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Insights into the dynamics of wolf occupancy in human-dominated landscapes

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ABSTRACT

Among large carnivores, wolves show a remarkable capability to persist in human-dominated landscapes. However, the temporal dynamics of variation in spatial use of these landscapes remains poorly understood. Considering the relevance of spatio-temporal variations of territorial marking on wolf behaviour, either to defend territory boundaries and core areas or to expand into new areas, the location of wolf signs should reflect the dynamics of spatial use. Taking advantage of a long-term non-invasive wolf monitoring dataset spanning from 2005 to 2022 we fit a dynamic occupancy model to investigate the effects of environmental and anthropogenic factors on the dynamics of wolf spatial use in human-dominated landscapes. We focused on two dynamic parameters – colonization and extinction – and developed a wolf habitat suitability map for Iberia. Colonization probability increased with higher altitude, livestock density, and unpaved road density, and with the decrease of burned areas, national-regional, and local road densities. Extinction probability decreased with higher unpaved road density.

In addition, we evaluated the wolf range dynamics in Iberia to understand if the ecological traits explained the expansion, stagnation or extinction sites observed since the beginning of the 2000s. Our results contribute to a sound understanding of wolf spatial use in human-dominated landscapes and its ability to adapt to these heterogeneous environments, allowing us to support adequate mitigation measures and conservation actions. The strong influence of livestock on the dynamics of wolf occupancy highlights the need to assess social factors, human dimensions, and direct wolf mortality causes for conflict management associated with livestock depredation.

1. Introduction

Large carnivores (LCs) are often at the core of public concerns because of the potentially negative interactions with humans and human activities. Their predatory behaviour (e.g., competition for game species or livestock depredation) and the impact this might cause on human

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activities is probably one of the most critical factors driving opposition to sharing the landscape with these species (López-Bao et al., 2017; Wolf and Ripple, 2016). These difficulties are aggravated in human-dominated landscapes and often result in the preemptive or retaliatory killing of LCs. Consequently, legal killing or poaching influences species persistence, particularly in human-dominated landscapes (Carter and Linnell, 2016; Lamb et al., 2020). These factors, together with other anthropogenic pressures, such as roadkills, habitat disturbance and fragmentation or food availability (Lovari et al., 2007; Zimmermann et al., 2014), may lead to adapted dynamics of LC occupancy in human-dominated landscapes. LCs have demographic or behavioural mechanisms to adapt and coexist with humans, such as spatial or temporal avoidance of human-disturbed areas, high reproduction rates and immigration to compensate for mortality in sink areas (Pease and Mattson, 1999; Pulliam, 1988). Co-adaptation is needed for successful coexistence in such landscapes (Carter and Linnell, 2016). Thus, by understanding the spatial dynamics of LCs adapted to human-dominated landscapes, we can also adapt by prioritizing actions to favour colonization, avoid extinction, and maintain LC persistence.

The wolf (*Canis lupus*) is a valuable model species to address LCs' dynamic occupancy in human-dominated landscapes due to its ability to persist in a wide range of environmental conditions. Wolves occur from the most remote landscapes with very low human interference, such as Ellesmere Island, in the Canadian Article Circle (Mech and Cluff, 2011) up to areas with high human population and road densities in Eurasia (Fechter and Storch, 2014; Sazatornil et al., 2016). Several studies addressed how habitat and anthropogenic features affect wolf distribution, and results often point to an increase in wolf occurrence with higher refuge availability and lower anthropogenic infrastructures such as roads (e.g., Llaneza et al., 2012). Some studies have used species distribution modelling approaches – based on different survey methods, such as sign surveys, camera trapping or citizen science – to predict the distribution of suitable habitats for the species or detect ecological corridors (e.g., Grilo et al., 2018; Louvrier et al., 2018; Rich et al., 2017). Though, most studies have short sampling periods and do not account for the dynamic effects of temporal variation of habitat or anthropogenic covariates on wolf distribution and spatial use, such as burned areas and human population density. Since species distribution is not static and can vary through time and space, particularly in expanding populations (Marucco and McIntire, 2010), dynamic occupancy models can be a powerful tool to address wolf spatial dynamics.

Here, we used a dynamic occupancy model to study the factors determining the dynamics of wolf persistence in human-dominated landscapes, taking advantage of wolf surveys (transects of sign surveys) carried out in different areas within the Iberian wolf range. With this approach, we accounted for the influence of dynamic processes such as colonization and extinction on the species range dynamics (MacKenzie et al., 2003; Royle and Kéry, 2007). Although wolves are well known for their long-distance dispersal ability (e.g., 233 km in Ražen et al., 2016), evidence in the Iberian Peninsula (IP) suggest low dispersal in Iberian wolves (e.g., 32 km in Blanco and Cortés, 2007; 24.8 km in Nakamura et al., 2021; see also Silva et al., 2018). After the 1970s, the north-western wolf population expanded in Spain (Blanco and Cortés, 2009; Chapron et al., 2014; López-Bao et al., 2018b), though it showed a remarkable regression pattern in Portugal, particularly in the south of Douro River (Monteiro, 2015). In the late 1990s, the species reached south of Castilla y León, north of Castilla-La Mancha (Guadalajara province) and Madrid (Blanco and Cortés, 2009, 2001). Genetic analyses have revealed that such expansion towards central Spain resulted from the expansion of wolves from the south-eastern Cantabrian Mountains (Silva et al., 2018). Currently, the population appears to have stagnated in eastern Castilla y León, the Basque Country, and north of Castilla-La Mancha (Guadalajara province) (Blanco and Cortés, 2009; López-Bao et al., 2018b) as well as in Portugal (Monteiro, 2015). For a detailed wolf distribution change since 1970, see Fig. 1.2.1. in Blanco and Cortés (2009) and Fig. A1 in Appendix A. Even though the wolf range in NW Iberia has been relatively continuous in recent times (Chapron et al., 2014; López-Bao et al., 2018a; Nores and López-Bao, 2022), the habitat can vary throughout the range. Here, we aim to understand how anthropogenic features influence wolf spatial use. As such, we expect low wolf occupancy and colonization probabilities and high extinction probabilities where human-related features are more abundant.

We hypothesize that high paved road densities negatively affect wolf colonization and occupancy since the persistence of wolves may be lower in areas with high road densities (Jedrzejewski et al., 2008; Mladenoff et al., 1995). However, we hypothesize that unpaved road density positively affects wolf colonization and occupancy because wolves often use forest roads less used by humans as travel corridors (Weaver et al., 1996; Zimmermann et al., 2014). We also hypothesize that higher human population density and higher proportions of human settlements, agricultural lands, and burned areas have a negative effect on wolf colonization and occupancy and a positive effect on extinction probability (Ballard et al., 2000; Mladenoff et al., 1995; Sazatornil et al., 2016). Even though livestock depredation can promote direct persecution and increase extinction probability (DeCesare et al., 2018), we hypothesize that livestock density positively affects occupancy and local colonization probability due to higher food availability (Fuller et al., 2003), both in terms of depredation or scavenging events on livestock (e.g., Planella et al., 2016). We also include environmental features related to wolf ecology and hypothesize that wolf colonization and occupancy increase with higher elevations and refuge availability (Grilo et al., 2018; Jedrzejewski et al., 2008; Llaneza et al., 2012; Stenglein et al., 2011). Even though we expected that anthropogenic variables (e.g., proportion of burned areas and population density) would have a generalized negative effect on wolf spatial use (e.g., Ballard et al., 2000; Sazatornil et al., 2016), previous studies have shown that some have a positive or no apparent effect (e.g., Geary et al., 2020; Lino et al., 2019). Table 1 presents several results from previous studies in which environmental and anthropogenic variables positively or negatively affected wolf distribution. We present several hypotheses for each covariate and possible explanations according to possible expected effects on colonization, extinction and occupancy probabilities.

