Adapted conservation measures are required to save the Iberian lynx in a changing climate

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The Iberian lynx (*Lynx pardinus*) has suffered severe population declines in the twentieth century and is now on the brink of extinction[1]. Climate change could further threaten the survival of the species[2], but its forecast effects are being neglected in recovery plans[3,4]. Quantitative estimates of extinction risk under climate change have so far mostly relied on inferences from correlative projections of species' habitat shifts[5]. Here we use ecological niche models coupled to metapopulation simulations with source–sink dynamics[6,7] to directly investigate the combined effects of climate change, prey availability and management intervention on the persistence of the Iberian lynx. Our approach is unique in that it explicitly models dynamic bi-trophic species interactions in a climate change setting. We show that anticipated climate change will rapidly and severely decrease lynx abundance and probably lead to its extinction in the wild within 50 years, even with strong global efforts to mitigate greenhouse gas emissions. In stark contrast, we also show that a carefully planned reintroduction programme, accounting for the effects of climate change, prey abundance and habitat connectivity, could avert extinction of the lynx this century. Our results demonstrate, for the first time, why considering prey availability, climate change and their interaction in models is important when designing policies to prevent future biodiversity loss.

The Iberian lynx is the world's most endangered cat. Its range contracted from 40,600 km² in the 1950s to 1,200 km² in 2005[1,8]. Recent counts estimate only 250 Iberian lynx in the wild[4]. This major decline is associated closely with sharp reductions in European rabbit (*Oryctolagus cuniculus*) abundance[8], caused by myxomatosis virus in the 1950s and, more recently, rabbit haemorrhagic disease[9] (RHD). Over-hunting of rabbits and the modification and fragmentation of its mixed grassland and forest habitat has exacerbated the problems of prey scarcity, because rabbits account for more than 80% of Iberian lynx consumption[10]. Non-natural mortality of Iberian lynx, such as trapping, poaching and road kills, have further reduced lynx population numbers[11]. Only two Iberian lynx populations persist in the wild at present compared with nine in the 1990s[1].

Ex situ captive breeding programmes have been launched to facilitate the reintroduction of a genetically diverse pool of Iberian lynx into suitable areas within their historical range[12]. Simultaneously, management effort is being directed

towards increasing the carrying capacity of reintroduction sites through habitat restoration, relocating rabbits and limiting direct anthropogenic-related fatalities[4,13]. Although a well-financed effort to avert the extinction of this charismatic species is underway (> €94 million funding since 1994)[4], non-accounted threats, such as climate change and its influence on prey abundance, are not being considered in recovery plans.

Here we provide the most comprehensive analysis of the likely effects of climate change yet for a threatened vertebrate. So far, models used to investigate how climate change will
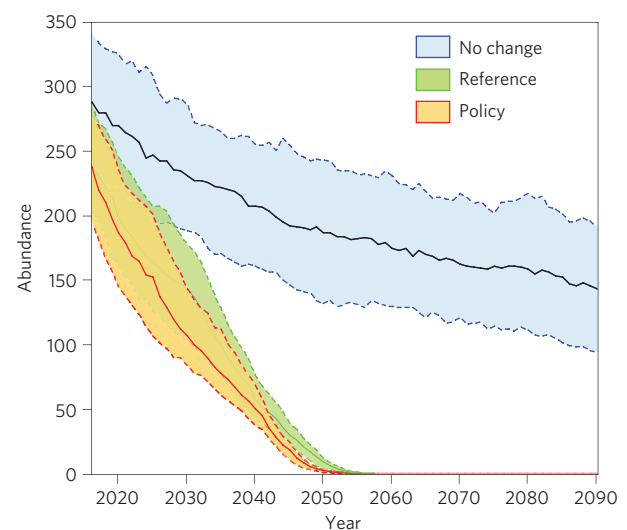
Figure 1 | Forecast lynx abundance in the Iberian Peninsula from 2015 to 2090 under three climate change scenarios. Scenarios are: no climate change—where temperature and precipitation remains unchanged from the year 2000; high CO_2 concentration Reference scenario (WRE750); and an alternative low CO_2 concentration Policy scenario that assumes strong mitigation of greenhouse gas emissions (LEV1). The solid lines show mean estimates for each scenario. Band widths represent 5th and 95th percentiles of population size derived from a stochastic metapopulation model with spatial habitat dynamics. Model variation characterizes demographic stochasticity, which is only one component of model uncertainty (see Supplementary Methods).

