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Large carnivore range expansion in Iberia in relation to different scenarios of permeability of human-dominated landscapes

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Abstract

Aim: Large carnivores are currently recolonizing parts of their historical ranges in Europe after centuries of persecution and habitat loss. Understanding the mechanisms driving these recolonizations is important for proactive conservation planning. Using the brown bear (*Ursus arctos*) and the Iberian lynx (*Lynx pardinus*) as examples, we explore where and when large carnivores are likely to expand into human-dominated landscapes and how varying levels of resistance due to human pressure might impact this recolonization process.

Location: Iberian Peninsula.

Methods: We used ensembles of species distribution models to relate species occurrence data to climate, topography and satellite-based land-cover predictors at a 10 km spatial resolution. Resulting predictions of suitable habitat areas were fed into a dispersal model to simulate range expansion over the 10 time-steps for different human pressure scenarios. Finally, we overlaid predictions with protected areas to highlight areas that are likely key for future connectivity, but where human pressures might hamper dispersal.

Results: We found widespread suitable habitat for both species (bear: 30,000 km², lynx: 170,000 km²), yet human pressure limits potential range expansions. For brown bears, core habitats between the Cantabrian and Pyrenean populations remained unconnected despite suitable habitat in between. For lynx, we predicted higher range expansion potential, although high human pressures in southern coastal Spain negatively affected expansion potential.

Main conclusions: Our results highlight that the recolonization potential of brown bears and lynx in the Iberian Peninsula is likely more constrained by lower permeability of landscapes due to human pressure than by habitat availability, a situation likely emblematic for large carnivores in many parts of the world. More generally, our

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approach provides a simple tool for conservation planners and managers to identify where range expansion is likely to occur and where proactively managing to allow large carnivores to safely disperse through human-dominated landscapes can contribute to viable large carnivore populations.

KEYWORDS

dispersal dynamics, habitat suitability, large carnivores, megafauna, niche models, range expansion, recolonization, simulation models

1 | INTRODUCTION

Large carnivores have recently been declining in many parts of the world (Ripple et al., 2014), as has historically been the case in Europe, where centuries of relentless human persecution and habitat loss have resulted in widespread extirpations and range contractions (Cimatti et al., 2021). This is worrisome, since large carnivores are threatened and are important for ecosystem functioning, given their role as keystone species and apex predators (Hoeks et al., 2020). However, since the mid-20th century, changing hunting regulations and legislation to better protect large carnivores have created more favourable conditions for large carnivores in Europe (Garrote et al., 2020). Simultaneously, human outmigration from rural areas, structural change in agriculture, as well as widespread agricultural abandonment have provided more space for these species (Boitani & Linnell, 2015; Cimatti et al., 2021; Estel et al., 2015). Together, this has put large carnivores on a recovery path (Chapron et al., 2014; López-Bao, Bruskotter, et al., 2017).

Despite recent population increases and range expansions of European large carnivores, many populations remain small and isolated, such as wolves in Scandinavia, lynx in Central Europe or brown bears in the Iberian Peninsula or Italy (Hindrikson et al., 2017; Krojerová-Prokešová et al., 2019; Morini et al., 2017; Pérez et al., 2010; Zedrosser et al., 2011). These small populations are likely to suffer from demographic and environmental stochasticity, as well as inbreeding depression (Palomares et al., 2012), which increases their probability of extinction (Benson et al., 2019). Therefore, safeguarding large carnivores in Europe and elsewhere critically depends on the continued recolonization of areas to ensure populations are connected and viable in the long run (Palomares et al., 2011; Zarzo-Arias et al., 2019). However, their return into fragmented landscapes with a high wildland-urban interface (Radeloff et al., 2005) leads to more frequent contact between people and carnivores, which can increase the mortality of large carnivores due to a range of factors (Dickman, 2010; van Bommel et al., 2020). Identifying where range expansion is likely to happen is thus essential to coordinate conservation planning and wildlife management to restore and maintain connectivity between carnivore populations (Chapron et al., 2014; Frank et al., 2019; Lamb et al., 2020).

The expansion of large carnivores across a landscape depends on the availability of suitable habitat, landscape connectivity and the dispersal ability of the species (Benton & Bowler, 2012). Yet, despite the importance of species' dispersal abilities for accurately

predicting range dynamics, only a few studies explicitly considered processes by which species shift their ranges (Urban et al., 2016; Zurell et al., 2009). Most studies still rely on static approaches to delineate potentially suitable habitats, assess landscape connectivity and permeability (Zurell et al., 2022) or examine the effects of anthropogenic barriers, for example, highways and railroads (Bordade-Água et al., 2019; Ceia-Hasse et al., 2017; Garrote et al., 2018). This is problematic as range expansion is a dynamic process that takes time (Gaston, 2003). From an ecological perspective, range expansion is affected by the biophysical resistance of the landscape as well as by ecological processes such as dispersal ability (Schurr et al., 2012). From a social-ecological perspective, human infrastructure (e.g. highways, fences) can constitute major barriers to dispersal (Barrientos et al., 2021). In addition, human pressure in landscapes through which carnivores have to disperse is essential in determining whether or not dispersal is successful (Cimatti et al., 2021; Morales-González et al., 2022; Tucker et al., 2018). With human pressure, we here collectively refer to human activities that can increase the mortality of large carnivores, such as hunting, the prevalence of livestock husbandry or shepherding, road traffic, institutional factors such as legal frameworks (e.g. hunting bans) or the attitude and tolerance of people living (Bautista et al., 2017; Behr et al., 2017; Dickman, 2010; Ghoddousi et al., 2021; Yackulic et al., 2011). Incorporating species-specific dispersal abilities and understanding how different levels of human pressure, in addition to physical barriers in the landscape, affect range expansion potential would improve our ability to anticipate large carnivore range dynamics and to guide large carnivore conservation and management.