Furthermore, we assess the parameters of extinction, colonization, and occupancy probabilities for the current wolf range in the IP and its surroundings to understand better the potential of wolf occupancy from an ecological perspective. By distinguishing areas of wolf persistence, expansion, regression, and potential recolonization – obtained from differences between the wolf range estimated at the beginning of the 2000s (Álvares et al., 2005) and the estimated current range (Kaczensky, 2018) – we compare the average probabilities of extinction, colonization, and occupancy among the areas considered. With the recent range expansion of most of the wolf populations in Europe (Boitani et al., 2022; Chapron et al., 2014), a better knowledge of wolf landscape use changes and tolerance between wolves and people are crucial to improve and guide management actions. By identifying areas with a higher probability of colonization and extinction for wolves, we can predict future recolonization sites to carry out actions ahead and help avoid and mitigate conflicts. Based on our findings, we propose mitigation measures and conservation actions and locate the areas where such actions should be prioritized within the current wolf distribution and potential areas of recolonization.

2. Material and methods

2.1. Wolf sampling areas

We used information collected between 2005 and 2022 from three areas in Portugal – Alto Minho (AM; 1075 km^2), South of Douro (SD; 1400 km^2), and Vila Real (VR; 1700km^2) – and one in Spain – Asturias (AST; 5700 km^2) within the Iberian wolf range (Fig. 1). The sampling years differed between study areas: 2007 through 2019 in AM, 2011 through 2020 in SD, 2005 through 2013 in VR, and 2019 through 2022

Table 1
Covariates included in the dynamic occupancy model, rationale and underlying hypothesis: a higher covariate value has a positive (+) or negative (–) effect on colonization (γ), extinction (ε), and occupancy (ψ) parameters. For the occupancy parameter, a hypothesis with no clear effect was added (=) when there may not be a clear positive or negative effect or when the effects are of a wide range. The considered hypotheses for the colonization and occupancy parameters are explained with reference to previous studies.

Covariate type	Covariate (units)	Hypothesis Col (γ)	Ext (ε)	Occ (ψ)	Hypothesis explanation	References
Anthropogenic	Paved road - Highway density (km/km^2)	-	+	= -	• Highway density has no clear effect on wolves in areas with well-established territories; • Wolves are less abundant in areas with higher road densities; • Wolves avoid high-level roads due to human disturbance (high traffic intensity).	Blanco et al., 2005; Dennehy et al., 2021; Jedrzejewski et al., 2008; Mladenoff et al., 1995; Rio-Maior et al., 2019; Zlatanova and Popova, 2013
	Paved road - National and regional road density (km/km^2)	+	-	+ = -	• Wolves are less abundant in areas with higher road densities; • Wolves frequently use mid-level roads for dispersal travelling and avoidance of resident wolves.	Jedrzejewski et al., 2008; Kabir et al., 2017; Mladenoff et al., 1995; Weaver et al., 1996; Zimmermann et al., 2014
		-	+		• Wolves are less abundant in areas with higher road densities; • Wolves avoid mid-level roads due to human disturbance (high traffic intensity); • Mid or low-level roads or high road densities increase mortality risk (roadkill) and decrease habitat connectivity that precludes dispersal.	Blanco et al., 2005; Dennehy et al., 2021; Jedrzejewski et al., 2008; Mladenoff et al., 1995; Rio-Maior et al., 2019; Zlatanova and Popova, 2013
	Paved road - Local road density (km/km^2)	+	-	+ = -	• Wolves frequently use low-level roads as travelling routes with less effort (both resident and dispersers);	Gurarie et al., 2011; Kabir et al., 2017; Mattisson et al., 2013; Weaver et al., 1996; Zimmermann et al., 2014
		-	+		• Wolves avoid low-level roads due to human disturbance (traffic and human activities). • Mid or low-level roads or high road densities increase mortality risk (roadkill) and decrease habitat connectivity that precludes dispersal.	Dennehy et al., 2021
	Unpaved road density (km/km^2)	+	-	+ = -	• Wolves frequently use low-level roads as travelling routes with less effort • Wolves frequently use forest/gravel roads as travelling routes as least-cost path; • Wolves frequently use unpaved roads and crossroads as territorial marking sites.	Barja et al., 2004; Gurarie et al., 2011; Kabir et al., 2017; Llaneza et al., 2014; Mattisson et al., 2013; Weaver et al., 1996; Whittington et al., 2005; Zimmermann et al., 2014
		-	+		• Wolves avoid potential human disturbance, resulting from higher accessibility for humans (e.g., 4 × 4 cars, hunting activities).	Rio-Maior et al., 2019
	Livestock unit density (LU/km^2)	+	-	+ = -	• High wolf productivity, survival, and/or densities due to high prey availability: a) high conflict/ poaching but the wolf population can strive; or b) low conflict/poaching;	–
		-	+		• Low wolf survival and/or wolf densities due to high conflict and poaching.	Blanco and Cortés, 2009; DeCesare et al., 2018
	Annual proportion of agricultural lands (%)	+	-	+ =	• Wolves have higher access to prey (livestock or wild).	–
		-	+	-	• Wolves avoid human disturbance (human presence due to agricultural activities); • Low wolf survival and/or densities due to high conflict and poaching.	Mladenoff et al., 1995; Sazatornil et al., 2016
	Annual proportion of burned areas (%)	+	-	+ = -	• Wolves opportunistically select burned areas due to higher prey availability after fires. • Wolves positively select burned areas or there is no apparent effect.	Geary et al., 2020; Lewis et al., 2022; Lino et al., 2019
		-	+		• Wolves have lower prey availability (absence of prey); • Wolves avoid high human disturbance: easier accessibility to humans and higher exposure of wolves to humans due to the absence of refuge.	Ballard et al., 2000
	Annual human population density (no. inhabitants/km^2)	+	-	+ = -	• Wolves have higher access to resources • Wolf population near carrying capacity (saturated population).	–
		-	+		• Wolves avoid human activity/disturbance.	Mladenoff et al., 1995; Sazatornil et al., 2016
Environmental	Altitude (m) a.s.l.	+	-	+	• Wolves select areas with higher elevations to avoid human activities.	Glenz et al., 2001; Llaneza et al., 2018, 2012; Rio-Maior et al., 2019
		-	+	-	• Dispersers select lower elevations to avoid resident wolves present in higher elevations.	Rio-Maior et al., 2019
	Annual proportion of refuge (forest, shrubland and bare rocks) (%)	+	-	+ = -	• Wolves select areas with higher refuge availability; • Wolves select areas with higher prey density.	Grilo et al., 2018; Jedrzejewski et al., 2008; Llaneza et al., 2012; Mladenoff et al., 1995; Oakleaf et al., 2006
		-	+		• Wolves use areas with less refuge (e.g. meadows) due to the high availability of prey.	Jedrzejewski et al., 2008