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Table 1 | Extinction risk for the endangered Iberian lynx in the twenty-first century according to different climate and conservation scenarios.
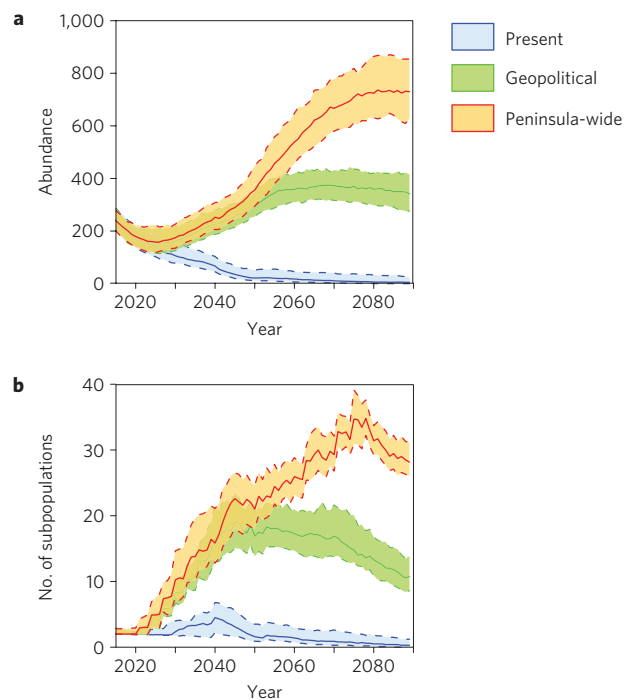
Conservation scenario	Climate scenario	EMA	Probability of extinction	Median time to extinction
No extra manag.	No change	58	12	—
	Policy	0	100	2051
	Reference	0	100	2054
Extra manag.	Policy	3	89	2066
	Reference	3	86	2065
Geopolitical	Policy	52	2	—
	Reference	52	4	—
Peninsula-wide	Policy	68	0	—
	Reference	78	1	—

Climate scenarios are a 'No change scenario' where temperature and precipitation remains unchanged from the year 2000, a stabilizing Policy scenario that assumes substantive mitigation of greenhouse gas emissions and a high CO_2 concentration Reference scenario. Conservation scenarios are: no additional management intervention beyond what is occurring in Doñana and Sierra Morena (No extra manag.); an increase in active population management in potentially suitable habitat patches across the Iberian peninsula (Extra manag.); moving animals with an underlying aim to establish viable lynx breeding populations in every autonomous region within its recent historical range (Geopolitical); moving animals to areas of most favourable habitat across the entire Iberian peninsula (Peninsula-wide). Extinction risk during this century is measured using expected minimum abundance (EMA), probability (%) of total population size declining to zero (Probability of extinction) and median time to extinction (Median time to extinction).

Figure 2 | The effect of management intervention on the persistence of Iberian lynx. a,b, Forecast lynx abundance (**a**) and number of populations (**b**) in the Iberian Peninsula from 2015 to 2090 according to three possible management options. Forecasts are for a Policy climate scenario that assumes strong mitigation of greenhouse gas emissions (LEV1). The interventions are: present-day conservation practices, including increasing prey (lagomorph) densities, habitat alteration, preventing disease and non-natural mortality (Present); reintroducing captive-bred lynx to unoccupied habitat according to a Geopolitical scheme that favours establishing lynx populations in every autonomous region in Spain (Andalucía, Castilla-La Mancha, Comunidad Valenciana, Extremadura and Murcia), plus Portugal as an additional region, within its recent historical range (Geopolitical); and a strategy focused on releasing animals into the best-quality habitat regardless of region (Peninsula-wide). The solid lines show mean estimates for each scenario. Band widths represent 5th and 95th percentiles, and characterize variation due to demographic stochasticity. They do not include error propagating from uncertainties in demographic parameters or forecasts of climate suitability (see Supplementary Methods).

affect biodiversity at broader geographical scales have failed to account explicitly for dynamic feedbacks of species interactions[14]. We address this key limitation using coupled ecological niche–population models with source–sink dynamics[6,7], simulating the stochastic demographic responses of Iberian lynx to: spatial patterns of rabbit abundance conditioned by disease, climate and land-use variation; and changes in climate suitability and landscape modification. We consider the interaction between rabbits and Iberian lynx as unidirectional, because lynx are extremely rare, whereas rabbits are abundant and have greater than 30 vertebrate predators, many of them widely distributed and locally abundant[15]. Rare efforts to account for species interactions in climate–ecological forecasts have used overly simple approaches; by adding an interacting species as an additional predictor in a correlative model, or by restricting the distribution of one species to the modelled distribution of the other[16]. Here we directly account for important per capita effects of rabbit abundance on the population growth rate of Iberian lynx in a climate change setting.

