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Landscape Features, Human Disturbance or Prey Availability? What Shapes the Distribution of Large Carnivores in Europe?

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Abstract: Knowledge concerning the relative importance of biotic and abiotic factors associated with the long-term settlement of large carnivores in human-dominated landscapes is important for effective species conservation. However, identifying the major drivers of large carnivore occurrences at a continental scale is challenging as several factors can act in concert to affect large carnivore distributions. Thus, we investigated the relationship between the permanent and sporadic occurrences of large carnivores (brown bear, Eurasian lynx, grey wolf and wolverine) and three groups of predictor variables (i.e., landscape attributes, human disturbance and prey availability) on the continental scale in Europe. Specifically, we used generalized linear models (GLMs) and variation partitioning to estimate the independent and cumulative effects of the three predictor groups on large carnivore occurrences. The explained variance for permanent vs. sporadic occurrence was highest for the wolverine (42.8% and 29.7%), followed by the brown bear (20.5% and 16.4%), Eurasian lynx (15.2% and 11.6%) and grey wolf (15.8% and 6.1%). Landscape attributes, such as forest cover, shrub-land cover, altitude and slope, were positively related to the occurrence of grey wolf, brown bear and Eurasian lynx, whereas human disturbance (human population density, distance to roads and to human settlements) was negatively related to wolverine occurrence. For all species, shared effects between landscape attributes and human disturbance accounted for a considerable portion of the explained variation in both permanent and sporadic occurrence, and landscape attributes were generally more important for explaining permanent than sporadic occurrence, except for the wolverine. Prey availability was marginally associated with the permanent occurrence of the grey wolf but we found no statistical effect of prey availability on the occurrence of the other large carnivores. In conclusion, the sporadic occurrence of large carnivores in Europe is more stochastic and less predictable than their permanent occurrence. Landscape attributes and their joint effects with human disturbance are the most important factors related to the recolonization dynamics of large carnivores, although wolverine distributions appear strongly limited by human disturbance itself. Domestic prey availability seems to play a subordinate role in driving the recent distribution dynamics of large carnivores at the continental scale. Thus, our results are relevant also in light of the ongoing recolonization of large carnivores which, in many rural areas, caused concerns among the locals, especially in relation to conflicts with human activities. For these reasons, we stress the need to continue and improve large carnivore monitoring across Europe.

Keywords: *Canis lupus*; *Lynx lynx*; generalized linear models; *Gulo gulo*; permanent occurrence; sporadic occurrence; *Ursus arctos*; variance partitioning

1. Introduction

Investigating why large carnivores permanently or sporadically occur in a given area and not in another has become increasingly important in the light of the ongoing recolonization dynamics of large carnivores in Europe. The availability of species occurrence records

and improved habitat data has brought forward a number of investigations providing insights into the factors associated with large carnivore distributions [1–5]. For example, prey availability has been suggested to preclude population expansion and the permanent population stabilization of grey wolf (*Canis lupus* L.) and Eurasian lynx (*Lynx lynx* L.) in the Carpathian Mountains [5]. In the Bohemian-Bavarian Eurasian lynx population, grasslands, croplands and altitude were the main environmental factors related to species occurrence, even though other factors, such as illegal killing, are expected to limit its expansion [6]. While these studies provide important regional insights into the factors related to single population dynamics, we know relatively little about the factors associated with large carnivore distribution dynamics at the continental scale [7].

After decades of persecution in Europe, large carnivores, such as the brown bear (*Ursus arctos* L.), Eurasian lynx, grey wolf and wolverine (*Gulo gulo* L.), are recolonizing their historical ranges and are now distributed across large areas of Europe [8]. The factors contributing to this recent expansion include improvements in natural or semi-natural habitat quality, the return of their prey species and public support, as well as favorable legislation [9]. The recolonization of large carnivores and their adaptability to persist in human-dominated landscapes has evoked strong debates [10–12]. Conflicts between humans and large carnivores primarily arise because of competition between people and predators for shared, limited resources, as large carnivores occasionally kill wild ungulates that humans hunt, harvest or farm for consumption [13–17]. Large carnivores are sensitive to disturbance and exploitation by humans, as well as to fragmented habitats, because they require wide contiguous areas where they occur at low densities [4,18–20]. Yet, large carnivores can persist at high human density and high levels of landscape exploitation, suggesting a considerable capacity to tolerate humans and their activities if other habitat features such as prey abundance and high-quality habitats prevail [11,12,21–26]. In human dominated landscapes especially, the occurrence and persistence of large carnivores appears to be driven by interactions between food availability, human activities and the landscape context, all of which affect reproductive rates and survival [4,11,22,26–30]. However, an integrative assessment of the relative effects of these factors for driving the recent recolonization dynamics of large carnivores at the continental scale is missing.

