-eastern border of Poland (regions with currently highest moose densities in Central Europe), while randomly sampling 500 occurrence points from the Western Pomeranian population as source nodes for E. bison. For both species, we used 1000 ground nodes randomly placed along the western limits of our study area. Each source node then emitted a current, with all available ground nodes as potential terminal points. We created maps of total current flow per cell, showing which regions are well-connected to source populations, and where potential recolonization corridors of E. bison and moose are located.

3 | RESULTS

3.1 | Environmental habitat suitability

Our final environmental habitat suitability models for E. bison had high predictive performance (Table S3) and performed robustly across different regions (Table S4). The most important predictors were the shares of natural vegetation at the home range scale, with suitable habitat characterized by high shares of forest cover and, at the same time, intermediate shares of grasslands (Figure S2). In total, we mapped 120,500 km² (13% of the study area) of environmentally suitable habitat for E. bison (Figure 2). In Poland, in addition to all regions with extant populations, we found large potential habitat complexes across forest landscapes in western Poland, as well as in the south of the Warmia-Mazury region, and in the Solska Forest area. Moreover, we mapped environmentally suitable habitats along the Carpathian Mountain range, across most of the lower mountain ranges (incl. Bohemian Forest, Giant Mountains, Jeseníky Mountains, Harz Mountains, Palatinate Forest), and in the wider area around the Austrian wilderness area Dürrenstein. Further aggregations of potential E. bison habitat in lowlands included the German regions of Müritz-Schorfheide and Lüneburger Heide, as well as along the eastern German border to Poland. Finally, the upland regions of Křivoklátsko and Brdy were highlighted as important potential E. bison habitats in Czechia.

Our models for moose showed lower, but satisfactory predictive performance (Table S3), with considerable variation when predicting to different regions (Table S5). Increasing shares of wet habitats (wet forests and grasslands) and high forest cover at the home range scale were important in determining habitat suitability (Figure S4). Environmentally suitable moose habitat was widespread (244,300 km², 26% of study area; Figure 2). We found large potential habitat complexes along the Carpathian Mountain range, in most of the lower mountain ranges in the study area, and across western and north-western Poland, including the Noteć and Warta River valleys, as well as the Oder Delta in the Polish-German border region. Moreover, the northern German lowlands harbored notable areas of environmentally suitable moose habitat, including the Müritz-Schorfheide and Lüneburger Heide regions, as well as several areas with wetlands and floodplains. Furthermore, potential moose habitat patches were scattered across Czechia, southern Germany and southern Austria (Figure 2).