We show that climate change is predicted to have a rapid and severe negative influence on Iberian lynx abundance (Fig. 1), exceeding its ability to adapt or disperse to more climatically favourable regions where prey densities are sufficient to support viable populations. We estimate time to extinction to be less than 50 years (Table 1), even with rapid and deep global cuts to anthropogenic greenhouse gas emissions (for instance, stabilization at an equivalent CO_2 concentration of 450 ppm (MiniCAM LEV1; ref. 17)). We forecast that population decline will occur at a slightly faster rate under a strong mitigation emission Policy scenario (Fig. 1), causing a slightly shorter median time to extinction (2051 compared to 2054 under the Reference scenario; Table 1). This apparently counter-intuitive result is because coal-fired power stations also produce atmospheric aerosols that suppress global temperatures through dimming[18]. Replacing coal combustion with cleaner energy alternatives results in conditions that are initially more adverse (warmer and drier before 2050) for Iberian lynx and rabbits under the Policy scenario compared with a high-CO_2 concentration Reference scenario (WRE750; ref. 19).

In trying to avert extinctions in the wild, managers have long considered the use of human-assisted colonization of individuals

to more suitable habitat[20]. However, as a climate adaptation strategy for Iberian lynx, such action has been criticized as inadequate if important factors relating to prey and habitat availability are ignored[21]. To avoid this simplification, we simulated a reintroduction scheme that accounted simultaneously for the velocity, extent and nonlinearities in rates of climate-induced change in habitat quality and the connectivity, prey availability and physiological conditions important to Iberian lynx. We show that a yearly release of six animals (aged between 1 and 4 years) of each sex into habitat patches ranked according to a combination of carrying capacity, initial population size, connectivity and rate of survival and fecundity, would avert the likely extinction of Iberian lynx this century (Fig. 2 and Table 1 and Supplementary Fig. S1). This reintroduction number is lower than that considered under the Iberian lynx reintroduction plan (release of 20–40 animals per year) and would not jeopardize the persistence of the breeding population (see Supplementary Methods).