We address these challenges by combining species distribution models (SDMs) with spatio-temporally explicit dispersal simulations to explore how two threatened large carnivores, the Iberian lynx (*Lynx pardinus*) and the Cantabrian brown bear (*Ursus arctos pyrenaicus*), could potentially expand their ranges across the Iberian Peninsula. Once on the brink of extinction, the Iberian lynx was considered the most endangered felid less than two decades ago (Simon et al., 2012). Similarly, the Iberian brown bear, a sub-species of the European brown bear (*Ursus arctos arctos*), suffers from fragmented, small populations and low genetic diversity (Naves et al., 2003). Safeguarding both species requires enlarging populations, which rests on increasing the connectivity between extant populations (Martin et al., 2012; Mateo Sánchez et al., 2014; Zarzo-Arias et al., 2019). At the same time, while range expansions are desirable from a conservation perspective, they will likely lead to exacerbated human-carnivore

conflict (Morales-González et al., 2020; van Bommel et al., 2020). Proactive conservation action to mitigate conflicts would be beneficial (Frank et al., 2019), but this requires understanding where and when range expansions will likely occur.

Our overarching aim here was to understand the potential range recolonization of large carnivores in the Iberian Peninsula, as well as potential constraints to such range expansions, in relation to human pressure in the landscape through which large carnivores would have to disperse. Specifically, we (i) estimated and mapped habitat availability and quality for the Iberian lynx and the Cantabrian brown bear across the Iberian Peninsula, (ii) ran a set of dispersal scenarios to evaluate how different assumptions about how human pressure influences landscape permeability affect range colonization and finally, (iii) overlapped potential habitat, dispersal scenarios and protected areas to highlight where human pressure is most likely to negatively affect range expansions. To proxy human pressure and its effect on the permeability of landscapes, we use the degree of human modification of landscapes.

2 | METHODS

Our overall methodological framework consisted of three main steps (Figure 1): First, we retrieved and processed the input data, including occurrence records for both species and the predictor variables. Second, we modelled the comprehensive extent of potential habitat using the occurrence records and predictors in a variety of models. Lastly, we simulated different dispersal scenarios assuming landscapes with different levels of human pressure would allow safe

passage of carnivores. Finally, we assessed conservation prioritization based on gap analysis. All analyses were carried out in R 4.1.1 (R Core Team, 2020).

2.1 | Distributional data

The presence records to model the potential range were based on the Global Biodiversity Information Facility (GBIF) database (GBIF.org, 2020). We differentiated between the two species with regard to the spatial extent considered for retrieving the records. For the Iberian lynx, we restricted the search to the Iberian Peninsula, while for the bear, we considered records from entire Europe (see sensitivity analyses, where we used only bear occurrences for the Iberian Peninsula, Appendix S5). Using records of the entire Europe for the bear ensures a complete description of the realized niche of the European brown bear, a procedure that has been shown to outperform models from individual populations (Ceia-Hasse et al., 2017; Kuemmerle et al., 2018). We retrieved all available records classified as “Human Observations” of the species *Ursus arctos* (Linnaeus, 1758) and *Lynx pardinus* (Temminck, 1827) between 1980 and 2020 using the “rgbif” package in R (Chamberlain et al., 2022), resulting in a total of 15,156 and 354 records for the bear and lynx, respectively. The records were further processed using the “CoordinateCleaner” package, which allows for filtering erroneous coordinates (i.e. incomplete coordinates or poorly georeferenced records) and those with large spatial uncertainties (>10 km) (Zizka, 2019). A substantial part of presence points exhibited an artificially increased coordinate uncertainty of 10 km to protect threatened species (iNaturalist

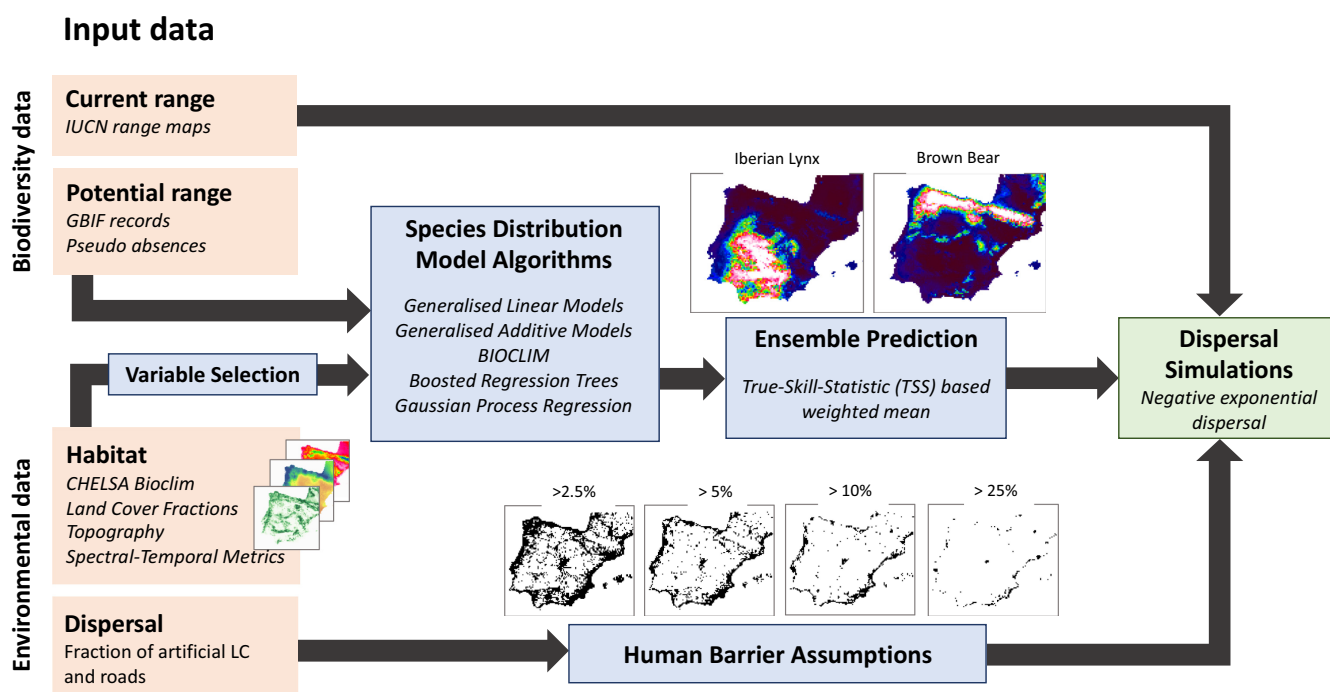


FIGURE 1 Methodological workflow applied to integrate species distribution models with dispersal simulations under different human barrier scenarios.

contributors, 2020). Consequently, we defined 10 km as the target resolution and aggregated the presence points to this resolution. In particular, we classified a 10 km cell as presence if at least one observation fell within it and removed all duplicate observations.