3.2 | Human pressure within potential habitats

About half (51%) of the environmentally suitable E. bison habitat was under low human pressure according to our models (Figure S3), while 37% were associated with high human pressure. We observed a clear east–west gradient of increasing pressure inside potential E. bison habitat (Figure 2), with half of the suitable habitat associated with low human pressure located in Poland (Figure 3). High levels of human pressure prevailed in the western part of our study region, with the
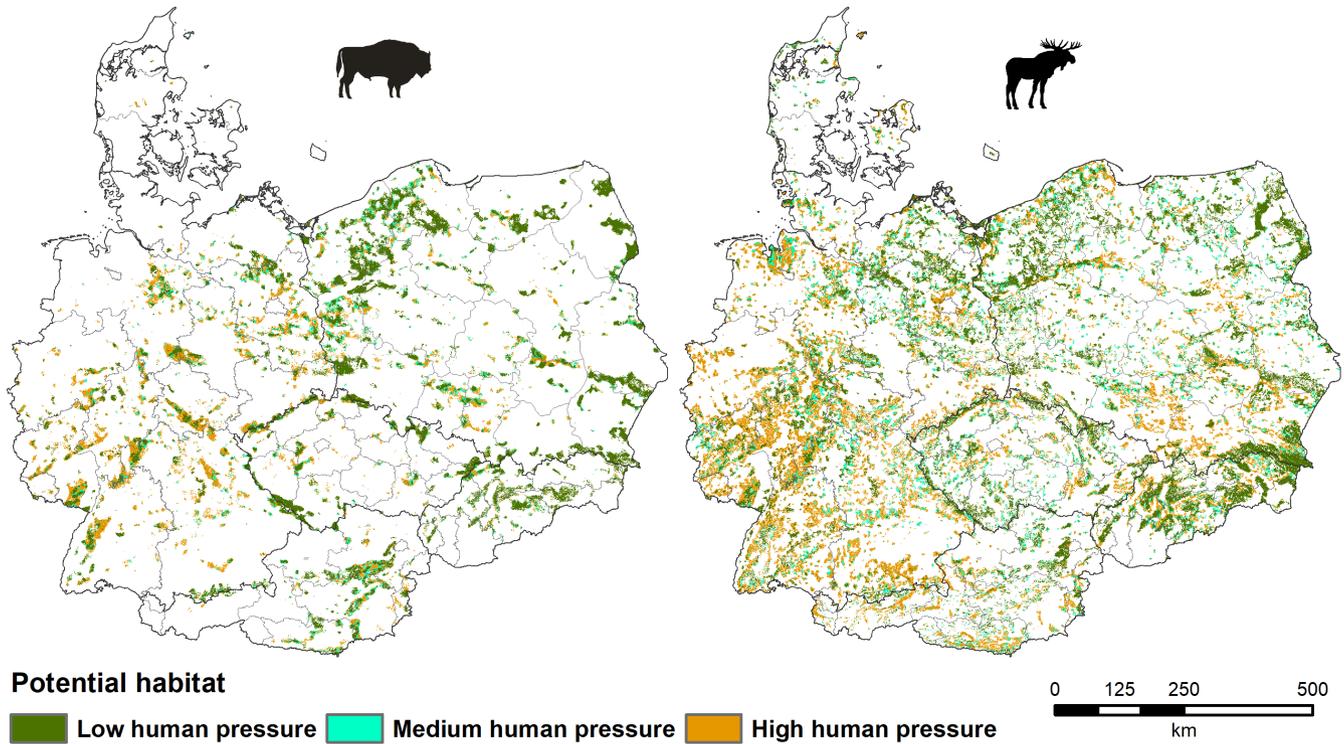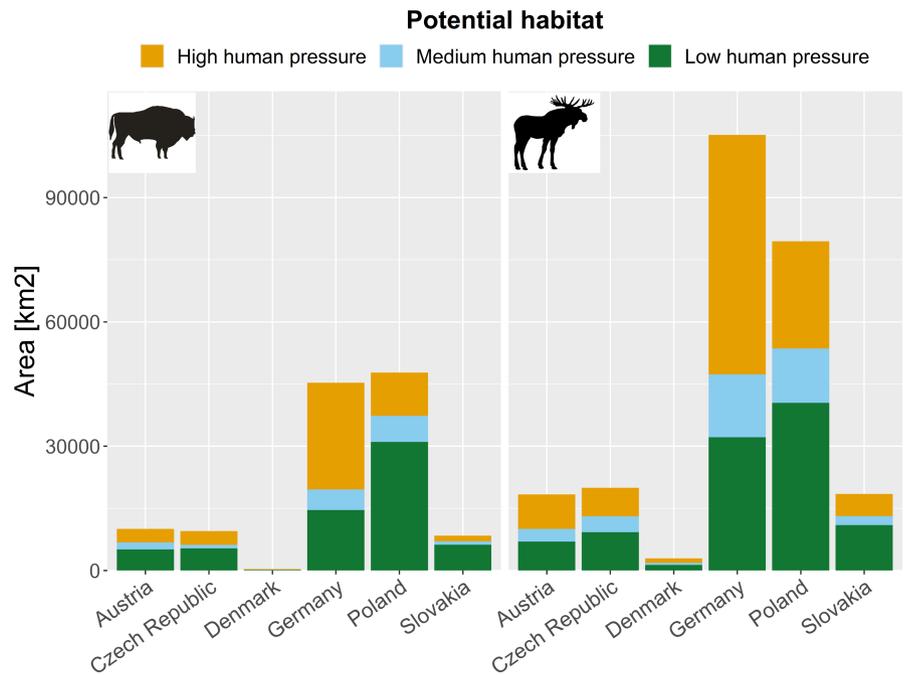
Potential habitat

Low human pressure | Medium human pressure | High human pressure

0   125   250   500
km

FIGURE 2 Potential environmentally suitable habitat for European bison and moose, and the associated level of human pressure within these habitat patches

FIGURE 3 Areas of environmentally suitable habitats for European bison and moose disaggregated by human pressure levels, per country

majority of potential E. bison habitat in Germany associated with high human pressure. The largest aggregations of currently unoccupied potential habitat associated with low human pressure were located along the Carpathian Mountain range in Poland and Slovakia, in the Polish Solska Forest, in the south of the Warmia-Mazury region, in several larger forest complexes across western Poland, in lower mountain regions of Austria and Czechia, in the Bohemian Forest and in the Müritz-Schorfheide region in eastern Germany (Figure 2).