In contrast, we show that implementing present-day conservation practices (increasing prey densities, habitat management, preventing disease and non-natural mortality[1,4]) at a regional level
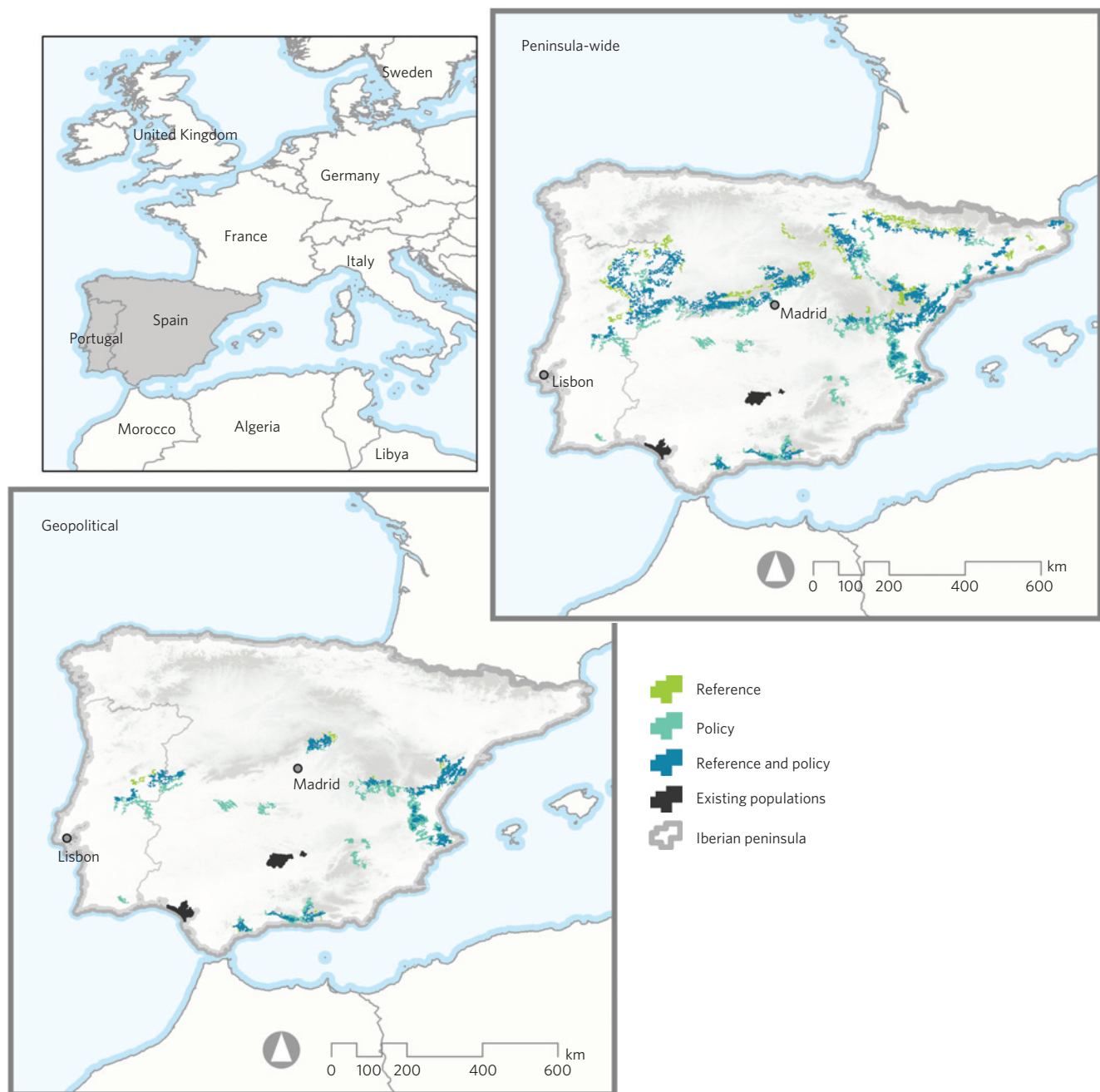
Figure 3 | Forecast location of lynx populations in the Iberian Peninsula in 2090. Occupied habitats are shown for the Peninsula-wide and Geopolitical reintroduction scenarios and two climate change scenarios: a high-CO_2 concentration stabilizing Reference scenario (WRE750) and an alternative Policy scenario that assumes strong mitigation (LEV1). Maps capture lynx demographic responses to spatial patterns of rabbit abundance (conditioned by disease, climate and environmental variation) and changes in climate suitability and landscape modification. Only grid cells where lynx were present in 90% of stochastic iterations of the demographic model were treated as populated. See Supplementary Information and Methods for further details.

would only serve to delay median time to extinction by <15years, irrespective of climate policy (Table 1). This is primarily because extensive clearing and destruction of natural habitats by humans has disrupted processes that underpin Iberian lynx dispersal and establishment. We predict that >40 discrete areas of suitable habitat would be available for potential colonization in 2050, but in the absence of managed reintroductions most of these would remain unoccupied because of limited connectivity caused by human modification of the landscape.

Policymakers are considering the feasibility of establishing viable Iberian lynx breeding populations in every autonomous region within its recent historical range[22]. We show, however, that

constraining reintroductions to only those suitable patches within the recent historical range of Iberian lynx (Supplementary Fig. S2), and spreading animals evenly across autonomous regions using a Geopolitical reintroduction strategy, results in fewer Iberian lynx living in fewer populations in the future compared with a Peninsula-wide reintroduction strategy, whereby animals are released into the best-quality habitat regardless of region (Fig. 2 and Supplementary Fig. S1). We predict final population size in 2090 to be between 190 and 275 animals (5th and 95th percentiles, respectively), approximately the same as today's population size[4], living in 7–10 subpopulations for the Geopolitical reintroduction strategy, compared with 654–896 animals living in 25–31 subpopulations