To contrast our presence-only data against the available background environment, we selected pseudo-absences within a spatial buffer around the presence cells. We chose this procedure to account for potential sampling bias and the currently restricted ranges. For the bear, we chose a 50km buffer, and for the lynx, a 15km buffer based on a combination of model performance results and ecological knowledge of the species (Blazquez-Cabrera et al., 2019; Senay et al., 2013; Zarzo-Arias et al., 2019). Both presence and pseudo-absence data were thinned separately using the “spThin” package (Aiello-Lammens et al., 2019), with a minimum distance of 11km between cells of the same class to avoid problems of spatial autocorrelation.

2.2 | Environmental predictors

The initial set of predictors consisted of 34 variables representing climate conditions, topography and land cover. All variables were resampled in GDAL to the target resolution of 10 km using an averaging (for continuous variables) and a majority approach (for categorical variables) and transformed using z-score standardization (GDAL/OGR Contributors, 2022).

The climate data comprised 19 bioclimatic variables obtained from CHELSA (Climatologies at high resolution for the earth's land surface areas), which provides global temperature and precipitation data at approximately 1 km resolution (Karger et al., 2017). The bioclimatic variables follow the scheme of WorldClim and are readily used in ecological applications, including species distribution models. Regarding topography, we derived elevation from the digital elevation model (DEM) Global 30 Arc-Second Elevation (GTOPO30), which was downloaded via the Google Earth Engine (GEE) (Gorelick et al., 2017). In terms of land cover, we used GEE to derive Landsat-based spectral-temporal habitat metrics as described in Oeser et al. (2020). These metrics include median Tasseled Cap greenness (TCG), brightness (TCB) and wetness (TCW) values for the three different phenological periods start- (SOS), peak- (POS) and end-of-season (EOS). These continuous metrics proxy different habitat features such as resource availability, vegetation density or moisture and have been shown to outperform SDMs based on categorical land cover data (Oeser et al., 2020). Furthermore, we transformed categorical land cover data into continuous fractions based on a European-wide LC map at 30m resolution for the year 2015 (Pflugmacher et al., 2019) resulting in five different land cover fractions: artificial surfaces, bare ground, cropland, high vegetation and low vegetation.

2.3 | Modelling potential suitable habitat

Species distribution models (SDMs) relate species presence data to environmental predictors and can be used to make predictions of

habitat suitability in space and time (Zurell et al., 2020). SDMs were implemented in R (R Core Team, 2020), using an ensemble of multiple algorithms, ranging from simple envelope to complex machine learning approaches, which reduce prediction error and capture the uncertainty inherent to model selection (Araújo & New, 2007; Dormann et al., 2018). In particular, we included the envelope approach BIOCLIM, two (semi)parametric methods, Generalized Linear Models (GLM) and Generalized Additive Models (GAM), and two machine-learning algorithms, Boosted Regression Trees (BRT) and Gaussian Process Regression (GPR). Based on the ODMAP (Overview, Data, Model, Assessment, Prediction) protocol by Zurell et al. (2020), we provide detailed information on SDM model inputs, assumptions, building and the validation process in the Appendix S4 (and see Appendix S6 for parameter estimates (GLM) and variable contribution (BRT)).

We checked for multicollinearity using Spearman's rank correlation coefficient and removed highly correlated variables using the “select07” method (Dormann et al., 2013). When a pair of variables showed a correlation $|r| > .7$, we removed the less important variable in terms of its univariate variable importance. Variable importance was determined by calculating the Akaike Information Criterion (AIC) for univariate GLMs with linear and quadratic terms. This resulted in a reduction to 21 predictors for the bear and 12 variables in case of the lynx (see Appendix S1).

As recommended by Barbet-Massin et al. (2012), we randomly sampled 10 times as many pseudo-absences as presence points and applied equal weighting of presences and absences for the GAM and GLM. In the case of the machine-learning algorithms, we used an equal number of presences and pseudo-absences during model fitting and fitted 10 models per algorithm, each with a different random set of pseudo-absences. We estimated out-of-sample accuracy for each model using fivefold cross-validation. Model performance was evaluated using the metrics Area Under the Curve (AUC) and True Skill Statistic (TSS) (Allouche et al., 2006). We constructed four ensemble predictions: mean, median, weighted mean of probabilities based on performance measured by TSS and a committee average of the binary predictions. The optimal threshold for binarizing the predictions into suitable/unsuitable habitat was retrieved for each model by maximizing the TSS using the *optimal.thresholds* function of the “PresenceAbsence” package (Freeman & Moisen, 2008). Based on the cross-validated accuracy metrics, we chose the ensembles with the highest TSS as the final predictions.

2.4 | Assessing range expansion

To explore the potential of habitat expansion of the Iberian lynx and the brown bear in Iberia, we implemented four alternative dispersal scenarios, using the “MIGCLIM” package in R (Engler et al., 2012). The colonization of suitable environments by the two carnivores was based on the species' initial distribution, habitat suitability, dispersal distance, barriers to dispersal and the number of time steps that would be involved to reach a location (Engler et al., 2012). From

the simulation output, we identified which areas were abandoned, stable, colonized at each of the 10 time-steps or not colonized at all, despite being suitable.

As an approximation of the initial distribution of the two species, we used the IUCN range maps, thus assuming that all 10 km cells inside these extent of occurrence polygons are actually occupied by the species. The best-performing ensemble SDMs served as a proxy of the ability of our two species to move through a cell. Permeability depended on the value for habitat suitability, while cells below the threshold used for binarizing the predictions were set to not suitable and hence could not be colonized. The probability that a pixel becomes colonized P_{Col} is the combined probability of all dispersing source cells which was defined through a negative exponential kernel as a function of the distance:

$$p_{\text{dispersal}}(d) = e^{-d/\theta}$$

where $p_{\text{dispersal}}(d)$ is the probability of dispersing from the potential source cell over a distance d given the expected mean dispersal distance for each species θ . The mean annual dispersal distance of brown bears varies by age and differs between sex and among regions and ranges from approximately 7 km to more than 30 km (McLellan & Hovey, 2001; Støen et al., 2006). Here, we used a mean dispersal distance of 20 km for the bear and 14.7 km for the lynx (Ferreras et al., 2010). These distances represent the overall population dynamic in the region, rather than the large distance dispersal of individuals as the simple dispersal model subsumes the process of movement and successful establishment. We assumed that both species disperse once a year and performed 10 dispersal steps to simulate a time period of 10 years. We did not account for reproductive potential. Hence, once a cell is occupied, it becomes a starting point for dispersing individuals in the next time step, yet not for producing propagules.