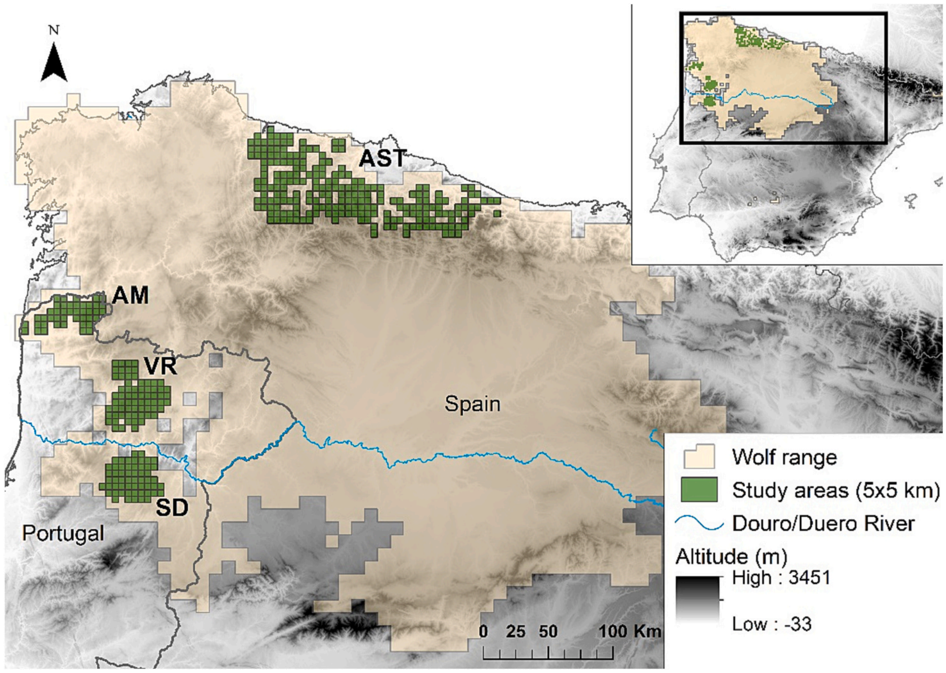

Fig. 1. Location of the study areas (AM - Alto Minho, SD - South Douro, VR - Vila Real, and AST – Asturias; 5 × 5 km sites) in the context of the estimated wolf range in north-western Iberia in recent times.
(Adapted from Kaczensky (2018).)

in AST. The number of packs detected across areas was: from 2 to 7 in AM, from 2 to 3 in SD, from 4 to 8 in VR, and around 40 packs in AST (Álvares et al., 2015; Nakamura et al., 2021; Regional Government of Asturias, 2022; Rio-Maior et al., 2020).

Across the study areas, there is a wide variation in human population density: AM 40.8 ± 48.1 inhabitants/km^2, SD 28.7 ± 26.2 inhabitants/km^2, VR 34.9 ± 64.4 inhabitants/km^2, AST 20.6 ± 36.3 inhabitants/km^2 (mean ± sd), reaching a maximum of 513.9 inhabitants/km^2 in VR (CIESIN, 2018); as well as in road densities: AM 0.77 ± 0.37 km/km^2, SD 0.58 ± 0.28 km/km^2, VR 0.71 ± 0.54 km/km^2, AST 0.42 ± 0.35 km/km^2, reaching a maximum of 2.89 km/km^2 in VR (OpenStreetMap contributors, 2022). Wolves feed mainly on livestock in all the study areas due to low wild prey availability and high livestock densities with inadequate husbandry practices or inefficient damage prevention measures (Álvares et al., 2015; Llaneza et al., 1996; Pimenta et al., 2018). Even though livestock depredations are compensated across the study areas, wolf predation on livestock is not properly adressed and managed, leading to major conflicts and retaliatory killing of wolves (Álvares et al., 2015; Blanco and Cortés, 2009; Fernández-Gil et al., 2016; Pimenta et al., 2017).

2.2. *Wolf data collection*

In all study areas, transects were carried out on foot or by car (<10 km/h) along unpaved roads and paths in order to detect wolf faeces. Particular attention was given to usual wolf scent marking places such as junctions (Barja et al., 2004; Llaneza et al., 2005). Most transects were conducted monthly or seasonally with year-round surveys or more focused on summer-autumn, depending on the year and study area. Seasons were defined as 'spring' (March–May), 'summer' (June–August), 'autumn' (September–November), and 'winter' (December–February). Sampling units were 5 × 5 km cells (hereafter referred to as sites) adapted from the 10 × 10 km European Environment Agency Reference Grid. The study areas differed in sampling coverage: 43, 56, 68, and 228 sites for AM, SD, VR, and AST, respectively (Fig. 1).

We summed transect lengths (i.e. total distance) to obtain the transect effort (km) per site and season (hereafter denominated 'site-season'). The effort varied over time and between study areas, with some transect changes throughout the sampling years. From autumn 2005 to autumn 2022, transects of sign survey effort was 8.72 ± 6.74 km (range 0.05–55.00 km) per site-season, which comprised 5672 site-seasons sampled. The dataset consisted of 68 seasons surveyed, with a sampling average of 78.8 ± 48.4 sites per season (range 2–233) and 14.4 ± 13.9 seasons per site (range: 2–41) (see Fig. A2 for sampled sites in the online Appendix A). We submitted the general protocol used from sampling faeces to molecular analysis. The success of wolf assignment for AM and SD until 2012 was 83.3 % (Nakamura et al., 2017).

Considering that wolf territory sizes are very variable between study areas (average minimum convex polygon of 408 km^2 for the IP, ranging between 14 and 2810 km^2; Silva et al., 2018) – the scale of 5 × 5 km used in this study is adequate for our analysis since it allows to detect variation in wolf spatial use within wolf territories as well as in inter-territorial areas, allowing to detect colonization and extinction patterns at a local level. A 10 × 10 km scale would be too large to detect spatial use variations within areas where wolves have smaller territories (e.g., Alto Minho 135 km^2; Álvares et al., 2015). Moreover, a smaller scale analysis (e.g., 2 × 2 km) is rarely used in long-term wolf monitoring studies in the IP and could result in high spatial autocorrelation.

2.3. *Environmental and anthropogenic covariates*

We selected predictor covariates based on factors important to wolf spatial use and distribution based on previous knowledge of the species and worldwide studies mostly conducted in areas with some anthropogenic disturbance (Table 1). We obtained the covariates for each 5 × 5 km site. As environmental covariates, we considered: 'Altitude' as average altitude (a.s.l.); 'Ruggedness' as average Terrain Ruggedness Index (Riley et al., 1999); and 'Refuge' as the proportion of refuge availability for wolves. According to local habitat specificities, we considered bare rocks as a refuge since these frequently have cavities for wolf refuge. As such, we joined the habitats of forest, shrubland, and bare rocks into a single covariate reflecting refuge availability. For anthropogenic variables, we considered: i) densities of three paved road types (from high to low traffic levels: 'highway', 'national-regional', and 'local' roads), ii) unpaved road density, iii) human population density, iv) livestock unit (LU) density, v) proportion of human settlements, vi) proportion of agricultural lands and vii) proportion of burned areas. We calculated road densities by obtaining road type length per site (OpenStreetMap contributors, 2022). Livestock availability was quantified considering LU density (1 LU of horse and cattle; 0.15 LU of goat and sheep), which represents the primary food resource for wolves in several areas of the IP (Blanco et al., 1992; Llaneza and López-Bao, 2015; López-Bao et al., 2013; Pimenta et al., 2017; Torres et al., 2015). We calculated the annual proportion of burned areas from the sum of monthly burned area per site from MODIS (Moderate Resolution Imaging Spectroradiometer). We determined the proportion of area covered by settlements, agricultural lands, and refuge per site from Corine Land Cover (CLC, 2018) and the European Settlement Map (Corbane and Sabo, 2019). For a detailed covariate description, calculation, and source of information, see Table A1 in Appendix A.

2.4. *Dynamic occupancy model: extinction and recolonization probabilities*

We fitted a dynamic occupancy model (MacKenzie et al., 2006) to scat detection data to identify anthropogenic and environmental variables potentially affecting wolf space use. Data on wolf scat detection and non-detection were organized per 395 sites in 72 surveys (i.e. seasons) from spring 2005 to winter 2022 (i.e. 18 years or primary occasions with four seasons each or secondary occasions).