Knowledge about the relative importance of biotic and abiotic factors associated with the occurrence and persistence of large carnivores in human-dominated landscapes is important for effective species conservation [6,11,31,32]. Large carnivores are most relevant from a global biodiversity conservation point of view but also because their maintenance or recovery at ecologically effective densities is crucial to maintain the structure and function of entire ecosystems [33]. However, across the globe, human activities pose threats to the conservation of large carnivores, due to habitat loss and degradation and hunting, as well as the over-exploitation and depletion of prey [20].

The complexity of large carnivores, their adaptability to a wide range of environmental and anthropogenic factors can determine a permanent or sporadic occurrence in a given area. Thus, sporadic occurrences might represent areas that have not yet been permanently filled or, alternatively, areas reached during dispersal with environmental conditions or anthropogenic factors that do not allow for permanent settlement of large carnivores [7,8]. In actual fact, many animals leave areas of permanent occurrence during dispersal and pass across sub-optimal habitats where other than landscape attributes (i.e., human disturbance or social factors) are the major driving factors [34].

At the regional scale, the permanent occurrence of large carnivores is expected to be mainly shaped by landscape structure and composition, human disturbance and food availability [6,11,35–38]. However, the relative importance of these factors for determining either permanent or sporadic occurrence at the continental scale in Europe is poorly studied. Yet, knowledge about the main factors related to large carnivore occurrence at multiple scales is needed to arrive at a general understanding of recolonization processes and the implications for species management and conservation.

Here, we investigate the independent and shared effects of three groups of predictors representing natural landscape attributes, human disturbance and prey availability, on both the permanent and the sporadic occurrence of brown bear, Eurasian lynx, grey wolf and wolverine across Europe (occurrence data available from [38]). We hypothesized that, compared to sporadic occurrences, the permanent occurrence of the four species is more closely related to natural landscapes and low human disturbance, and should therefore be better explained by these factors than sporadic occurrences. We also hypothesized that the four species differ in their susceptibility to landscape attributes, human disturbance and prey availability due to species-specific adaptability to these factors. Specifically, we expect that the occurrences of wolves, a distinct habitat generalist [11,23,35,39], are less related to habitat characteristics, less limited by human disturbance and more closely related to prey availability [40,41] compared to the other three species. On the other hand, we expect that the brown bear, an opportunistic omnivore [42,43], would not be strictly related to prey availability, while the Eurasian lynx, being a specialist and a forest-dependent species [1,22], and the wolverine, which is expected to be strongly influenced by human disturbance and environmental conditions [37,44–47], would be more related to habitat characteristics and limited by human disturbance.

2. Materials and Methods

2.1. Study Area and Species Data

Our study area covers all continental European countries, excluding Belarus, Russia and Ukraine (Figure 1). Ranging from 0 to 4810 m.a.s.l., the study area is characterized by coniferous, deciduous and mixed forest (15.6%, 10.4% and 7.3% of the total area, respectively), shrub-lands (11.5%) and grasslands (7.8%). Croplands (32.4%) and human settlements (4%) are concentrated in the lowlands.

We used the dataset [38] which covers the distributions of the grey wolf, brown bear, Eurasian lynx and wolverine in Europe in the period of 2012–2016. This dataset is separated into two categories: (i) areas with permanent occurrences, confirmed in ≥ 3 years in the last 5 years or in >50% of the time or reproduction confirmed within the last 3 years) and (ii) areas of sporadic occurrence, highly fluctuating observations, confirmed in <3 years in the last 5 years or in <50% of the time, without reproduction. The species occurrence data from [38] is represented in a grid with a size of 10×10 km^2, because all four large carnivore species have large spatial requirements. Using this dataset, we derived a total of 9558 permanent and 5943 sporadic grey wolf occurrences, 6735 permanent and 4524 sporadic brown bear occurrences, 9368 permanent and 2641 sporadic Eurasian lynx occurrences and 3423 permanent and 3741 sporadic wolverine occurrences.

According to [38], the grey wolf permanently occurred in 10 regions (Alpine, Baltic, Carpathian, Central European, Dinaric-Balkan, Italian peninsula, Karelian, North-West Iberia and Scandinavian), for a total of 1,550,100 km^2, while the brown bear occurred in 10 regions (Alpine, Baltic, Cantabrian, Carpathian, Central Apennines, Dinaric-Pindos, East-Balkan, Karelian, Pyrenean and Scandinavia), corresponding to a total of 1,125,900 km^2. The Eurasian lynx permanently and sporadically occurred in 11 regions (Alpine, Balkan, Baltic, Bohemian-Bavarian, Carpathian, Dinaric, Harz Mountains, Jura, Karelian, Scandinavian and Vosges-Palatinian), corresponding to a total of 1,200,900 km^2. The populations of Eurasian lynx in the Dinaric, Bohemian-Bavarian, Alpine, Jura, Vosges-Palatinian and Harz Mountains are the result of recent reintroduction initiatives in these areas [8]. Finally, the wolverine, distributed only in the three Fennoscandic countries in two regions (Scandinavian and Karelian) and occurred in a total of 716,400 km^2.