We further included barrier masks in our dispersal simulation, indicating cells across which dispersal cannot occur. If such barriers separate source cells from the target cell, then the source cells will be ignored and not contribute to the combined probability P_{Col} (Engler & Guisan, 2009). In the simulation, barrier cells are considered as permanently unsuitable, but unlike regular unsuitable cells, they also impede dispersal across them. Dispersal is modelled as a random process such that colonization of an unoccupied cell is determined from a Bernoulli trial $\text{Bern}(P_{\text{Col}})$.

We defined four different barrier maps that mirrored a gradient of how general human pressure translates into effective barriers, meaning that large carnivores cannot safely move through these landscapes. General human pressure was approximated via the density of built-up area that the animals perceive as impermeable to dispersal. We used the land-cover classification at 30 m resolution and complemented this with detailed information on roads and railways from OpenStreetMap (<https://www.openstreetmap.org>), which are typically underestimated in classifications based on medium resolution remotely sensed imagery. The resulting binary mask indicating the presence or absence of artificial surfaces

at 30 m resolution was then aggregated to the 10 km target resolution by calculating artificial surface cover fractions as a percentage per 10 km cell. Comparing the cover fractions with high-resolution imagery in Google Earth, we devised four different artificial surface cover thresholds (2.5%, 5%, 10%, 25%) to construct binary masks of dispersal barriers (Appendix S3). The resulting four dispersal scenarios represent different assumptions about the level of human pressure, proxied by the proportion of artificial surface, which would be needed to render a cell unsafe for large carnivores to transverse through and thus render a cell to act as a barrier to dispersing carnivores. Consequently, with a threshold of 25%, only cells with dense urban settlements act as barriers to population expansion. In contrast, a threshold of 2.5% assumes that even cells with only a few roads and settlements functionally act as barriers because carnivores will avoid such cells. The different dispersal scenarios allowed us to assess how the human pressure assumptions influence our range colonization estimation. In the main text, we only present results from the most extreme scenarios with 2.5% (restrictive dispersal scenario) and 25% (optimistic dispersal scenario) thresholds for artificial surface fraction, while results for the other thresholds are provided in the Appendix S3.

2.5 | Identifying priority areas for effective conservation planning

To identify and prioritize areas where conservation interventions and wildlife management would likely be beneficial, we overlap our predictions of habitat suitability, the different dispersal scenarios and protected areas. We used the European Natura 2000 network of protected areas (<http://eunis.eea.europa.eu>) for our analysis that is composed of SPAs (Special Protection Areas following Birds Directive 1979) and SACs (Special Areas of Conservation following Habitat Directive 1992). All SPA sites (type codes A for the study area) were removed from the network because as they aim at protecting bird species and would not be different from other landscapes from the perspective of our target species (Santini et al., 2016).

For each species, we identify the top-ranking cells with the highest suitability per species, defined as those cells with predicted suitability above the 85% quantile, regardless of whether species can get there or not. We then assessed how much of this habitat is under protection. Second, we identify those areas that will likely be colonized under a low human-pressure dispersal scenario (25% artificial surface cover threshold) to assess how much of this is adjacent or close to protected areas (using a 50-km buffer for the bear, and a 15 km buffer for the lynx). This proximity and the lower human pressure will help protected area expansion to increase protection levels. Finally, we identified areas where recolonization is uncertain. This applied to areas that are colonized under our optimistic dispersal scenario but remain uncolonized under the more restrictive dispersal scenario (2.5% artificial surface cover threshold). In these areas, implementing conservation management measures will be crucial to mitigate potential negative impacts arising from high

human pressure and ensure the long-term viability of large carnivore populations (López-Bao, Frank, et al., 2017).

3 | RESULTS

Our SDMs performed well for both species (evaluation metrics in Table 1). Measured by the TSS, BIOCLIM performed poorest for both bear and lynx, while the remaining models showed similarly high results in their predictive power. AUC values ranged from 0.84 to 0.98, indicating high overall levels of predictive accuracy. Differences among the ensemble models were subtle, as TSS values ranged from 0.78 to 0.80 (see Table 1 and Appendix S2). We chose the weighted mean ensemble as the final model to predict habitat suitability because it topped the others regarding its predictive performance according to TSS and AUC metrics. Also, overlaying predictions with independent IUCN range maps suggested the high plausibility of our results (Figure 2).

For both species, climate and land-cover indicators largely determined habitat suitability. While both sets of SDMs comprised generic climatic parameters and spectral-temporal metrics-derived vegetation signals as the most important indicators, suitability for the bear was also substantially explained by human land-cover alterations (fraction of cropland and artificial land) and elevation. SDMs for bear habitat classified the Pyrenees and the Cantabrian Mountains as most suitable, while the remaining areas in Iberia were generally of low suitability. The results for the lynx suggest a more extensive suitable habitat in Iberia compared with the brown bear. While the highest lynx suitability was found in the mountainous

regions of Sierra Morena, the Betic Chain and the Mountains of Toledo, the potential lynx range covered the largest part of Southern and central Spain in our results.

According to binary classifications of the continuous suitability predictions based on TSS-optimizing thresholds (Table 1), there were nearly 170,000 km² of suitable, unoccupied habitat for the lynx, which constitutes almost a 50-fold increase compared with its current range size of 3400 km² (Figure 2b). Contrarily, suitable but unoccupied habitat for the brown bear was less widespread, amounting to approximately 30,000 km², compared with 8400 km² of currently occupied habitat (Figure 2a).