We were interested in the dynamics of wolf occurrence in a given area. To do this, we assume that: i) the detection of scat markings confirms the presence of the species and reflects sites that wolves preferentially use or scent mark, and ii) the non-detection of scat markings reflects unused or non-preferentially used nor scent marked sites. Thus, we highlight that the meaning of the terms 'colonization' and 'extinction' used for interpreting the occupancy model results are not actual colonization and extinction of the species but instead refer to a probability of a site becoming, respectively, used and unused from one year to another.

By correcting for imperfect detection (i.e. the species is undetected in occupied sites), occupancy approaches facilitate obtaining unbiased estimates of variables relevant to species conservation and management implications (MacKenzie et al., 2006, 2002). Covariates can be modelled to infer relationships between observed patterns and the underlying processes that cause them, thereby projecting patterns in un-surveyed areas (MacKenzie et al., 2006). Occupancy models rely on a spatial closure assumption, i.e. the ecological state of a site (occupied vs not occupied) remains unchanged over seasons j (from spring to winter) within a year. Considering the sampling methodology and wolf scent-marking behaviour, we included effort (transect length), unpaved road density, and average ruggedness as covariates for the detection parameter. For a detailed description of the dynamic occupancy model and covariates considered for the colonization, extinction, initial occupancy, and detection parameters, see Appendix A1.

We estimated posterior distributions of initial occupancy, colonization, and extinction parameters, considering detection probability using Markov Chain Monte Carlo (MCMC) implemented in JAGS (version 4.3.0) using R2jags (Plummer, 2011) in RStudio (Posit team, 2022). We generated two chains of 40,000 iterations after a burn-in of 3000 iterations. We assessed model convergence visually by inspecting the chains and by checking the Gelman-Rubin statistic (Rhat < 1.1) (Gelman et al., 2004). We used posterior means and 50 % and 95 % Bayesian credible intervals (BCI's) to summarise parameter posterior distributions. Additionally, we considered the mass of the posterior distribution on the negative or positive side to interpret the results. To assess the effect of a covariate on a given parameter, we set the other covariates to their mean value. Considering the posterior estimate distributions of the model and the first 5000 iterations after burn-in, we obtained the annual colonization, extinction, and occupancy probabilities of all sites in the study areas.

We obtained the annual detection rate estimates from the model. Moreover, to ensure that wolf detection by transects of sign survey is adequate to assess wolf spatial use, and considering that the locations of GPS-collared wolves give the most accurate information on spatial use, we compared an available dataset from AM study area to calculate the seasonal proportion of sites with presence confirmed by GPS-collared wolves that had successful detection by transects (details in Appendix A2).

2.5. *Assessing changes in estimated wolf range in the last two decades*

Considering the posterior estimate distributions of the model, we predicted the annual parameter estimates for sites within the latest known wolf range (Kaczensky, 2018) to identify areas with higher probabilities of colonization, extinction and persistence. We also predicted these parameter estimates for the sites out of the current distribution range to identify areas with ecological potential for recolonization in the IP.

Moreover, we evaluated the wolf dynamics on a broad scale for the last two decades in the IP to better understand if the ecological traits of the model are in concordance with the species' range expansion progression, stagnation or extinction observed since 2000 (Álvares et al., 2015; López-Bao et al., 2015, 2018a). To do this, considering the last estimates for the entire wolf range in the IP, we attributed an occurrence area type for each 5×5 km site based on wolf presence or absence at the beginning of the 2000s (1999–2003, Álvares et al., 2005) and in recent times (Kaczensky, 2018). We considered four area types regarding wolf occurrence: i) persistence (a site with wolf presence in both periods; 129,475 km^2); ii) expansion (wolves became present from 2000s to present; 20,724 km^2); iii) regression (wolves became absent; 13,497 km^2); and iv) potential recolonization (i.e. 100 km buffer around the latest wolf range as the most potential recolonization area for wolves in the near future; 271,811 km^2). We defined this buffer considering the short dispersal distances observed in the IP (Blanco and Cortés, 2007; Nakamura et al., 2021; Silva et al., 2018) and the average dispersal distance of wolves in Europe (Morales-González et al., 2021; excluding outliers of $>$1000 km and wolves from Scandinavia that are in expansion and have very high dispersal distances compared to the rest of Europe) (see Fig. A1 in Appendix A for a detailed map with the four area types). To understand if our dynamic occupancy model predicts differences between area types, we obtained the average annual probabilities of colonization, extinction, and occupancy estimated by the model over the 5×5 km sites of each area type. Here, we assume that known wolf ranges are the most recent and accurate information for the IP and that no sites were mistakenly attributed.

3. Results

Wolves were detected in 1481 out of 5672 site-seasons, based on 9672 wolf scats (AM 5886; SD 509; VR 1637; AST 1640). For detailed results per site-season and study area, see Fig. A2 in Appendix A. The annual occupancy probabilities for each study area and the average annual detection probability (41.2 $\pm$ 8.8 %; range: 22.7–68.1 %) are presented in Fig. 2A. Wolf detection probability increased with transect effort ($\beta = 0.89 \pm 0.11$), ruggedness ($\beta = 0.89 \pm 0.14$), and unpaved road density ($\beta = 0.20 \pm 0.14$) (Fig. 3A). Comparatively, in AM, the detection estimated by transects of wolf signs and by GPS-collared wolf locations (n = 40,282 locations) was similar. We detected the species through transects of sign survey in most sites where GPS-collared wolves were present (seasonal average: 82 % $\pm$ 22 %; range: 17–100 %), supporting the approach used here.

Regarding the dynamic process of wolf occupation in these human-dominated landscapes, the probability that an area will become marked by wolves (i.e. colonization probability) increased with altitude ($\beta = 3.36 \pm 2.14$), livestock density ($\beta = 3.01 \pm 1.64$), and unpaved

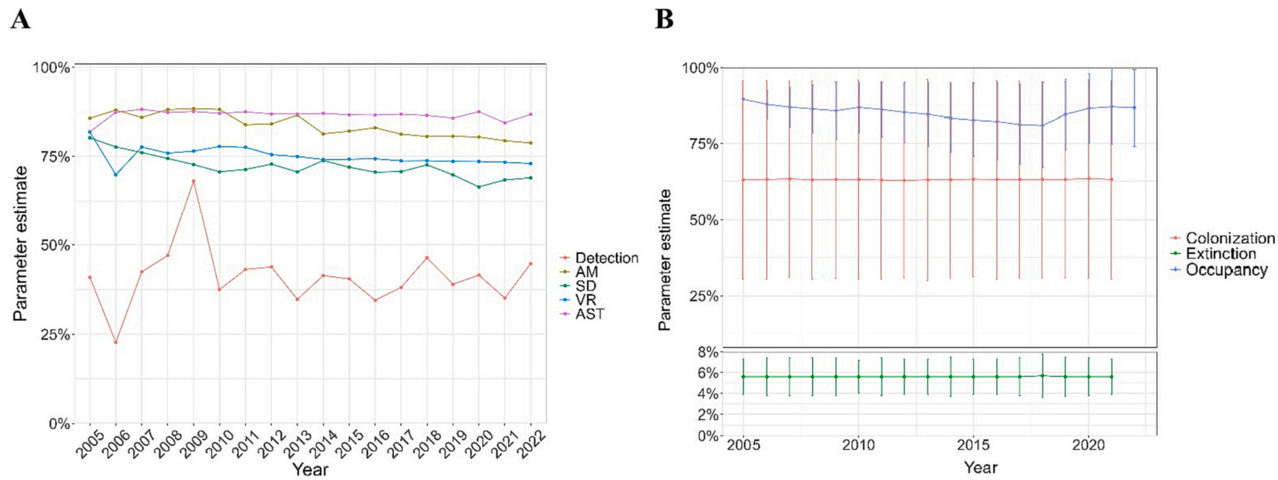

Fig. 2. A) Annual detection probability ('Detection') and annual occupancy probabilities for each study area (AM-Alto Minho, SD-South Douro, VR-Vila Real, AST-Asturias); B) annual average parameter estimates for the overall study area (bars represent standard deviation values).