2.2. Predictor Variables

We considered an initial set of 18 predictor variables (Table 1) for which continuous spatial data were available for the entire study area and which represented the main ecological requirements of the four large carnivore species [4,11,22,36,45,47–54]. All predictor

variables were resampled at a 10 × 10 km² grid cell size and grouped into three main groups namely (i) landscape attributes, (ii) human disturbance and (iii) prey availability.
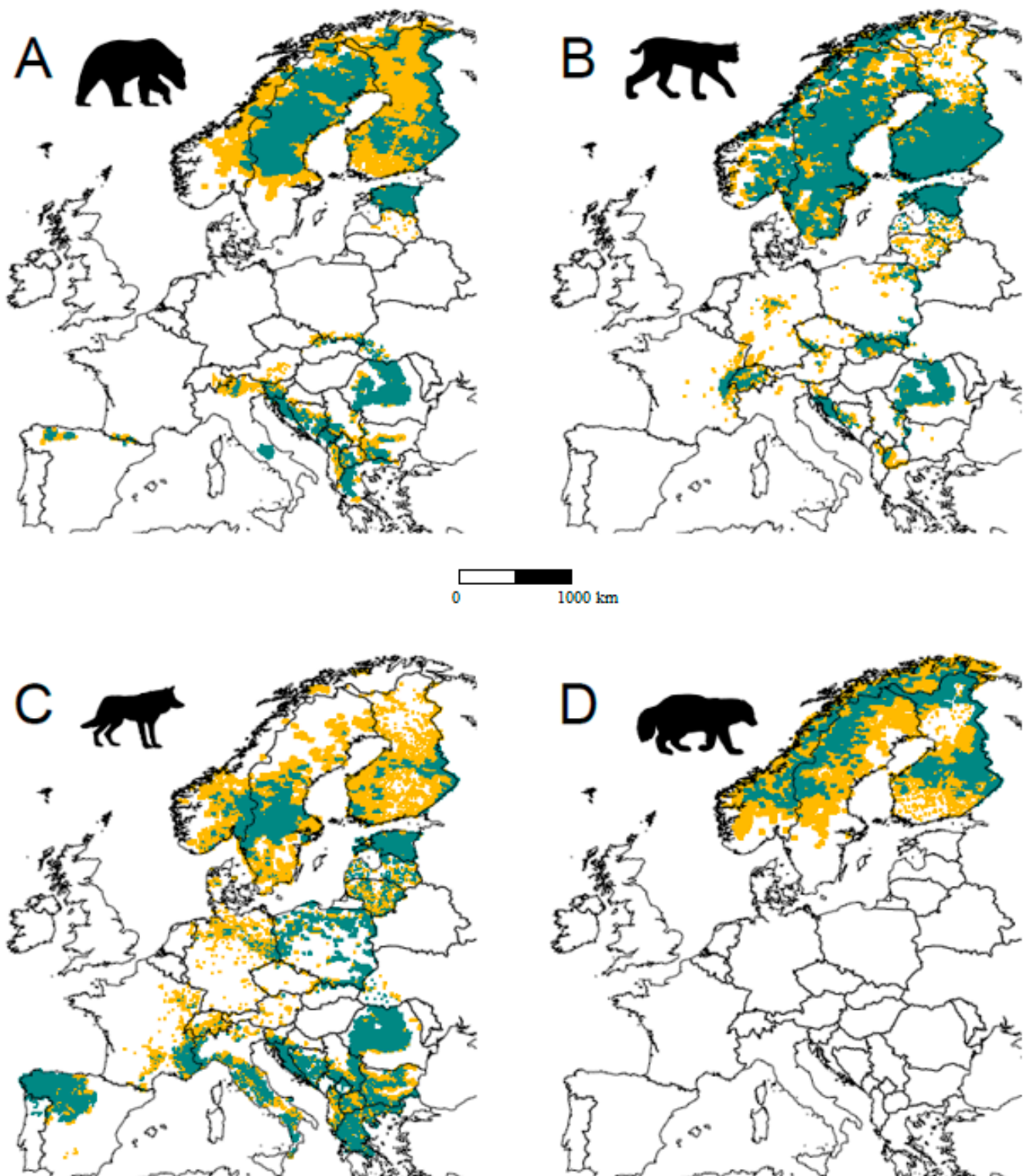
Figure 1. Permanent (green) and sporadic (orange) occurrences of (**A**) brown bear, (**B**) Eurasian lynx, (**C**) grey wolf and (**D**) wolverine in Europe estimated by [38]. Country borders in black. Large carnivore black icons from https://www.lcie.org/Large-carnivores (accessed on 19 September 2022).