Dispersal simulation outcomes after 10 time-steps strongly depended on the underlying human barrier assumption (Appendix S3). While all models were characterized by uniform, radial dispersal around initially occupied cells, the extent of potential connectedness among currently isolated populations varied considerably among dispersal scenarios as well as among the two species. In the following, we will focus on the two extremes of low and high level of assumed human pressure to dispersal. For the brown bear, the restrictive dispersal scenario (artificial surface cover threshold 2.5%) resulted in very little dispersal, particularly beyond the fifth time-step (Figure 3). Although colonization potential increased slightly with the most optimistic dispersal scenario (artificial surface cover threshold 25%), brown bear core habitat areas, as well as more marginal habitat areas, remained unconnected in all dispersal scenarios. In particular, potential exchange between the Cantabrian and Pyrenean bear populations did not emerge in our scenarios, leaving major areas of suitable habitat that could connect extant populations unoccupied. Although larger habitat areas were colonized after 5–10

Species	Algorithm	AUC	TSS	Sens	Spec	tresh
Brown bear	Generalized linear models	0.925	0.703	0.865	0.838	0.54
	Generalized additive models	0.940	0.757	0.887	0.869	0.56
	BIOCLIM	0.844	0.550	0.687	0.863	0.04
	Boosted regression trees	0.950	0.784	0.909	0.875	0.5
	Gaussian Process Regression	0.961	0.797	0.902	0.895	0.56
Iberian lynx	Generalized linear models	0.975	0.856	0.989	0.866	0.29
	Generalized additive models	0.977	0.852	0.957	0.895	0.29
	BIOCLIM	0.904	0.747	0.893	0.854	0.01
	Boosted regression trees	0.972	0.831	0.930	0.901	0.51
	Gaussian Process Regression	0.973	0.834	0.968	0.866	0.49

TABLE 1 Model performance metrics obtained from fivefold cross-validation: Area Under the Curve (AUC), True Skill Statistic (TSS), sensitivity (Sens), specificity (Spec) and the TSS-optimizing threshold for binary classifications.

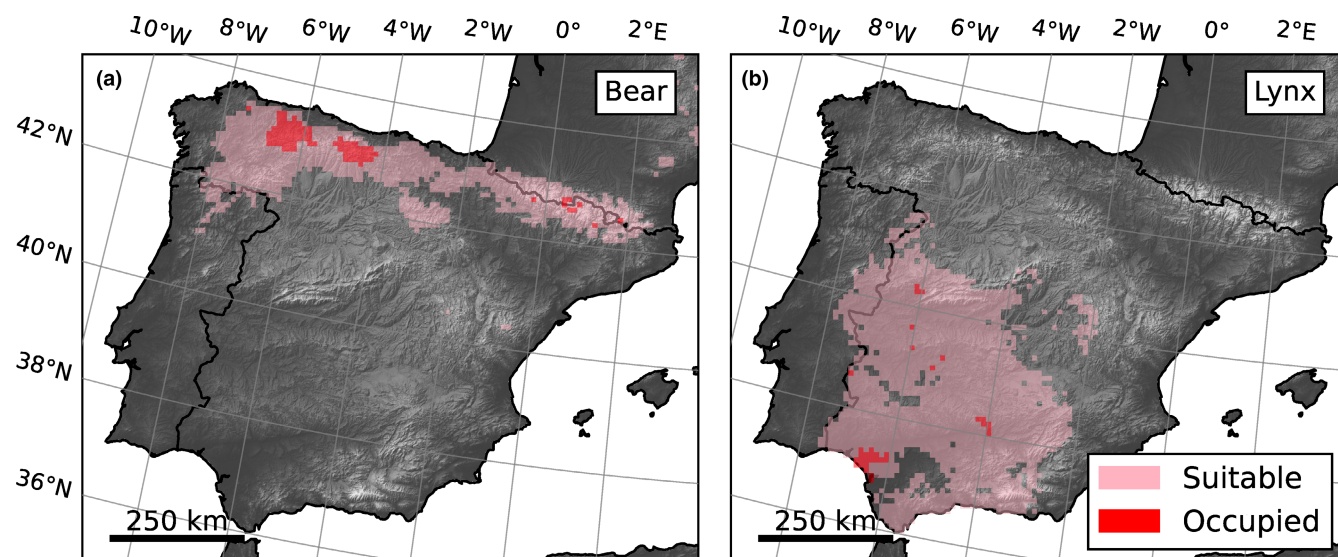


FIGURE 2 Classification of suitable habitat for the brown bear (a) and Iberian lynx (b). Suitable habitat is obtained by thresholding the TSS (TSS = 0.46 for bear; TSS = 0.28 for lynx) based on the SDMs. Occupied habitat is defined as the currently occupied cells based on IUCN range maps for both species. The SDM predictions capture 100% of the bear's and 91% of the lynx's currently occupied habitat, respectively.