The overall extent of suitable moose habitat under high and low human pressure was similar (43% and 41%, respectively), while the spatial distribution showed a gradient of increasing human pressure from east to west (Figure 2, Figure S5). More than half of the habitat associated with high human pressure was located in Germany, whereas Poland held the largest share of potential moose habitat under low human pressure (Figure 3). In addition to prevailing high human pressure in the western parts of Germany and Austria,

most of the potential moose habitat in central as well as southern Poland (except for the Carpathians) was associated with medium-to-high human pressure. Large complexes of suitable moose habitat associated with low human pressure were distributed across eastern Poland, along the Carpathian Mountain range in Slovakia and Poland, and across western Poland. Moreover, moose habitat with lower human pressure occurred in the lowlands of north-eastern Germany, notably the Müritz-Schorfheide region and the floodplains along the river Elbe. Finally, we found larger aggregations of low-pressure moose habitat in mountain regions of Czechia and eastern Austria.

3.3 | Assessment of habitat connectivity

Landscape connectivity for E. bison (Figure 4a) was high across large parts of eastern Poland as well as in western and north-western Poland, while permeability in central Poland was considerably lower. Further regions facilitating E. bison movements included the Bohemian Forest, and mountainous regions in Slovakia, as well as in southern Austria. Moreover, north-eastern Germany harbored numerous areas facilitating E. bison movement, yet these were often markedly separated from highly permeable regions in neighboring Poland. In western Germany, across most of Czechia, and in northern Austria, connectivity was very limited. Generally, landscape connectivity decreased from east to west, becoming increasingly patchy and disrupted. The directed westward movement simulation for E. bison, originating from extant herds in Western Pomerania (Figure 4b), showed a similar east–west gradient of decreasing connectivity, highlighting two broader corridors running north and south of Gorzów Wielkopolski. On the German side of the border, connectivity strongly decreased and potential corridors became narrower and more disrupted. Cross-border connectivity was highest in the Oder Delta region. Moreover, the wider Müritz-Schorfheide region and several areas south of Berlin showed higher connectivity, while E. bison movements appeared severely limited further westwards.

For moose, our landscape connectivity assessment (Figure 4c) revealed generally similar patterns to E. bison, yet portions of the landscape contributing to high connectivity for moose were more continuous and more widespread. Moreover, connectivity across wetlands and floodplain areas was markedly higher, notably including the Biebrza wetlands, the Noteć and Warta River valleys and several areas in northern Germany. Continuous tracts of highly permeable areas for moose occurred throughout large parts of eastern and western Poland, as well as in north-eastern Germany. Moreover, favorable conditions for moose movements prevailed in large parts of Slovakia, in the Bohemian Forest region and in southern Austria. Similar to the results for E. bison, landscape connectivity for moose was notably lower in central Poland, limiting movements between the eastern and western parts of the country. Moreover, we mapped a wide belt of low connectivity along the Czech-Polish border and across central Czechia. The directed westward movement

simulation for moose (Figure 4d) confirmed the general patterns of the landscape-wide assessment. The initially high levels of connectivity in north-eastern Poland gradually diminished across central Poland, leaving increasingly narrow corridors, particularly in the Noteć and Warta River valleys. Permeability for moose movements toward and across Czechia was limited, while higher connectivity remained toward the Polish-German Oder Delta region, as well as north and south of Berlin.