road density ($\beta = 1.86 \pm 1.62$). Conversely, linear infrastructure development (national/regional roads: $\beta = -1.49 \pm 1.99$, local roads: $\beta = -1.01 \pm 1.48$) and the proportion of burned areas ($\beta = -1.26 \pm 2.12$) influenced the probability of colonization negatively (Fig. 3B). In contrast, the probability that wolves will stop using an area (i.e. extinction probability) increased with the surface of burned areas ($\beta = 0.09 \pm 0.15$), and major linear infrastructures (national-regional roads: $\beta = 0.09 \pm 0.23$, highways: $\beta = 0.08 \pm 0.27$) (Fig. 3C). On the contrary, extinction probability decreased with unpaved road density ($\beta = -0.25 \pm 0.42$; 50 % BCI) and, to a lesser extent, with higher human population densities ($\beta = -0.10 \pm 0.30$), altitude ($\beta = -0.06 \pm 0.31$), and local paved road density ($\beta = -0.09 \pm 0.25$) (Fig. 3C). For detailed model results, see Figs. A3 and A4, and Tables A2 and A3 of Appendix A.

The initial occupancy probability for the overall sampled area was 89.5 ± 0.9 % (95 % BCI: 67.9–99.7 %), and the average annual colonization and extinction probabilities were 63.1 % and 5.6 %, respectively. The average occupancy probability for the overall sampled areas was 85.2 ± 0.2 % (range: 81.0–89.5 %) and constant from 2005 to 2022 (Fig. 2A).

According to the predictions obtained for the overall IP, in the last year (2020–2021), 49 % of the IP had a colonization probability higher than 50 % (range 0–100 %), 90 % had an extinction probability higher than 10 % (range: 3–58 %), and 89 % had an occupancy probability higher than 50 % (range: 23–97 %) (Fig. 4).

The average annual colonization probability was relatively high in the areas of wolf expansion and persistence ($\gamma_{expansion} = 76.2 \pm 0.3$ %; $\gamma_{persistence} = 66.9 \pm 0.1$ %) but lower than 50 % in the area of regression ($\gamma_{regression} = 43.1 \pm 0.0$ %) (Fig. 4). The average annual extinction probability was generally low and similar across areas types ($\boldsymbol{\varepsilon}_{expansion} = 5.8 \pm 1.2$ %; $\boldsymbol{\varepsilon}_{persistence} = 5.8 \pm 0.2$ %; $\boldsymbol{\varepsilon}_{potential} = 6.9 \pm 0.1$ %; $\boldsymbol{\varepsilon}_{regression} = 6.4 \pm 0.0$ %). The mean annual occupancy probability was always higher than 80 % regardless of the area type ($\psi_{expansion} = 90.0 \pm 3.6$ %; $\psi_{persistence} = 88.3 \pm 3.4$ %; $\psi_{regression} = 81.0 \pm 4.5$ %) (Fig. 4). The colonization and occupancy probabilities for the potential recolonization area ($\gamma_{potential} = 49.5 \pm 0.1$ %; $\psi_{potential} = 82.1 \pm 4.7$ %) were relatively higher than the values obtained for the regression area. Additionally, 48 % (103,141 km^2) of the considered potential recolonization area has over 50 % of probability of being colonized (Figs. 4 and 5).

4. Discussion

By properly accommodating the detection process and landscape dynamics, our occupancy model helped us to identify environmental and anthropogenic variables influencing wolf spatial use in highly anthropogenic and heterogeneous landscapes of Western Europe. We obtained high average annual colonization probabilities (63 %) and low extinction probabilities (6 %) for the sampled study areas. The overall occupancy probabilities in the study areas were high (85 %) throughout the study period, though they were generally higher in AM and AST compared with SD and VR, which indicates that the latter study areas have less suitable areas for wolves.

Our results suggest that higher altitude, livestock density, and unpaved road densities substantially increased the colonization probability. Our results also suggest that: the increase of burned areas and national-regional and local roads have potential negative effects on colonization; the increase of local and unpaved road densities have a potential negative effect on the extinction probability; and the increase of highway and national-regional road densities and the proportion of burned areas have a potential positive effect on the extinction probability. Our results indicate that human population density and the proportion of agricultural lands have no evident influence on wolf spatial dynamics.

Altitude was the covariate with the most decisive influence in the occupancy model, with areas over 750 m a.s.l. having >75 % colonization probabilities (see also Llaneza et al., 2012). In human-dominated landscapes with small mountainous formations that can only encompass one or two packs, wolf territories are often bounded or surrounded by lower altitude areas and river valleys with higher human disturbance (Rio-Maior et al., 2019). Consequently, core areas of home ranges (e.g., breeding sites) are often located in mountainous and inaccessible areas with fewer human activities (Llaneza et al., 2012; Sazatornil et al., 2016), resulting in constant scent re-marking in such places (Barja et al., 2005; Llaneza et al., 2014). Unlike in core areas, space use and scent marking are potentially less constant on the territory edges with lower altitudes (Llaneza et al., 2014; Sazatornil et al., 2016), which can explain the tendency of higher extinction probability in these areas. Furthermore, colonization and extinction events are more likely to occur in territory edges due to annual territory shape differences and to elude intraspecific competition with neighbouring packs or dispersing wolves (Mech and Harper, 2002; Schlägel et al., 2017). On the other hand, wolves were absent or locally extinct in some sites at the beginning of the sampling period, even in areas with relatively high altitudes (e.g., Alto Minho; Nakamura et al., 2021). The recolonization of such areas throughout the sampling years can partly explain our results (Nakamura et al., 2021).

Wolves feed primarily on livestock in several regions of the IP (Blanco et al., 1992; Torres et al., 2015). Thus, as expected, wolves increasingly use areas where food availability is abundant, either in the form of live prey or carcasses (Llaneza and López-Bao, 2015; Mateo-