Table 1. Description of predictor variables, including the expected relationship with species occurrence (positive (+), negative (−), hump-shaped (∩)) and variance inflation factor (VIF) used to assess the degree of multicollinearity among the predictor variables. Variables with (VIF) > 3 were removed from further analysis (*).

Group	Variable	Expected Relationship	VIF Value
Landscape attributes	Altitude (m a.s.l.)	+, ∩	2.385
	Slope (°)	+, ∩	2.203
	Roughness (ratio of the average length of isoipses in the cell over cell side) *	+, ∩	>3
	Grasslands (%)	+, ∩	1.701
	Shrublands (%)	+, ∩	1.518
	Forest cover (%)	+, ∩	1.816
	Croplands (%) *	−, ∩	>3
	Shannon diversity index of habitat ($H' = -\Sigma \, (p_i \times lnp_i)$)	+, ∩	1.485
Human disturbance	Human settlements (%)	−	2.735
	Distance to human settlements (m)	+	1.484
	Distance to roads (m)	+	1.871
	Artificial night light brightness (nanowatts/cm^2/sr)	−	2.031
	Human population density (number/km^2)	−	2.217
Prey availability	Cattle density (number/km^2)	+	1.198
	Goats density (number/km^2)	+	1.221
	Sheep density (number/km^2)	+	1.271
	Livestock density (number/km^2) *	+	>3
	Wild ungulate richness (number of species)	+	1.519

In the first group, landscape attributes, we included topographic variables, such as altitude, slope and landscape roughness, all of which were derived from a Digital Elevation Model (DEM) with a spatial resolution of 15 m (ASTER GDEM; https://www.jspacesystems.or.jp/ersdac/GDEM/E/, accessed on 10 September 2022), and land-cover variables, obtained from the Coordination of Information on the Environment (CORINE Land Cover 2012 vector data; https://land.copernicus.eu/pan-european/corine-land-cover/clc-2012, accessed on 10 September 2022). Landscape roughness was estimated in R (http://www.R-project.org/, accessed on 10 September 2022) with the package "raster" [55] (Table 1).

To represent human disturbance, we considered the percentage and Euclidean distance to human settlements (derived from CORINE) and the distance to roads (derived from OpenStreetMap; www.openstreetmap.org, accessed on 25 July 2022), as well as human population density, which is available at the spatial resolution of 1 km (GEOSTAT 2011 grid dataset–Eurostat–European Commission; https://ec.europa.eu/eurostat/web/gisco/geodata/reference-data/population-distribution-demography, accessed on 10 September 2022). We also considered artificial night-time light brightness, available at a spatial resolution of 350m (NOAA, NPP VIIRS–NASA 2012; https://ngdc.noaa.gov/eog/viirs/download_dnb_composites.html, accessed on 10 September 2022). Distances to human settlements and roads were calculated by rasterizing human settlements and roads at a grid cell size of 1 × 1 km^2 and then averaging the resulting straight-line distances within a 10 × 10 km grid cell size.

To represent prey availability, we calculated wild ungulate richness by stacking individual maps of 18 wild ungulate species in Europe provided by [56] (at a 10 × 10 km^2 resolution). Specifically, this dataset included 18 wild ungulate species, namely, Alpine and Iberian ibex (*Capra ibex* L. and *Capra pyrenaica* S.), barbary sheep (*Ammotragus lervia* P.), European bison (*Bison bonasus* L.), Northern chamois (*Rupicapra rupicapra* L.), Pyrenean chamois (*Rupicapra pyrenaica* B.), Chinese water deer (*Hydropotes inermis* S.), fallow deer (*Dama dama* L.), moose (*Alces alces* L.), mouflon (*Ovis ammon* L.), Reeves's muntjac (*Muntiacus reevesi* O.), red deer (*Cervus elaphus* L.), roe deer (*Capreolus capreolus* L.), sika deer (*Cervus*

nippon T.), while white-tailed deer (*Odocoileus virginianus* Z.), wild boar (*Sus scrofa* L.), wild reindeer (*Rangifer tarandus* L.) and muskox (*Ovibos moschatus* Z.). We must specify here that we could not include wild ungulate densities as these are not available on a European scale. However, we considered livestock density (FAO's Gridded Livestock of the World 2010–GLW3; https://dataverse.harvard.edu/dataverse/glw_3, accessed on 10 September 2022) as individual maps of cattle, sheep and goat as predictors and also generated a map of livestock density by stacking the three individual densities. The livestock density should thus represent reasonable estimates of biomass available per species and in total.