4 | DISCUSSION

In the face of ongoing global defaunation, the recent rebounding of large-mammal populations in Europe is a hopeful trend (Enquist et al., 2020; Malhi et al., 2016). Large herbivores are particularly important, as they are of conservation concern, have historically been extirpated across much of their former ranges and fulfill unique ecological roles (Lundgren et al., 2020; Schowanek et al., 2021). Knowing where suitable habitat for large herbivores is located, how that overlaps with human pressure and where recolonization might happen provides important information for conservation planning and wildlife management. Nevertheless, broad-scale, up-to-date information on the range expansion potential for large herbivores is lacking. We used large datasets of E. bison and moose occurrences to identify suitable habitat and to assess their ongoing westward range expansion. We uncover widespread, environmentally suitable habitat for both species, yet also show a clear east–west gradient of increasing human pressure on these habitats. Furthermore, a large portion of potential habitat likely remains inaccessible, as we also identified a strong east–west gradient of decreasing landscape connectivity that threatens to seriously limit natural recolonization. Together, our assessments pinpoint areas where recolonization is imminent and where mitigating human-wildlife conflicts will be needed, as well as where measures to improve landscape connectivity might increase recolonization potential. More generally, our study shows that large herbivores can find suitable habitat, even within strongly human-modified landscapes, such as in Europe.

Our habitat models performed well and yielded plausible mapping results, as our habitat distribution overlapped broadly with smaller-scale assessments, such as for Poland (Perzanowski et al., 2019) or the northern Carpathians (Ziółkowska et al., 2016), in the case of E. bison; and a local habitat assessment for the border area of Germany, Austria and Czechia, in the case of moose (Janík et al., 2021). The widespread, currently unoccupied suitable habitat we found for both species suggests a major potential for further range expansion in Central Europe, similar to the ongoing expansion of large carnivores in these landscapes (Chapron et al., 2014). Similar to the case of wolves, potentially important sites for the establishment of E. bison and moose could be protected areas and abandoned and active military training grounds that provide refuges in otherwise human-dominated landscapes (Reinhardt et al., 2019; Zentelis & Lindenmayer, 2015), as in the case of the growing E. bison population in Western Pomerania (Poland).
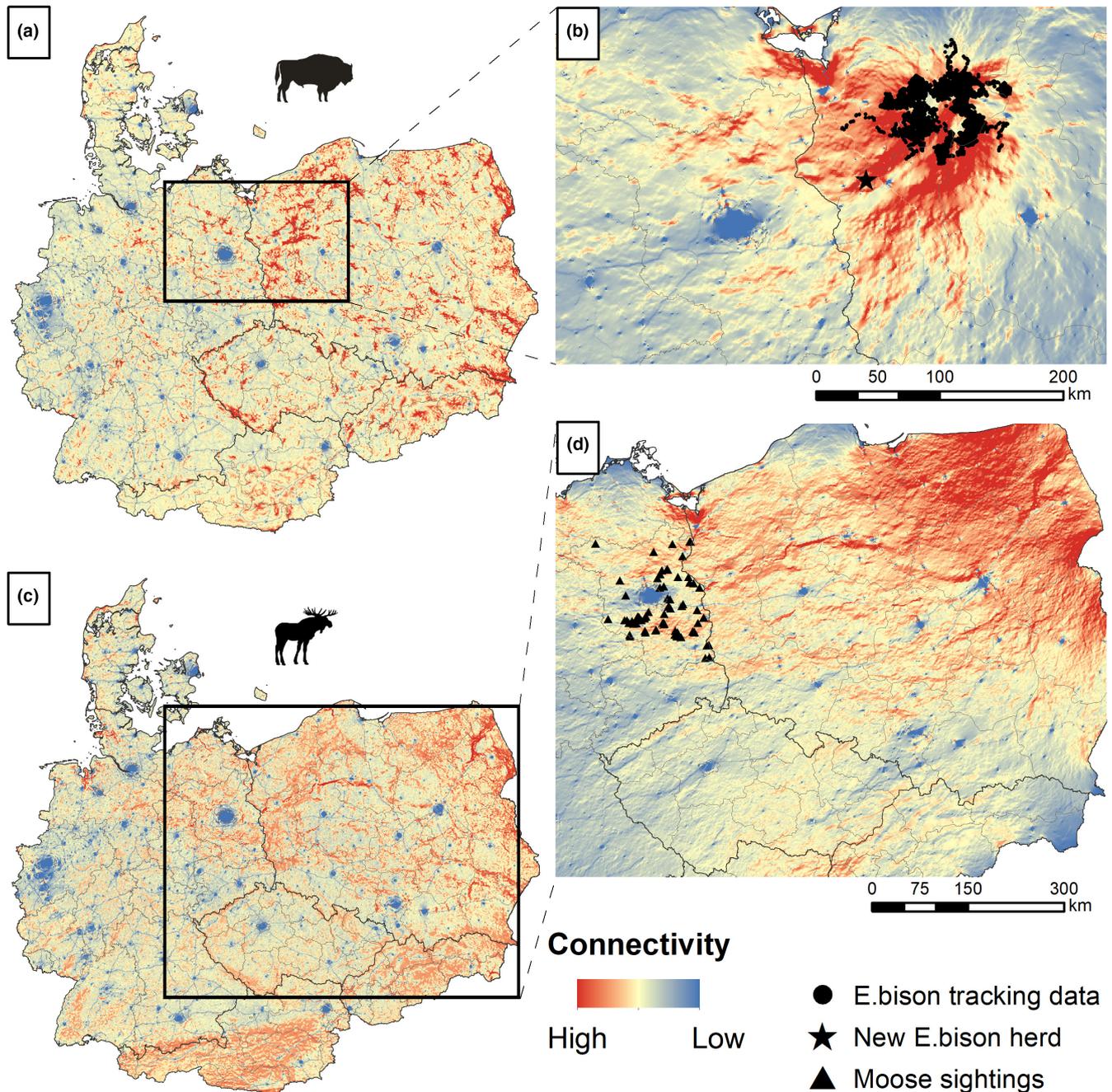
FIGURE 4 Landscape-wide (panels a and c) and directed westward (b and d) connectivity maps for European bison (a and b) and moose (c and d). Landscape-wide connectivity shows the general permeability of the landscape, whereas westward connectivity shows the potential for dispersal from east to west (see Methods section). In the regions where range expansion is ongoing, we overlayed the locations of collared E. bison individuals from our GPS-tracking datasets (used in the models) and the (independent) locations of a newly established E. bison herd that recently dispersed and reported sightings of moose in eastern Germany.