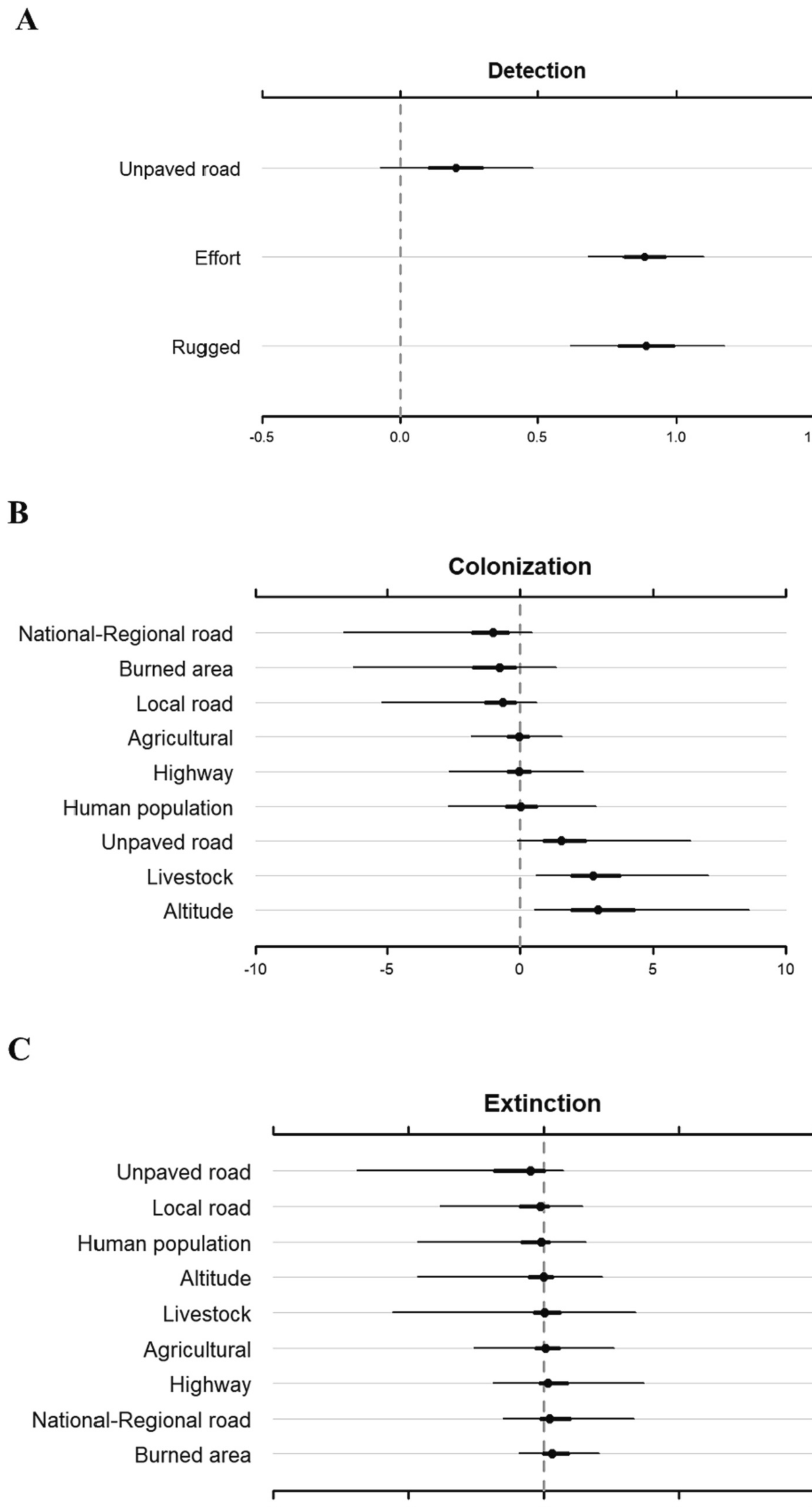

Fig. 3. Plots with mean covariate estimates of the dynamic occupancy model for each parameter (A-detection, B-colonization, and C-extinction), with 50 % CI (thick bars) and 95 % CI (thin bars). Covariates: 'Effort'- transect effort; 'Rugged'- ruggedness index; 'Altitude' – average altitude (a.s.l); 'Highway', 'National-Regional road', 'Local road', and 'Unpaved road' densities; 'Burned area' - proportion of burned area; 'Agricultural': proportion of agricultural land; 'Livestock' - livestock unit density; and 'Human population' - human population density.

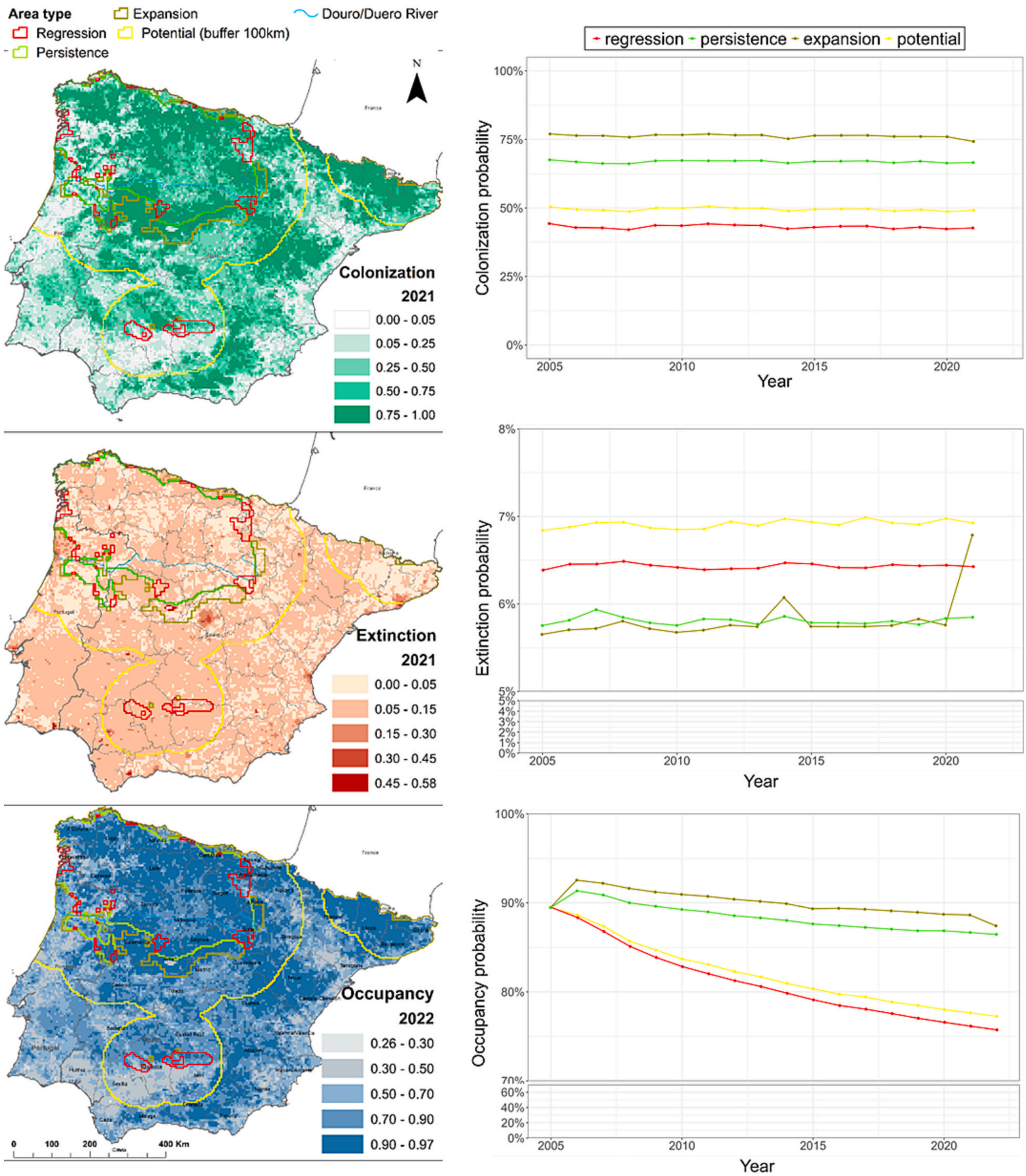

Fig. 4. Predicted wolf colonization, extinction and occupancy probabilities: i) of 2021–2022 for the Iberian Peninsula (left side maps); ii) from 2005 to 2022 in four area types, according to differences in wolf distributions between the beginning of the 2000s and recent years (right side graphs). Area types: regression, persistence, extinction and potential (i.e. 100 km buffer of the current wolf distribution).