2.3. Statistical Analyses

We used variation partitioning to test for the independent and shared effects of our three groups of predictor variables on permanent as well as sporadic species occurrence [57]. Variation partitioning was based on generalized linear models (GLMs) with binomial errors and the logit link function. For each large carnivore species, we considered 10,000 species-specific pseudo-absences derived by randomly sampled cells among those available to each large carnivore. Specifically, we considered as available all the cells of the countries in which a given large carnivore occurred, except those of its permanent and sporadic occurrences. For instance, all the cells of Finland, Norway and Sweden, except those in which the wolverine occurred (permanently or sporadically) were initially considered to randomly select 10,000 pseudo-absences for the wolverine.

To arrive at the final GLMs to partition the variation, we followed a strict variable selection procedure: first, similar to [58], we excluded all variables with a variance inflation factor (VIF) higher than 3 (Table 1) to reduce the multi-collinearity within our entire predictor variable set; second, we fitted GLMs, including all remaining variables in each predictor variable group (eight different species datasets times three predictor variable groups = 24 models in total) and excluded all non-significant ($p > 0.05$) variables. All variables for which we expected a hump-shaped response were included with the second order polynomial (quadratic) term. The resulting variable sets were then used to run the final GLMs for which we decomposed the explained variation (pseudo-R^2) into independent and shared effects of the three predictor variable groups, following [57]. All final models were checked for spatial independence by using the residuals to calculate correlograms and Morans'I values over various lag distances. We found no statistically significant spatial autocorrelation (all $p > 0.05$) and thus we did not investigate it further. We also checked for the potential effects of interaction terms between the retained landscape attributes as well as human disturbance indicators and domestic prey availability, but including interactions terms did not or only marginally improve the model fits. For reasons of parsimony and to facilitate the interpretation of the result, we did not further analyze the interaction terms. All analyses were carried out in the R statistical programming language [59].

3. Results

For all four species, our predictor variables explained permanent occurrence better than sporadic occurrence, with total R^2 values ranging from 42.8% to 15.2% for permanent occurrence and 29.7% to 6.1% for sporadic occurrence (Figure 2).