for the Peninsula-wide strategy. Uncertainties in these estimates are due to demographic variation, driven by multiple stochastic runs of the metapopulation model and the coupled dynamics of the rabbit–lynx bi-trophic interaction. They do not include error propagating from uncertainties in demographic parameters or forecasts of climate suitability (see Supplementary Methods for a detailed description of model uncertainty). The reason for this large difference is that the Peninsula-wide strategy considers habitats in the northern half of Iberia as potential refugia from climate-induced shifts in physiological conditions, rabbit abundance and habitat availability (Fig. 3 and Supplementary Fig. S3). However, even then, a negative imbalance between the rate of establishment of new potential relocation sites and the extirpation of old is expected to occur for the Peninsula-wide strategy after 2065 (Fig. 2). Thus, in the future, managers might need to consider moving Iberian lynx beyond their Pleistocene refugia (where they evolved[23]), to other parts of Europe, where the biophysical characteristics of the new location better match the needs of the species and its staple prey[24]. For example, fossil data show that the Iberian lynx or its near relatives were distributed in southeastern France in the Pleistocene[8].

Another potential management option is to improve the quality, connectivity and permeability (of the non-habitat landscape matrix) of Iberian lynx's present and future habitats, by developing habitat corridors along climate pathways[25]. However, the immediacy of the climate threat faced by Iberian lynx (high probability of extinction in the wild within the next 50 years; Fig. 1), paired with both the tremendous cost associated with establishing large-scale movement corridors[26] and the technical feasibility of translocating Iberian lynx[4], implies strongly that the dispersal processes that have been disrupted by loss of habitat connectivity can be most cost-effectively and quickly restored using carefully managed reintroductions, not corridors[24].

Our results suggest that Iberian lynx abundance is declining (Fig. 1, see also ref. 1). However, lynx abundance at Doñana and Sierra Morena (the two extant populations) may have increased in recent years in response to intensive management operations[4]. Recent conservation measures have included efforts to decrease anthropogenic mortality among dispersing Iberian lynx and broker conservation agreements with private landholders[4], two management actions not fully captured in our models, both of which could potentially influence trajectories of population growth in the absence of global warming. Our systematic sensitivity analysis (see Supplementary Information), which identified primary sources of demographic parameter uncertainty in model predictions, supports this premise. Although our forecast final mean and expected minimum abundance estimates for Iberian lynx proved to be most sensitive to the frequency of outbreaks of feline leukaemia virus (see Supplementary Methods), lynx survival (aged ≥2 years) was the second most important parameter in the model (Supplementary Table S1). Although it remains unclear whether management intervention in the two extant populations of Iberian lynx in Doñana and Sierra Morena is definitely reversing population declines[1,4,22], present-day efforts will be insufficient for achieving the long-term conservation of Iberian lynx. Our dynamic metapopulation model results clearly show that habitat connectivity today is inadequate to support sufficient range movement for an effective natural-adaptation response to the velocity of environmental change forecast for Iberian lynx this century. Refining field estimates of Iberian lynx survival will strengthen model precision and should be a priority for future Iberian lynx research.

The risk of extinction faced by Iberian lynx within the next 50 years is high. Although existing breeding programmes and reintroduction plans promote the persistence of Iberian lynx (at least in the near term), we have demonstrated that the implementation of a carefully planned relocation strategy,

accounting simultaneously for the effects of climate change, prey availability conditioned by disease, and habitat connectivity, will be crucial, irrespective of any global decision on mitigating greenhouse gas emissions.

Methods

We used coupled niche–population models[7] to simultaneously model Iberian lynx and European rabbit range dynamics and climate change. We generated an annual time series of climate change layers for annual rainfall and mean temperature of the hottest and coolest months for the period 2000–2100 using regionally skilful ensemble-averaged climate forecasts[27]. Occurrence records (since 1950) were used to fit ecological niche models (ENMs) separately for the Iberian lynx and European rabbit. Models were parameterized to represent present climatic–habitat preferences and to forecast potential future distributions. The rationale is that ENM-modelled suitability provides a surrogate for species' carrying capacity[28], capturing more than the physiological constraints that define presence/absence at a given location, which can then be used in demographic models[7]. As projections from alternative ENMs can vary substantially under the same climate change scenario, we computed seven different ENM approaches (BIOCLIM, Mahalanobis and Euclidean distances, generalized linear models, random forest, maximum entropy and GARP) and obtained a consensus forecast by assigning equal weights to a subset of skilful methods. We separately identified CORINE land-use categories (centred on the year 2000) appropriate for breeding habitat for Iberian lynx and rabbit occupancy (Supplementary Tables S2 and S3). As land-use modification has left a strong historical legacy on the distribution of Iberian lynx and rabbits[8], this information was used to constrain the suitability of ENM predictions, both for the present-day and future[29]. Our projections assume that lynx and rabbits will conserve their climatic–habitat preferences in the future and that land-use remains spatially constant.