Given the high plasticity of habitat requirements of both E. bison and moose (Hofman-Kamińska et al., 2019), both herbivores could likely persist in many regions where they are currently absent. However, we also show that many habitat areas are associated with high levels of human pressure. As both species show an ability to tolerate human presence and can adapt to human-modified landscapes (Eldegard et al., 2012; Haidt et al., 2018), recolonization is still likely to occur. However, conflicts with land use and people might become a hindrance to long-term coexistence in such shared landscapes (DW, 2018; Schröder et al., 2019). Large herbivores such as E. bison and moose can inflict major damage on crops and trees (Edenius et al., 2002; Hofman-Kamińska & Kowalczyk, 2012; Nieszała et al., 2022), although likely less than the damages caused by other, much more abundant ungulates such as red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*) or wild boar (*Sus scrofa*) (Carpio et al., 2021; Linnell et al., 2020). Another potential source

of conflict with E. bison and moose are traffic collisions, which can threaten human lives (Niemi et al., 2017), inflict major economic damage (Gren & Jägerbrand, 2019) and negatively impact population viability of small populations (Janík et al., 2021; Teixeira et al., 2020). Measures to lower the risk of animal-vehicle collisions are important in areas expecting range expansions of large herbivores, such as the provision of safe road crossings (i.e. wildlife bridges or underpasses and guiding structures), speed limits and warning signs in risk-prone locations, as well as awareness raising among drivers (Borowik et al., 2021; Huijser et al., 2016). Overall, the social acceptance of moose and E. bison—in areas where they return—will determine whether or not coexistence is possible (Klich et al., 2021; Linnell & Kaltenborn, 2019), depending on context-specific wildlife management, measures to reduce and compensate for damages (Linnell et al., 2020; Neumann et al., 2022) and educational campaigns (Klich et al., 2018).