Landscape attributes accounted for the largest independent share of explained variance in the permanent occurrences of grey wolves, brown bears and Eurasian lynxes, followed by the shared effect between landscape attributes and human disturbance. This pattern was also found for the sporadic occurrence of these three species, although at a reduced level of explained variance. This reduced level of explained variance in sporadic occurrence was mainly attributed to a smaller independent effect of landscape attributes, suggesting a higher tolerance level towards landscape attributes in areas of sporadic occurrence. We further found that for grey wolves, brown bears and Eurasian lynxes, the independent share of explained variance of human disturbance was slightly higher in areas with sporadic occurrences than permanent occurrences (Figure 2).
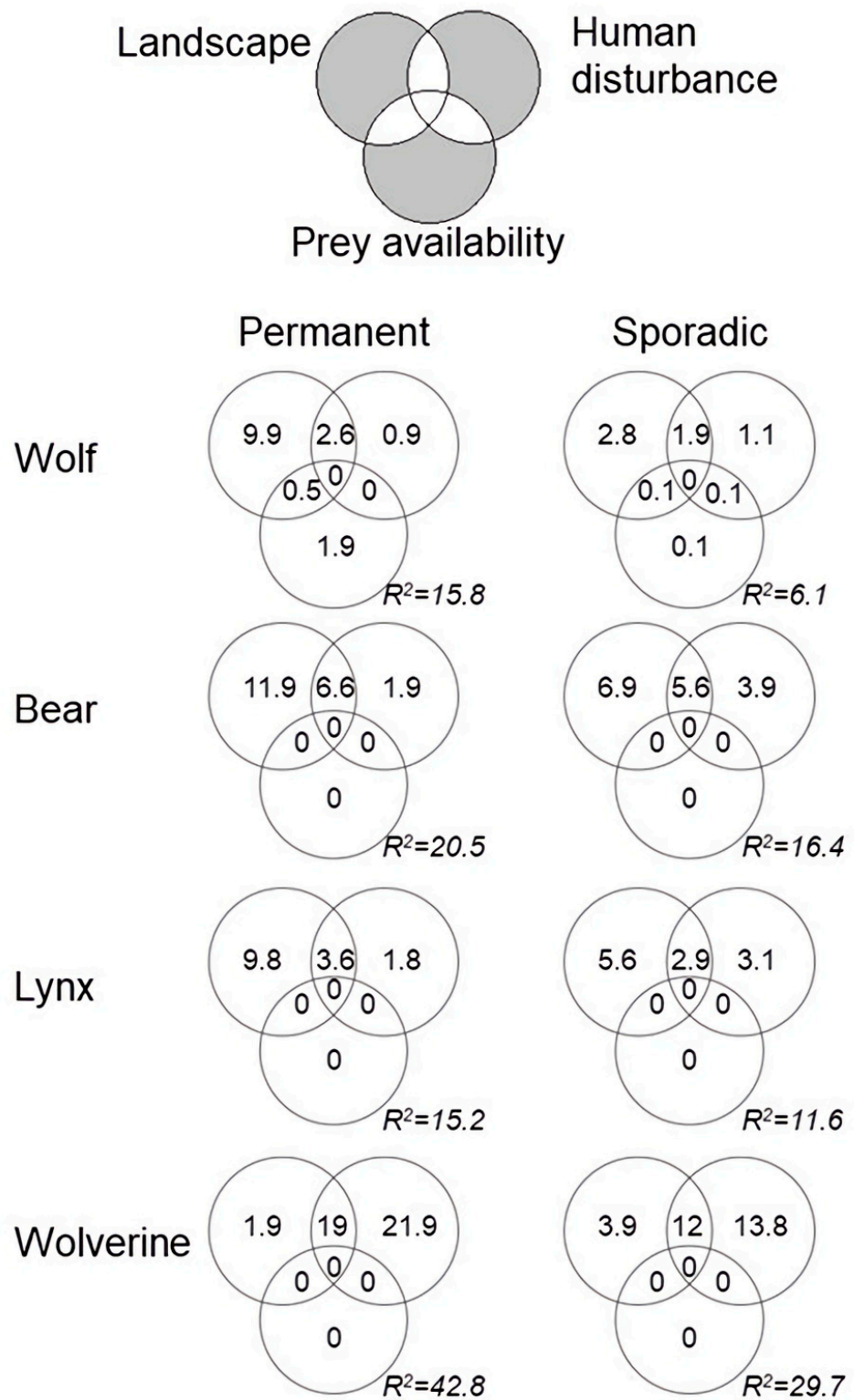
Figure 2. Results from variation partitioning based on GLMs relating landscape attributes, human disturbance and prey availability to permanent as well as sporadic occurrences of the four species studied. Following the structure shown in the inset, we report the independent (grey) and shared (white) percentage of explained variation by each variable group. The R^2 values from the total model are shown below the circles.

Contrary to the other three species, the permanent occurrence of wolverine was best explained by human disturbance and the shared effect between landscape attributes and

human disturbance (Figure 2). The same also held true for sporadic wolverine occurrence, but with a considerably lower level of explained variance.

In line with our hypothesis that the occurrence of the grey wolf—a distinct habitat generalist—is less related to landscape attributes and human disturbance than the other three species, we found relatively small effects of these two attributes on the permanent and, in particular, in the sporadic occurrence of grey wolf. Prey availability showed a weak statistical relationship with the permanent occurrence of wolves, and we found no such effect on the permanent and the sporadic occurrence of the other three large carnivores (Figure 2).

The probability of permanent occurrence of brown bear and grey wolf significantly increased with increasing altitude, but this relationship weakens at high altitudes, as indicated by the negative estimate for the quadratic term (Table 2). Slope was positively related to sporadic occurrence of brown bear, the permanent one of Eurasian lynx and both permanent and sporadic occurrence of wolverine, while the quadratic effect of slope was inversely related to permanent occurrence of Eurasian lynx and wolverine (Table 2). Shrublands were significantly and positively related with both the permanent and sporadic occurrence of all the four large carnivore species considered, while its quadratic effect was negatively related to both the permanent and sporadic occurrence of the brown bear, grey wolf, Eurasian lynx and the sporadic occurrence of wolverines (Table 2). Forest cover was significantly and positively related to both permanent and sporadic occurrence of all large carnivores, except for the sporadic occurrence of wolverine (Table 2). Among the variables representing human disturbance, human population density and distance to human settlements, as well as artificial night light brightness were the main factors related to carnivore occurrence. Finally, the estimated probability of grey wolf permanent occurrence increased significantly with increasing goats and sheep density, as well as with increasing wild ungulate richness, but in sporadic occurrences only with increasing sheep density (Table 2).

Table 2. Beta coefficients of generalized linear models carried out on permanent and sporadic occurrences of the four large carnivores in Europe in relation to the predictor variables of landscape attributes, human disturbance and prey availability.