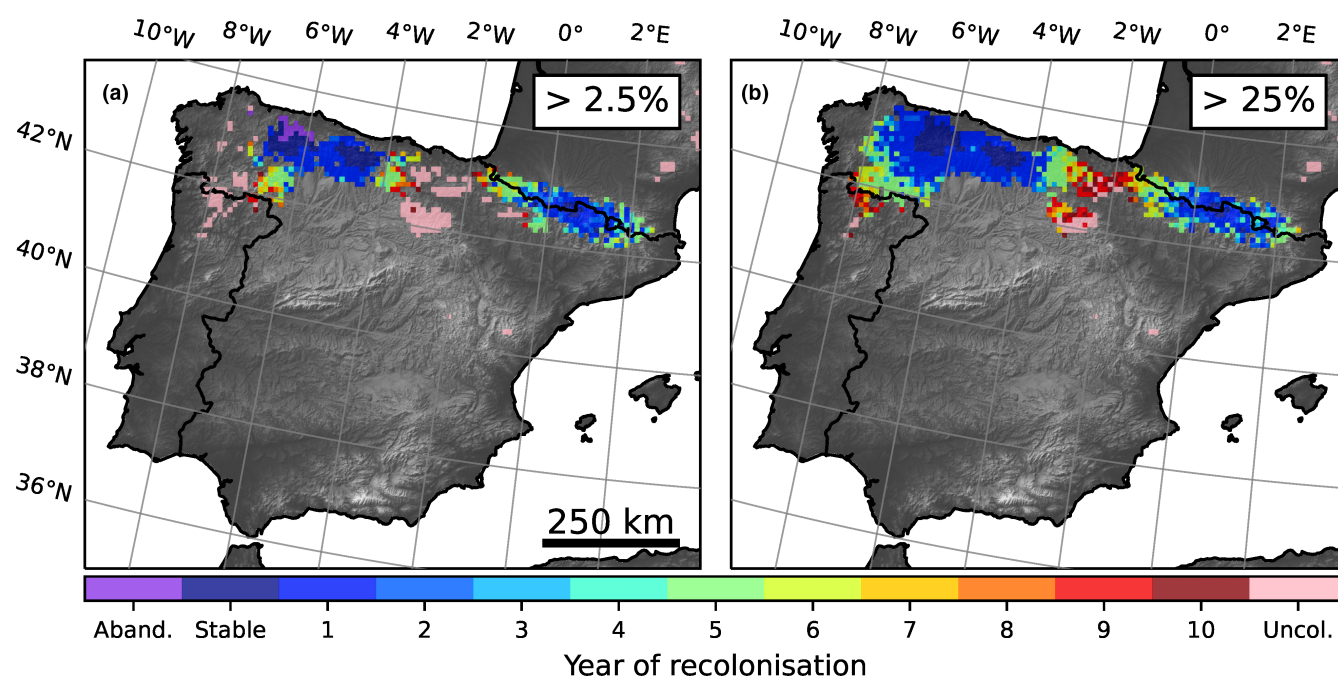


FIGURE 3 Simulated dispersal scenarios for the Cantabrian bear under different barrier assumptions, (a) restrictive dispersal scenario based on 2.5% artificial surface cover threshold and (b) optimistic/low human-pressure dispersal scenario based on 25% artificial surface cover threshold. The artificial surface cover threshold indicates how much area can be covered by artificial surfaces before the cell is perceived as barrier to bear dispersal.

time-steps in the most optimistic dispersal scenario, there was still a lack of connectivity between these two brown bear populations.

In contrast, for the Iberian lynx, dispersal simulations suggested less fragmented habitat within the current and potential range of the species (Figure 4). Within 5–10 time-steps, most suitable habitat patches were colonized by dispersing lynx in all our dispersal scenarios. This predicted range expansion showed high potential

for creating connectivity between extant populations and would substantially expand the lynx' current distribution in the Iberian Peninsula. However, the most restrictive dispersal scenario (artificial surface cover threshold 2.5%) predicted some cells around the Doñana National Park on the southern coast of Spain to become unsuitable for lynx, indicating that these areas have a comparably high level of landscape modification and constitute suboptimal habitat.

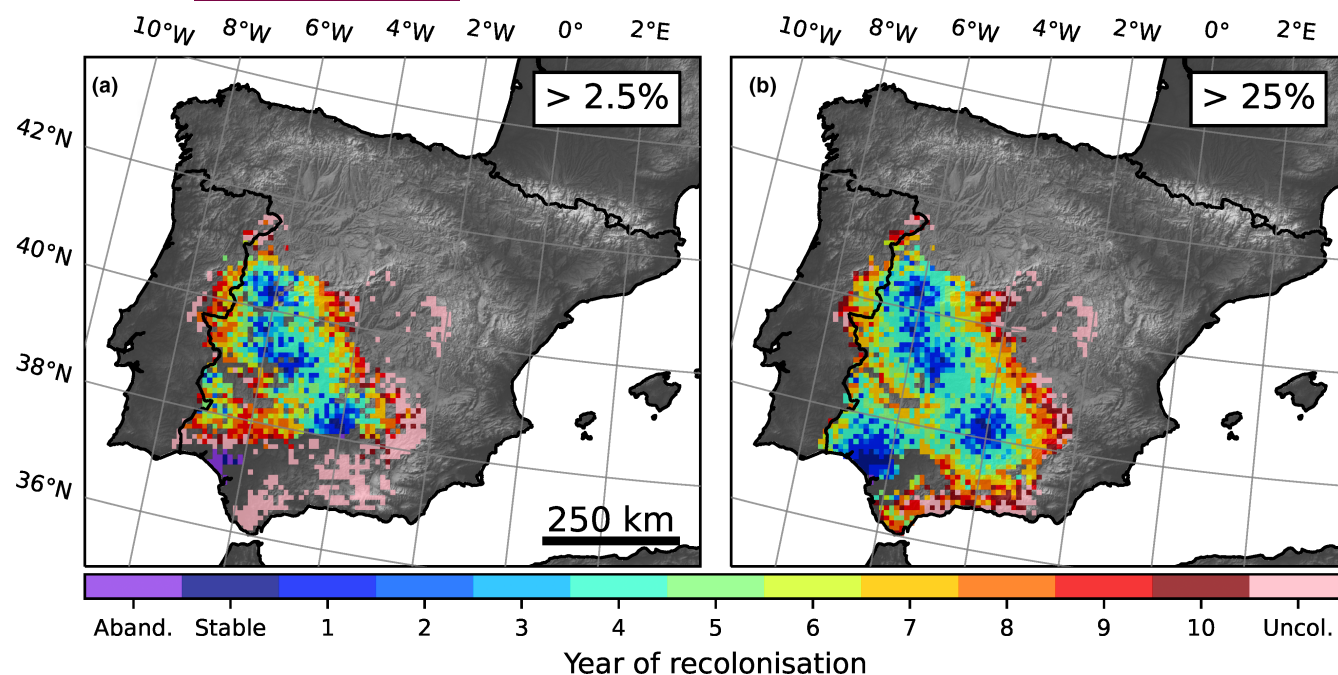


FIGURE 4 Simulated dispersal scenarios for the Iberian lynx under different barrier assumptions, (a) restrictive dispersal scenario based on 2.5% artificial surface cover threshold and (b) optimistic/low human-pressure dispersal scenario based on 25% artificial surface cover threshold. The artificial surface cover threshold indicates how much area can be covered by artificial surfaces before the cell is perceived as barrier to lynx dispersal.