Tomás et al., 2019). We obtained high colonization probabilities (>75 %) when livestock density exceeds 60 LU/km^2. Livestock densities could positively affect extinction probabilities due to conflicts with humans, though we failed to detect such an effect. Nevertheless, poaching rates could be high since wolf productivity (e.g., Llaneza et al., 2023) can overcome poaching rates in this human-dominated landscape. In a population of 2200–2500 wolves of Iberia (Chapron et al., 2014) with remarkable annual wolf productivity (approximately 1570 pups/year; see Table A4 in Appendix A), high extinction probabilities may be difficult to obtain even when mortality rates (mostly poaching) are high, as observed in the IP (Rio-Maior et al., 2018: poaching was the cause of death of 47 % of 17 GPS collared wolves in Portugal between 2007 and 2017). This highlights the need to include a variable of wolf mortality probability in future occupancy studies to obtain better estimates of extinction probability and calls for increasing efforts in understanding wolf mortality causes in Iberia (mainly throughout GPS collaring).

Higher unpaved road densities increased the colonization probability and decreased extinction probability, possibly because wolves often use them to scent mark as territorial behaviour (Barja et al., 2004; Llaneza et al., 2004), for ease of travel (Whittington et al., 2005; Zimmermann

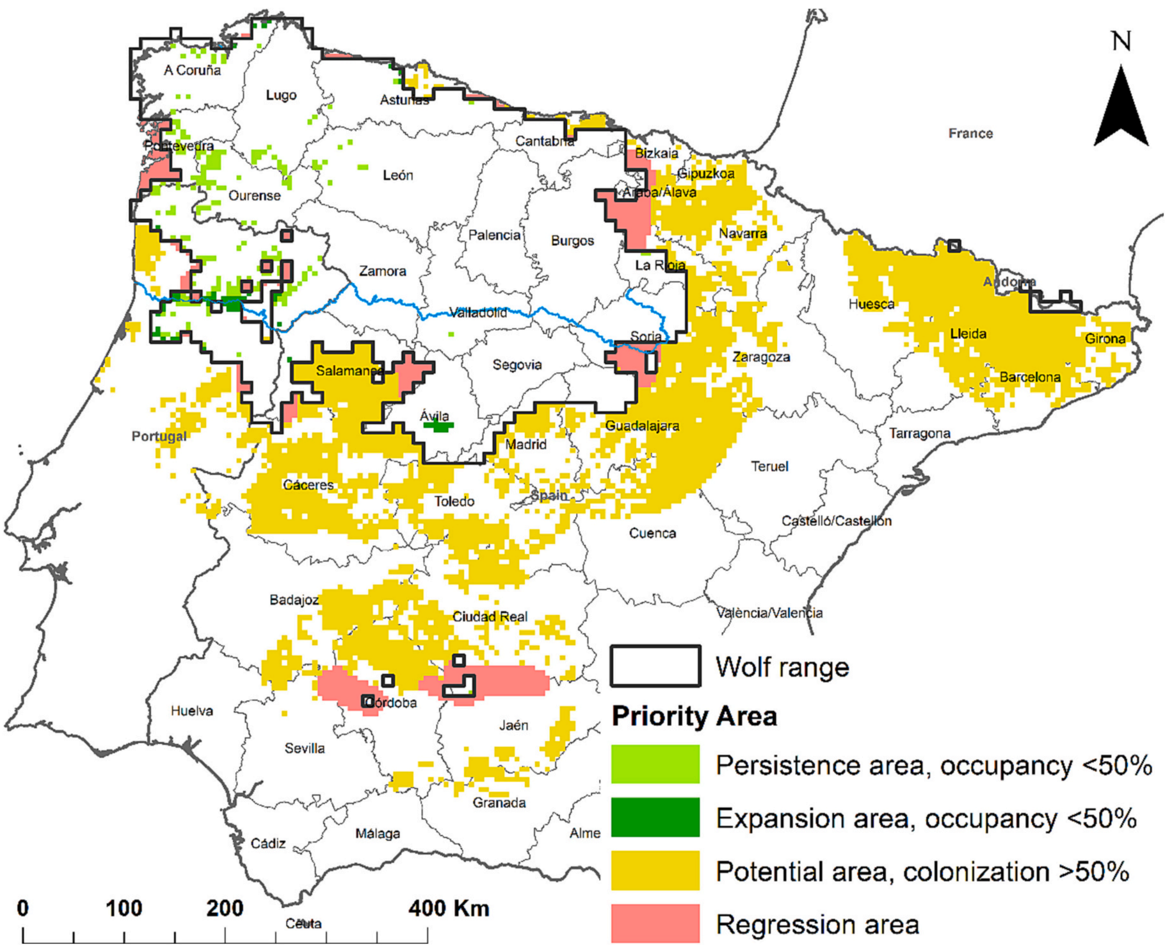

Fig. 5. Priority areas for implementing mitigation measures and conservation actions within the current wolf range (persistence and expansion areas with occupancy probability lower than 50 %) and out of the range (potential recolonization area with colonization probability higher than 50 % and regression area).

et al., 2014), and because such roads are often associated to mountainous or forested areas, which can be more easily colonized. In contrast, wolves tend to colonize fewer areas with higher national-regional and local road densities, possibly due to high human disturbance since these roads often connect urban areas and have constant traffic or other human activities. Extinction probabilities tended to increase with national-regional road densities, which may be related to human disturbance and habitat fragmentation that preclude dispersal and to higher wolf mortality caused by traffic collisions on lower-level roads than highways (Dennehy et al., 2021).

Some studies have shown that predators can select burned areas due to the presence of prey (Geary et al., 2020; Lewis et al., 2022), avoid them immediately following disturbance and re-occupy relatively rapidly, or avoid them during the following years (Ballard et al., 2000). According to our model, wolves tended to avoid using areas with a higher proportion of burned areas and were less likely to colonize such areas. Since forest fires in the IP are often human-related (Nunes, 2012), our results indicate that wolves tend to avoid burned areas, likely due to direct human disturbance, low prey availability, or low refuge availability that increases their exposure to humans.

Taking advantage of wolves' high territoriality and marking behaviour, scat surveys are often used to assess spatial use and detect core areas (Barja et al., 2005; Llaneza et al., 2014). Our study identified some variables that explain habitat suitability for colonization of wolves, though it fails to detect factors clearly related to the extinction parameter. From an ecological perspective, this could be because of the species' overall expansion trend and its typical resilience in human-dominated landscapes (Blanco and Cortés, 2009; Weaver et al., 1996). Furthermore, extinction sites in our study areas are less frequent and may lack variability compared to sites with stable pack territories that are constantly used or colonized.

Considering the differences in the estimated wolf ranges for the IP in the last decades, higher mean colonization and occupancy probabilities were obtained for wolf expansion and persistence areas than for regression and potential recolonization areas. The opposite occurred for mean extinction probabilities, with higher values for regression and potential areas than for expansion and persistence areas. While the differences were not significant, the model still predicts a gradient of higher to lower wolf occupancy probabilities from expansion, persistence, potential and regression areas, in this order. However, the relatively high occupancy (81 %) and low colonization (43–50 %) in sites where wolves were absent in recent times (i.e. potential and regression areas) indicate that the recolonization may not occur easily or quickly and that other factors rather than those considered in this study may be operating.

According to the maps of parameter probabilities obtained for the IP, there are some large extensions of sites with low occupancy probabilities within the current wolf distribution. This is the case in southern Galicia (Pontevedra and Ourense) and northeastern Portugal. Wolf is believed to have gone extinct since the beginning of the 2000's in a large area at the boundaries of Álava, Burgos, and La Rioja, Soria, and eastern Salamanca (in Spain), and in the southwestern area of Vila Real and some areas of the southern range limit (in Portugal). The model also predicted part of this area as having low occupancy probabilities. According to the model, Sierra Morena (southern Spain) has some sites with high colonization probability. If wolves are still present in that area, colonization would likely occur in the surroundings. On the other hand, if this relict population did not resist, recolonization is unlikely to occur shortly due to low colonization probabilities or non-continuous areas with relatively high occupancy probability and considerable distance to the remnant wolf distribution.