Group	Variable		Brown Bear		Eurasian Lynx		Grey Wolf		Wolverine	
			Permanent	Sporadic	Permanent	Sporadic	Permanent	Sporadic	Permanent	Sporadic
Landscape attributes	Altitude	linear	83.984 *	-	-	−74.048 *	95.703 *	-	-	-
		quadratic	−20.375 *	-	-	23.193 *	−23.033 *	-	-	-
	Slope	linear	-	30.690 *	6.077 *	-	-	-	6.594	17.360 *
		quadratic	-	−13.203 *	−21.466 *	-	-	-	-4.974	−10.003 *
	Grasslands	linear	-	-	-	-	31.971 *	-	-	-
		quadratic	-	-	-	-	−57.191 *	-	-	-
	Shrublands	linear	39.674 *	76.970 *	62.669*	35.121 *	36.380 *	12.576 *	9.979 *	22.682 *
		quadratic	−25.930 *	−19.195 *	−8.644*	−5.846	−37.850 *	−54.579 *	0.399	−31.497 *
	Forest cover	linear	1.016 *	0.685 *	0.942*	0.382 *	0.647 *	0.434 *	0.019 *	0.012
		quadratic	-	-	-	-	-	-	-	-
	Shannon diversity index of habitat	linear	22.658 *	-	-	-	-	-	-	-
		quadratic	−32.574 *	-	-	-	-	-	-	-
Human disturbance	Human settlements		-	-	-	-	-	-	-	-
	Distance to human settlements		0.087 *	0.197 *	0.033 *	0.161 *	-	0.214 *	0.095 *	0.041 *
	Distance to roads		0.127 *	-	-	-	-	-	0.033 *	-
	Artificial night light brightness		−0.303 *	-	-0.008	-0.048	−0.061 *	−0.046 *	-	-
	Human population density		−1.161 *	−1.188 *	−1.304 *	−0.261 *	−0.328 *	−0.306 *	−21.112 *	−2.012 *
Prey availability	Cattle density		-	-	-	-	-	-	-	-
	Goats density		-	-	-	-	0.246 *	-	-	-
	Sheep density		-	-	-	-	0.254 *	0.356 *	-	-
	Wild ungulate richness		-	-	-	-	0.151 *	-	-	-

*: $p < 0.0001$.

4. Discussion

In this study we investigated how the permanent and sporadic occurrences of the grey wolf, brown bear, Eurasian lynx and wolverine are related to landscape attributes, human disturbance and prey availability at the continental scale in Europe. Landscape attributes and human disturbance accounted for most of the explained variance and were most important for explaining the permanent occurrence of the four large carnivores. Our findings have important implications for the understanding and management of the recent recolonization of large carnivores in Europe, as discussed in the following section.

We found that the permanent occurrence of all four large carnivore species can be explained much better than sporadic occurrence. This implies that large carnivores mainly select the least disturbed areas, especially for mating, while sporadic occurrences often take place in sub-optimal habitats used during dispersal [60–63]. The sporadic occurrence of large carnivores in Europe appears more stochastic and less predictable than permanent occurrence. Large carnivores can adapt to human-dominated landscapes [11,64], although human tolerance towards these species is fundamental for their persistence in new areas of colonization.

Considering the single groups of predictors independently, landscape attributes were the most important factors to explain the permanent occurrence of the grey wolf, Eurasian lynx and brown bear. Natural and semi-natural habitats in which these species find refuges and suitable conditions for reproduction are thus crucial for their persistence [7]. However, for the sporadic occurrence of grey wolf, Eurasian lynx and brown bear, landscape attributes had a smaller independent effect, while human disturbance became slightly more important compared to permanent occurrences. This suggests that during dispersal, these three species can tolerate large areas of unsuitable or poor-quality habitats with relatively high human disturbance. Dispersing wolves have been shown to move over large areas of unsuitable or poor quality habitats, but the successful establishment of packs is limited to large areas of high quality habitats [61–63,65]. Our results are also in agreement to those of studies carried out on Eurasian lynx [22,24,45,66,67], showing that even if this species could also permanently occur in areas with medium degrees of human disturbance, it needs sloped terrain and high forest cover. Forest cover is also strongly related to the movements and dispersal of the Eurasian lynx [68,69], and thus it is likely that forest cover, even in relatively small patches, provides sufficient shelter for the Eurasian lynx to avoid human disturbance even at a high human density [24]. Additionally, the permanent occurrences of the brown bear showed that this species avoids human disturbance, while forests on mountains most likely provide bears with more opportunities to conceal den sites [70].