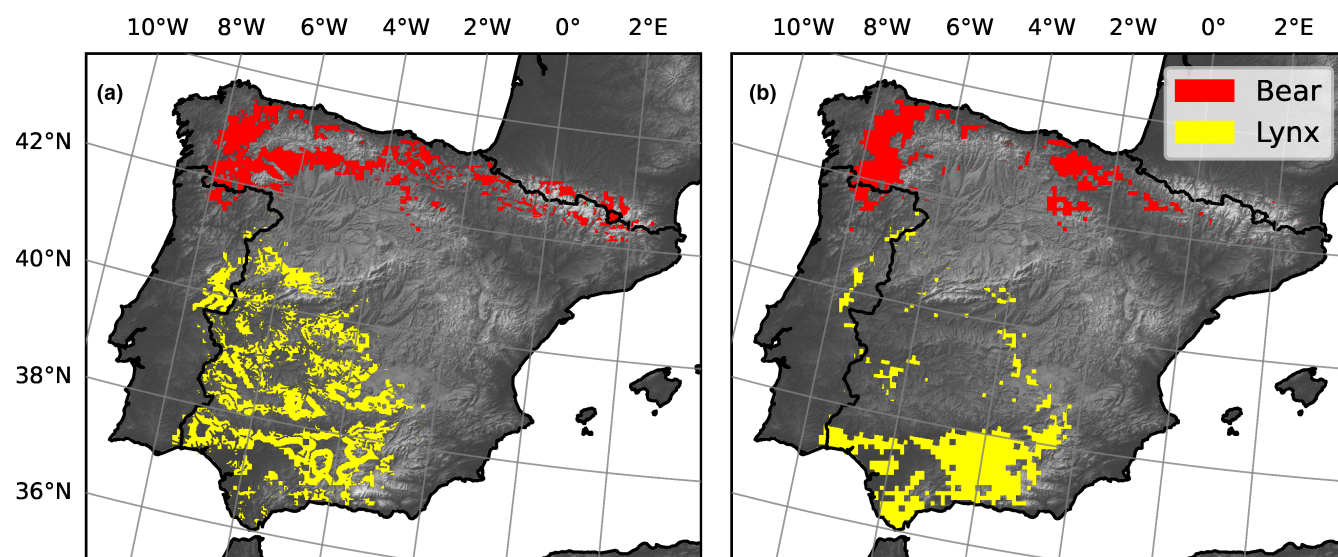


FIGURE 5 Priority areas for effective conservation planning for the brown bear (red) and Iberian lynx (yellow) showing (a) areas potentially important for protecting suitable habitat, meaning areas that are colonizable under the low human-pressure dispersal scenario (25% artificial surface cover threshold) and close to current Natura 2000 protected areas (within 50km for the bear, and within 15km for the lynx). And (b) areas where human pressure critically affects possibility of dispersal, meaning areas that are colonizable under the low human-pressure dispersal scenario but not under the restrictive dispersal scenario (2.5% artificial surface cover threshold).

Comparing potential range expansion scenarios of the network of protected areas showed, for the brown bear, that 41.90% of the current range and 30.19% of the most suitable potential habitat would fall inside Natura 2000 area. However, we found potentially important habitat areas for range expansion and for fostering connectivity between the Cantabrian and Pyrenean bear populations

that are currently unprotected (Figure 5). Our gap analyses highlighted habitat areas that could be colonized under our optimistic dispersal scenarios and close to current protected areas. These cells would be good candidates for the enlargement of protected areas. Furthermore, we identified areas where human pressure could hamper successful range expansion (Figure 5). These areas would

be priority areas for implementing measures to foster coexistence between brown bears and people and mitigation measures to lessen potential conflicts.

For the Iberian lynx, 19.27% of the current species range and 46.63% of the top suitable potential range are covered by the Natura 2000 network of protected areas. We found numerous cells likely to be colonized that are close to protected areas (Figure 5). These cells are candidate areas for increasing protection and fostering functional connectivity between current Iberian lynx populations. Finally, our simulations indicated that high values of human pressure would likely hamper colonization of critical habitat patches that connect the main Iberian lynx population in Sierra Morena with the Doñana population or with other multiple populations nuclei (Figure 5).

4 | DISCUSSION

Large carnivore populations are currently recolonizing their historical ranges in Europe after centuries of persecution and declining populations (Chapron et al., 2014). Understanding what determines range expansion patterns is key to ultimately foster coexistence between humans and large carnivores. Using the brown bear and the Iberian lynx as examples, we integrated land-use indicators, species distribution models and dispersal simulations in a simple and transferable approach. This allowed us to assess where and how fast these large carnivores might expand their ranges in the Iberian Peninsula and how varying levels of resistance due to human pressure might impact recolonization. Specifically, how different assumptions about how human pressure might hinder dispersal would impact this recolonization process. Our results show large areas of suitable habitat across the Iberian Peninsula that the brown bear and Iberian lynx could colonize. However, the direction and speed of range expansions will potentially be limited by high levels of human pressure in landscapes through which these species have to disperse. Comparing dispersal scenarios based on different levels of human pressure allowed us to highlight areas that are likely key for future population connectivity but where range expansion is uncertain. These areas constitute potential target sites for proactive conservation planning, such as establishing safe corridors, expanding protected areas or mitigating human–carnivore conflict, and thus benefit long-term large carnivore conservation in the Iberian Peninsula (Bautista et al., 2019). More generally, we showcase an assessment of recolonization potential that can be used for evidence-based and adaptive conservation planning.

Suitable areas for brown bears in the Iberian Peninsula in our analyses were concentrated in mountainous regions with low human impact. This matches previous evidence, where suitable habitat was found to be characterized by the same factor, suggesting bears make a trade-off between resource availability and security, avoiding human activity (Martin et al., 2012; Piédallu et al., 2019; Zarzo-Arias et al., 2019). Overall, we found large areas of suitable habitat that are unoccupied (42,400 km²) (Milanesi et al., 2017). Currently, less than half of these areas are protected, and our simulations suggested that

colonization of unoccupied, suitable patches will be hindered by dispersal limitations due to high levels of human pressure. In particular, critical areas for the connectivity between the Cantabrian and the Pyrenean bear populations show a very low colonization potential under the restrictive dispersal scenario. In addition to physical barriers (e.g. infrastructure), the suitable habitat for the brown bear is patchy and fragmented and interspersed with human-dominated landscapes. This results in closer proximity to humans and, therefore, a range of human pressures on dispersing brown bears, including conflict between bears and humans, especially where people have abandoned practices such as traditional stone walls and/or electric fences as prevention measures that have enabled coexistence in the past (Bautista et al., 2019; Penteriani et al., 2016; Recio et al., 2021). Developing appropriate strategies to minimize human pressure on bears, such as from poaching, retaliation killing or road traffic, in those areas that harbour suitable habitats but where dispersal is currently hampered (Figure 5) is key to ensuring long-term population viability for bears (Lischka et al., 2018; Lozano et al., 2019; Scharf & Fernández, 2018).