Our connectivity assessments identified areas with high potential for recolonization of suitable habitat, especially in western Poland and north-eastern Germany, and several factors enhance the plausibility of our results. First, our connectivity maps align well with reported moose sightings in the German federal state of Brandenburg, for example explaining the high density of sightings south of Berlin (Figure 4d). Second, our assessment broadly aligns with other, smaller-scale connectivity assessments, such as for E. bison in the Carpathians (Ziółkowska et al., 2012) or for large mammals in Czechia (Romportl et al., 2013). Finally, our connectivity maps for E. bison across Poland are in line with an assessment identifying isolated habitat patches for 'reservoir herds' for E. bison (Perzanowski et al., 2019). Together, this suggests that our maps are helpful for estimating where westward expansion of E. bison and moose is likely to happen. Yet, our assessments reveal substantial barriers to this range expansion, explaining, for example, why suitable moose habitat remains uncolonized in western and southern Poland. Moreover, lacking connectivity for moose from Poland toward and across Czechia, primarily due to recent infrastructure development, underlines the high level of isolation of the southernmost extant moose population, which is currently undergoing critical decline (Janík et al., 2021). Across the globe, large herbivore movements and migrations are increasingly limited by people (Tucker et al., 2018). Despite the ability of large herbivores, like E. bison and moose, to disperse over large distances (Krasińska & Krasiński, 2013; Niedziałkowska et al., 2016), increasing landscape fragmentation from Europe's east to west explains why large herbivores are "lagging behind" the recolonization dynamics of large carnivores. Ongoing construction of new highways in Poland and Czechia, as well as a surge in border fencing (e.g. Polish-Belarussian border wall, African swine fever fence along Polish-German border) seriously limit the natural recolonization potential (Jaroszewicz et al., 2021; Linnell et al., 2016). Moreover, these barriers limit genetic exchange among different subpopulations, potentially leading to genetic drift in isolated populations which can ultimately decrease population viability through inbreeding and loss of adaptive capacity (Plumb et al., 2020).

Therefore, consideration of transboundary connectivity restoration is urgently needed (Liu et al., 2022).

In addition to landscape connectivity, we stress that population density likely plays an important role in range expansion, as dispersal is density-dependent in large herbivores (Bonenfant et al., 2009; Plumb et al., 2009), and many populations (e.g. of E. bison) are likely below ecological carrying capacity. The comparatively slow expansion of E. bison in some areas is thus likely also related to wildlife management keeping populations below carrying capacity (Krasińska & Krasiński, 2013). For moose, further westward expansion will depend on the sustained growth of the Polish moose populations, in turn relying on a continued hunting ban in Poland. However, environmental stochasticity and changes in habitat quality due to, e.g. wildfire, flood, drought or harsh winter conditions may also trigger dispersal independent of local population density (McCullough, 1999). Moreover, it is important to note that E. bison and moose are different in their life history and dispersal behavior. Natural range expansion of herd-living E. bison requires the dispersal of mixed-age and mixed-sex groups, which does not commonly occur over long distances, especially when supplementary feeding reduces animal movements away from established areas (Kowalczyk et al., 2013; Krasińska & Krasiński, 2013). Moose are solitary and frequently disperse over long distances (Niedziałkowska et al., 2016), explaining their faster expansion.

While we highlight well-connected areas with suitable habitat where the expansion of E. bison and moose can be expected, our assessments also reveal many isolated habitat patches that are unlikely to be colonized naturally yet can be candidate locations for reintroductions. Particularly for E. bison conservation, such herds can be highly valuable (Plumb et al., 2020). Given the species' high vulnerability due to its low genetic diversity (Tokarska et al., 2011), isolated reservoir populations can be an important backup for restocking other herds (Perzanowski et al., 2019). Moreover, reintroducing large herbivores can restore lost ecological functions even in isolated habitats, including contributions to maintaining valuable, open habitats (Dvorský et al., 2022; Kowalczyk et al., 2021) and to wildfire prevention (Rouet-Leduc et al., 2021). Finally, reintroductions, even in isolated patches, will contribute to the global conservation of iconic wildlife and threatened species and can support regional development in rural areas (Helmer et al., 2015; Margaryan & Wall-Reinius, 2017). While our maps reveal potential candidate sites for reintroductions, we caution that any reintroduction project must pair our top-down analyses with bottom-up assessments of land use, acceptance of people and institutional conditions. Moreover, we caution that our analysis is static and considering habitat quality under expected future climates could be important. While our study area is distant to the historical range limits of E. bison and moose (Kuemmerle et al., 2012; Schmölcke & Zachos, 2005), thus suggesting some adaptive capacity of both species, assessing the impact of warmer climates could be particularly important for moose as a cold-adapted species (Ruprecht et al., 2016; Thompson et al., 2020). However, the overall effects of warming on moose are unclear as they have a high capacity for behavioral thermoregulatory responses to mitigate the negative effects

of rising temperatures (Borowik et al., 2020; Thompson et al., 2021), and warming might reduce calf mortality in winters (Ferguson, 2002; Holmes et al., 2021). Closely monitoring the responses of E. bison and moose to changing climatic conditions will be important to understand the adaptive capacity of these species.