We built a demographic projection for rabbits with a grid-based spatial structure, whereby each grid cell was modelled with its own scalar–stochastic model. The carrying capacity of rabbits in each cell was based on ENM predictions, scaled by the maximum and minimum recorded annual rabbit abundance per hectare. The impact of myxomatosis on rabbit abundance was modelled implicitly, whereas the impact of RHD was modelled explicitly. Diseases were modelled as temporally uncorrelated and non-interactive, because empirical data directly describing disease interactions and their effects on rabbit vital rates across a wide spectrum of rabbit densities are not available. To account for uncertainty in RHD estimates, 100 rabbit models were built, each with different grid cell frequencies of RHD occurrence and severity (sampled from within the likely upper and lower parameter bounds), and run for a single iteration under both a Reference and Policy CO_2 concentration scenario; and a no-climate change scenario, where temperature and precipitation remained unchanged from the year 2000. Using these outputs, we then mapped rabbit density each year (2000–2100) for each model, capturing stochasticity in interactions between rabbit demography, disease and source–sink dynamics.

Following the rabbit modelling step, we built spatially structured metapopulation models for the Iberian lynx, where each subpopulation was represented with a sex-structured, stage-structured, stochastic model. The size and location of subpopulations was generated using ENM predictions, forecast spatial patterns of rabbit abundance (see previous step) and an estimate of on-ground management effort. The density-dependence sub-model accounted for individuals with and without territories and modified survival and fecundity as functions of rabbit and lynx density. Populations located outside protected areas were modelled with an additional 10% fixed increase in mortality. Dispersal accounted for the interaction between movement rates and land cover. We modelled the probability of an outbreak of feline leukaemia virus as a per-population catastrophe.

Using a single-population lynx model, we calculated a sustainable number of young animals (aged between 1 and 4 years) that could be removed annually from a captive breeding population of 60 lynx. We evaluated and ranked which patches to release Iberian lynx into on the basis of a composite metric that accounted for important ecological processes. Reintroductions were spread, where possible, evenly across autonomous regions (Supplementary Fig. S2) for the Geopolitical strategy—targeting the most suitable patch of habitat in each of two autonomous regions, for three consecutive years, whereas for the Peninsula-wide strategy, the two best ranked habitats were used regardless of provincial location. Vulnerability of lynx during the 80-year interval 2010 and 2090 was measured using expected minimum abundance, probability of total population size declining to zero and median time to extinction for persistent model runs. Annual average abundance and metapopulation patch occupancy were also used to provide a measure of population stability.

The level of the complexity in the rabbit and Iberian lynx models reflected a balance between the need for management actions to be based on realistic models that do not exclude major biological processes, and making the model as robust as possible to underlying uncertainties. Bayesian approaches can be used to explore model error in niche–population models[30]; however, using them to propagate uncertainty in complex models, such as the Iberian lynx model, would be computationally demanding. Furthermore, independent evaluation

of such models is extremely difficult[7] and is beyond the scope of this study. We report uncertainties in Iberian lynx abundance derived from the internal dynamics of the stochastic population model and the coupled dynamics of the rabbit–lynx relationship. We used sensitivity analysis to determine how the rabbit model was sensitive to assumptions surrounding disease, carrying capacity and population growth rates; and whether assumptions surrounding spatial and/or non-spatial demographic parameters largely influenced our lynx model. A more detailed explanation and justification of data and methods is given in the Supplementary Methods.

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Author contributions

The design of this project was the result of discussions involving all authors. M.B.A generated the ENMs. D.A.F., H.R.A., A.R., P.C.A, E.C. and M.T. coupled the ENMs to metapopulation simulations. D.A.F., H.R.A., B.W.B. and M.J.W. performed the analysis. D.A.F. and M.B.A. wrote the initial draft of the manuscript; and all authors contributed to the writing of the final version of the paper. All authors discussed the results and commented on the manuscript.

Additional information

Supplementary information is available in the online version of the paper. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to M.B.A.

Competing financial interests

The authors declare no competing financial interests.