As in the case of brown bears, a potential range expansion by the Iberian lynx habitat was not so much limited by the amount of potential suitable habitat, but more so by dispersal limitations caused by high human pressure in the landscape (Blazquez-Cabrera et al., 2019). Our results highlight a large, continuous area of suitable habitat for the lynx in the southwestern part of the Iberian peninsula, overlapping with the species' historical range (Palomares, 2001). This area is characterized by Mediterranean scrub and woodlands (Fernández et al., 2006; Palomares, 2001) as well as anthropogenic landscapes (Garrote et al., 2020). Successful efforts to increase the Iberian lynx population, which grew from <100 individuals in the year 2000 to almost 1000 in 2020, have taken place there, particularly in Andujar-Cardena and Doñana, saving the species from extinction (Delibes et al., 2000; Simon et al., 2012). Likewise, recent reintroductions have taken place in this part of the Iberian Peninsula, expanding the lynx range area with new populations nuclei (Simón, 2017). Our analyses of further potential habitat areas and dispersal potential can guide such conservation efforts, particularly those targeted at ensuring natural colonization of the historical range of Iberian lynx (e.g. the Life+ project LYNXCONNECT).

However, our dispersal simulations assuming different levels of human pressure will inhibit or allow for safe dispersal of large carnivores also showed that the Iberian lynx is unlikely to colonize several large patches of suitable habitat. Mortality is high in dispersing individuals, primarily through poaching and road accidents (Delibes et al., 2000; Garrote et al., 2018; Rodríguez & Delibes, 2004). Conservation programmes carried out during the last decade have reduced non-natural mortality by implementing numerous prevention measures, such as compensating losses or the installation of electric fences (Garrote et al., 2013; Simon et al., 2012). While lynx might be able to expand without such measures in place, conservation measures will make dispersal more likely, mainly if they help to create safe habitat patches that function as stepping stones (Blazquez-Cabrera et al., 2019).

This is particularly important in the context of conflicts related to predation on livestock by the Iberian lynx (Garrote et al., 2013). While conflict is currently uncommon, an expanding and growing lynx population will likely be connected to higher levels of conflict, which can undermine conservation success (Bautista et al., 2019). Previous quantitative estimates of extinction risk for the Iberian lynx population showed that long-term population viability strongly depends on conservation interventions at multiple scales (Fordham et al., 2013). Our broad-scale assessment highlights specific areas where such interventions will improve functional connectivity between Iberian lynx nuclei, making a contribution towards the viability of the global population.

Our models performed well and resulted in highly plausible predictions that converge well with prior work (Chapron et al., 2014; Cimatti et al., 2021; Garrote et al., 2020; Palomares et al., 2011) as well as historical range estimations (Clevenger et al., 1987; Gil-Sánchez & McCain, 2011; Rodríguez & Delibes, 1992). Still, a few limitations need mentioning. First, we did not consider fine-scaled processes, such as individual landscape features and or individuals' behaviour, which can play an important role in carnivore habitat selection and movement (Blazquez-Cabrera et al., 2016; Martin et al., 2012; Piédallu et al., 2019; Recio et al., 2021; Zarzo-Arias et al., 2019). For example, GPS tracking data can yield realistic movement estimates (Blazquez-Cabrera et al., 2016; Recio et al., 2021). Yet, more fine-scaled movement analyses are unlikely to alter the broad-scale patterns we found. Second, our dispersal scenarios could be further ecologically more refined by considering processes and factors such as demography or food resource availability (Chapron et al., 2014). For example, mapping food resources, such as rabbit distributions for the Iberian lynx, could refine our habitat selection models (Real et al., 2009; Zarzo-Arias et al., 2019). Third, we proxy human pressure, and its effect on enabling or hindering dispersal, through the level of human landscape modification. More detailed, social-ecological assessments could map people's attitudes towards and tolerance of carnivores (Behr et al., 2017), which could help to more directly map anthropogenic resistance in the landscape (Ghoddousi et al., 2021). Similarly, incorporating land-use change projections could assess how anthropogenic resistance changes with continued land abandonment and the decline of the rural population (Pereira & Navarro, 2015). Finally, fully assessing population viability will require incorporation of additional demographic processes within spatially explicit population or individual-based models (Zurell et al., 2022). Importantly, all of this could easily be incorporated into our framework once sufficient data become available.

More generally, our results provide guidance for large carnivore conservation planning to promote large carnivores' range expansion. By coupling species distribution models with different dispersal scenarios, we highlight that the ability of large carnivores to colonize and ultimately coexist with people in shared landscapes is likely most constrained by human pressure and their impact on dispersal behaviour and not by available habitat (Recio et al., 2021; Tucker et al., 2018).

This situation is likely emblematic for many human-dominated landscapes across the world. Likewise, although the protected area network in the case of Iberian carnivores partly overlaps with current and potential suitable habitat, potentially critical stepping stones for dispersing individuals remain often unprotected. Most of the protected area network in our case was designed prior to the recent range expansion of these species (Evans, 2012), and successful large carnivore conservation will benefit from a flexible, adaptive protected areas network that incorporates species range dynamics in response to varying human pressures and climate change (Santini et al., 2016). Our results provide a step towards such an adaptive conservation planning approach, as we highlight suitable, unprotected areas close to current Natura 2000 protected areas as candidates to expand protection (Figure 5). Importantly though, protected areas cannot sustain large carnivores populations by themselves (Santini et al., 2016; Woodroffe & Ginsberg, 1998). Conservation efforts thus require a social-ecological view that acknowledges that human aspects are likely the most critical determinant of carnivore distribution in anthropogenic landscapes (Kuijper et al., 2016).

We showed how integrating species distribution models with dispersal scenarios can provide important insights into potential range expansion and recolonization patterns of large carnivores. Our simple approach, which can be easily updated and transferred to other geographies and species, can therefore help devise long-term conservation plans that include recovering population connectivity and metapopulation dynamics (Boitani & Linnell, 2015). In order to achieve these conservation goals, proactive conservation interventions are needed (e.g. protecting livestock and preparing society for the return of the large carnivores; López-Bao, Frank, et al., 2017), and our analyses provide a top-down view of where such conservation actions are potentially most relevant to facilitate the return and persistence of large carnivores in human-dominated landscapes.

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CONFLICT OF INTEREST

The authors declared no conflict of interest for this article.

DATA AVAILABILITY STATEMENT

Code and data sets used are available on GitHub (https://github.com/leonsnill/iberian_conservation.git).

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BIOSKETCH

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SUPPORTING INFORMATION

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