On the contrary, the wolverine showed higher sensitivity to human disturbance compared to the other large carnivores, and spatial segregation patterns between wolverines and humans were found [4,44], as large carnivore' home ranges are usually at high elevation (often covered by snow), far from the lowlands where density of human settlements and roads is high. The denning sites of this species are mainly placed away from infrastructure, indicating that successful reproduction may be influenced by human activities [4]. However, this species is also able to pass across artificial barriers that occur within their home territories [71]. Wolverines may thus have a relatively low tolerance towards human disturbance but show flexible behavior during dispersal (sporadic occurrence).

The low variance explained by the models for the wolf—often considered a generalist species—is likely related to the highly adaptable behavior of this species to different conditions [72,73]. In reality, due to their high mobility, high reproductive rate and low dependency on particular habitats, wolves have higher ecological resilience compared to other large carnivores [74]. Contrary to the Eurasian lynx, being a specialist and a forest-dependent species [1,22], and to the wolverine, the most sensitive species to human disturbance and habitat changes [44], wolves can persist in different habitats such as tundra, boreal and temperate forests, as well as steppes, as long as they are tolerated by humans and find safe refuges [8,72,75].

Our results suggest that prey availability plays a subordinate role in driving the distribution dynamics of large carnivores at the continental scale in Europe, although they are important at the regional scale [22,76–78]. In fact, the only independent (and positive) effect of prey availability on species occurrence was found for the occurrence of wolves. Other predictors, such as the density of different wild ungulate species, are expected to play a fundamental role. The Eurasian lynx, for example, mainly preys on relatively small wild ungulates, such as roe deer (*Capreolus capreolus*) and chamois (*Rupicapra rupicapra*) [79–83], and the lack of abundance data for roe deer and chamois may partially explain why we did not find any effect of prey availability on lynx occurrence. Wolverines, however, mainly prey on reindeer [44,47,71,84], one of the most sensitive ungulate species to habitat fragmentation and human disturbance [44,85]. We expect that the non-exhaustive availability of wild reindeer density data at the European level may have contributed to the low variance explained by prey availability on wolverine occurrence. On the other hand, it is not surprising that the occurrence of brown bears is not related to prey availability as this species is an opportunistic omnivore that feed on a variety of food sources (e.g., nuts, cherry, ants, etc.) [42,43]. The grey wolf was the only species among the four large carnivores that showed a marginal effect of prey availability, indicating that prey availability is not necessary a limiting factor for wolves [11], even if we cannot exclude that other factors of grey wolf occurrence not considered in this study (e.g., human attitudes toward carnivore's occurrence, poaching, wild ungulate abundances, etc.) could explain the large amount of unexplained variance [11]. Another explanation could be related to the recent growth of wild ungulate populations in Europe, leading to both increasing densities and distribution ranges [86].

Finally, here we stress that, while we considered fundamental factors related to large carnivore distribution, unfortunately we could not include in our analyses another relevant parameter which is currently not spatially available at a continental scale, i.e., human attitude. This is an important factor as large carnivores often suffer from a negative reputation and direct persecution due to conflict with human activities. In reality, recolonization by large carnivores is likely to be strongly opposed, especially in landscapes where the species have been extinct throughout the past centuries, and thus, the unfamiliarity of local people with coexistence with large carnivores can lead to fear and intolerance, and negative attitudes are often translated into illegal killing [87]. Since human attitude is a crucial factor shaping large carnivores' distribution and persistence, we encourage a continental strategy to collect explicit spatial human attitude data, e.g., following the country scale example of [87], to create spatially explicit socio-ecological models of human acceptance. This is also relevant in light of the various legal regimes that apply to large carnivores under the Bern Convention and the EU Habitats Directive in different parts of Europe, which determine the legal bandwidth within which local authorities can design and implement specific management and conservation actions [88].

Last but not least, considering the ongoing increase of species occurrence reports in online biodiversity platforms and how they can potentially be used to assess species distribution [89–91], here we stress that citizen science can dramatically contribute to the assessment of both permanent and sporadic occurrence of large carnivores, and thus we suggest their integration in the next update of [8,38].

5. Conclusions

The occurrence of the grey wolf, brown bear, Eurasian lynx and wolverine in Europe is mainly related to landscape attributes and the negative impacts of human disturbance. Thus, while we provided general insights into the ongoing distribution dynamics of large carnivores at a continental scale, partially confirming those found at a local/regional scale in previous studies, we found that prey availability (i.e., domestic prey abundance and wild prey richness) was not or only marginally related to carnivore occurrence at the European scale. Specifically, the lack or low relationship between domestic prey abundance and carnivore occurrence is an important result in light of the ongoing debate about the regional

impact of large carnivores on livestock, as negative impacts of large carnivores on livestock appear not to increase at the continental scale.

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