The model predicted high colonization and occupancy probabilities for recently recolonized areas in Spain (La Rioja/Soria, northern Guadalajara, northern Madrid, Ávila and northern Salamanca). From an ecological point of view, we predict that in the recent future, wolf recolonization could proceed through the central mountainous massif of Portugal (Serra da Estrela), remnant Salamanca and into the area of Cáceres. In the eastern front of the wolf distribution, eastern Guadalajara and the borders with Teruel and Cuenca also have high probabilities of recolonization. However, over the last decades, population expansion has nearly stagnated in such areas, apparently caused by the wolf persecution triggered by high livestock damage (Blanco and Cortés, 2009). The wolf population has not expanded to several mountain areas free from man-made barriers, with high densities of wild ungulates or well-preserved *dehesa* areas (i.e. savannah-like wood pasture where livestock graze unguarded) (Blanco and Cortés, 2009). In opposition, since the 1970s, a significant expansion of the Spanish wolf population occurred into less suitable agricultural habitats with a low density of wild ungulates, little vegetation cover, and a high density of roads (Blanco and Cortés, 2009; López-Bao et al., 2018a). Since frequent damages to livestock alone are enough to prevent wolves from expanding into ecologically suitable habitats (Blanco and Cortés, 2009), such unexpected expansion fronts and stagnations emphasize the strong effect and the need to assess social factors on the recovery of wolf populations. Lastly, recent evidence indicate that wolf expansion from the Italian population is recolonizing the eastern Pyrenees (Louvrier et al., 2018), which is in concordance with the high colonization probabilities obtained by the model. Nevertheless, wide areas with low colonization probabilities between the expansion from France and the eastern front of the Iberian wolf range indicate that these populations are not expected to mix in the near future.

Wolf detectability increased with higher survey effort (see also Jiménez et al., 2016; Llaneza et al., 2014), landscape ruggedness, and density of unpaved roads. Wolves' seasonal variation of space use and marking behaviour may have influenced on lower detection rate than expected (Roda et al., 2022). Detection probability also increased with a higher density of unpaved roads, possibly because wolves often use these structures as preferred travel routes and marking sites (Stępniak et al., 2020). Furthermore, higher unpaved road density leads to a higher frequency of crossroads and intersections, known to be preferred scent-marking sites for wolves (Barja et al., 2004). The selection of conspicuous substrates at crossroads amplifies the visual component of deposited scats, increasing scat detectability for other wolves (Barja et al., 2004; Bojarska et al., 2020) and for the observer as well. In landscapes with lower ruggedness, wolves have more travelling route options and can travel more randomly across the landscape since effort is likely to be similar between untrailed paths or unpaved roads. Conversely, more rugged landscapes provide fewer options, and therefore wolves tend to travel through least cost paths that exist in limited availability (e.g. roads; Zimmermann et al., 2014). The regular use of such routes likely results in higher marking intensity and detectability of scats.

We propose long-term monitoring surveys in areas where packs are permanently present and in the neighbouring areas in order to detect recent wolf population expansions (see Nakamura et al., 2021). Transects of sign surveys, and camera trapping approaches, between known pack territories and close to the limit of wolf distribution can help detect dispersal events and recent recolonizations that would be harder to detect through other methods. Here, we performed a prediction based on the occupancy model to identify the potentially suitable areas where the wolf population could expand in the near future; although wolf dispersal patterns accounting for habitat availability and connectivity deserves further investigation. Considering the high wolf capabilities for dispersal, the sampling area for the national wolf population estimates should also include a buffer of 100 km of the last known distribution, particularly close to areas where wolves appear to be recolonizing (Fig. 5).

GPS-collared wolves in the expansion borders would facilitate detailed information on dispersal movements that is unobtainable through any other method. Additionally, intensive non-invasive sampling with molecular individual identification and genealogy analyses can also provide information on habitat connectivity and dispersal, especially relevant for recolonizing areas, particularly if included in a spatial capture-recapture framework (e.g., Caniglia et al., 2014; Kervellec et al., 2023). Integrating data on additional socio-ecological factors, such as wild prey density, hunting pressure, or other human infrastructures, could also benefit further investigations. It would be expected that wild prey availability, together with livestock vulnerability, influence on wolf diet, although detailed data on wild prey densities in the IP is limited. To address this knowledge gap, we recommend that more studies on wild ungulate density estimations should be conducted in the IP, such as wild boar density estimates obtained by ENETWILD-consortium et al. (2019) based on species occurrence and hunting bags or studies based on camera trap data (Gilbert et al., 2021). These density estimates could be incorporated into wolf occupancy studies to improve our understanding on the influence of both livestock and wild prey availability on wolf occurrence and persistence in such human-dominated landscapes.

Based on our findings, the sites where the wolf was recently extinct or with low occupancy probabilities within its distribution range should be the main priority for implementing conservation actions and mitigation measures (Fig. 5). These areas are potential indicators of conflicts around the presence of wolves and poaching. Increasing awareness among the local communities, including livestock owners or hunters, would be highly relevant in such areas. Efforts should be focused on implementing livestock damage preventive methods (e.g., Eklund et al., 2017), developing patrolling activities, and improving law reinforcement to fight against poaching. We also recommend implementing roadkill mitigation measures (particularly on national-regional and local roads) and improving landscape management regarding habitats with a higher probability of large fires. Moreover, areas with high probabilities of colonization beyond the current wolf range should also be given priority (Fig. 5). Efforts should be intensified in these areas to raise awareness about facilitating human-wolf coexistence, promoting livestock damage preventive methods, and explaining how compensation schemes work. We also propose that future studies incorporate a social component, human dimensions, or estimated wolf mortality rates across space to shed light on the slow recovery and recolonization of the population in Iberia.

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CRediT authorship contribution statement

Mónia Nakamura: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. **José Vicente López-Bao:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Writing – review & editing, Supervision. **Helena Rio-Maior:** Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Writing – review & editing, Project administration, Supervision. **Sara Roque:** Data curation, Investigation, Methodology, Writing – review & editing, Supervision. **Patrícia Gil:** Data curation, Investigation, Writing – review & editing. **Ana Serronha:** Data curation, Investigation, Writing – review & editing. **Emilio García:** Investigation, Writing – review & editing. **Orencio Hernández Palacios:** Methodology, Writing – review & editing. **Gonçalo Ferrão da Costa:** Data curation, Investigation, Methodology, Writing – review & editing. **Francisco Álvares:** Funding acquisition, Methodology, Writing – review & editing, Project administration, Supervision. **Francisco Petrucci-Fonseca:** Funding acquisition, Writing – review & editing, Project administration, Supervision. **Olivier Gimenez:** Conceptualization, Formal analysis, Funding acquisition, Methodology, Writing – review & editing, Supervision. **Pedro Monterroso:** Conceptualization, Formal analysis, Funding acquisition, Methodology, Writing – review & editing, Supervision.

Research data

The processed data file (.Rdata) and code of the dynamic occupancy model (.Rmd) are available on the Zenodo Digital Repository (https://zenodo.org/record/8377581). The processed data files include the data frame with detection/non-detection results and standardized values of covariates included in the final model, per 5x5 km site (N=395) of the sampled study areas from March 2005 to February 2022.

Declaration of competing interest

The authors declare that they have no conflict of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2023.110316.

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