We used the most comprehensive datasets of E. bison and moose occurrences ever collected for Central Europe, spanning a wide range of environmental conditions. Our habitat models performed well, yet several sources of uncertainty need to be mentioned. First, despite thoroughly accounting for spatial sampling bias, some bias likely remained, especially for moose. Including more records from moose populations in central and eastern Poland would have been desirable. Second, our habitat maps are likely conservative, given that both species are currently not in equilibrium with their environment and had larger ranges historically. Likewise, our habitat models relied on occurrence data based on current distributions, which are heavily influenced by past reintroductions. For E. bison, which have been reintroduced mainly to forest landscapes, this could mean that more open areas are also or even more suitable than the areas currently occupied (Kerley et al., 2012; Kuemmerle et al., 2020). Moreover, E. bison's association with forest habitat might be lower without management such as supplementary feeding inside forests (Krasińska & Krasiński, 2013). Thus, there are likely further regions harboring suitable E. bison habitat, especially more mosaic-type landscapes (Kuemmerle et al., 2018). Third, our maps included extrapolation to areas outside the value range of our training data, particularly, in alpine regions (Figure S7), where we might overestimate connectivity. Fourth, several factors could have enhanced our models but were unavailable to us, including forest understory productivity, snow depth, a distinction between natural and managed grasslands, or the location and extent of winter feeding. Fifth, while habitat suitability is a reasonable proxy for movement resistances, GPS-tracking data from dispersing individuals, as well as more detailed information on road barriers (e.g. traffic volumes, road fencing), could further enhance our connectivity assessments (Ziółkowska et al., 2016).

Finding ways of preserving large mammals in the Anthropocene is challenging. The ongoing comeback of large mammals in Europe provides a unique opportunity to restore lost functionality (Perino et al., 2019), thereby contributing to the UN Decade on Ecosystem Restoration goals. Large herbivores are often neglected in restoration efforts, despite many ecological (Dvorský et al., 2022), economic (Margaryan & Wall-Reinius, 2017) and cultural (Cooper et al., 2016) benefits, provided their populations are properly managed (Apollonio et al., 2017; Linnell et al., 2020). Restoring large herbivore populations can also be key for mitigating human-carnivore conflicts by creating a better wild prey base for carnivores (Kuijper et al., 2019). Overall, our maps highlight that range expansion from Europe's east to west for E. bison and moose is possible and plausible. This provides important information for conservation efforts and wildlife management in at least three ways. First, by identifying areas where natural recolonization is likely imminent, requiring proactive measures to mitigate human-wildlife conflict. Second, by highlighting where barriers prevent such a natural recolonization, requiring measures to improve landscape connectivity if recolonization is desired. Third, by highlighting isolated habitat patches where reintroductions are needed, but that can make a contribution to safeguarding threatened species and to restoring lost functionality. Similarly, our assessment highlights how for wide-ranging large mammals, conservation and management efforts urgently require joint, transboundary cooperation. Finally, our study advances the understanding of the considerable potential for large-mammal recoveries in landscapes, which have historically undergone major episodes of land-use change and defaunation, providing hope during times of accelerating biodiversity loss.

CONFLICT OF INTEREST

We declare no conflict of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The species location records, the input data used to generate the species distribution models, and the output maps, will be made available via the Dryad data repository under the following link: doi:10.5061/dryad.280gb5mrz. We provide the species location records at a coarsened resolution (50 km) due to the sensitive nature of these data, as E. bison is an internationally protected species (Bern Convention Annex III and Habitats Directive), and both E. bison and moose are threatened by poaching in several regions.

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BIOSKETCH

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SUPPORTING INFORMATION

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