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Research article

Exploring the ecological feasibility of restoring Eurasian lynx to Great Britain using spatially explicit individual-based modelling

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ABSTRACT

Ecological restoration offers a multitude of benefits for the human-nature system, which has put it at the forefront of international initiatives opposing environmental degradation. In Great Britain, the reintroduction of Eurasian lynx has been proposed to help improve ecosystem health, raising the question; what is the ecological feasibility of lynx reintroduction in Great Britain? Combining a lynx-specific spatially explicit individual-based model and contemporary habitat suitability mapping would shed new light on this question. We hypothesised potential drivers of reintroduction success, including demographic parameters, behavioural responses in habitat selection, and management strategies. We further hypothesised that reintroductions may not be viable in some regions, therefore, we considered scenarios with improved habitat to understand the potential effect of national habitat creation policies. We aimed to provide evidence on practical and ecological conditions necessary for successful reintroduction to support stakeholder discussions. We found that the release site was critical to ensure low extinction probability and advantageous population expansion for demographic viability and maintenance of neutral genetic diversity. Specifically, Aberdeenshire, Galloway, and Kielder Forest had robust reintroduction success under diverse conditions, even without the hypothesised habitat improvements. Our simulations suggested a population of 240 individuals could emerge from a release in Aberdeenshire and population of 60 individuals from a release in either Kielder Forest or Galloway, all with allelic richness >2 and extinction probabilities ≤5 %. Our work suggests a well-planned, legal, lynx reintroduction in Great Britain could be feasible, provided there is acceptance in key stakeholder groups.

1. Introduction

The impacts of human activities on nature and the environment threatens ecosystems globally (Sage, 2020). The interdependency between nature and humans means natural ecosystems are also vital for human existence due to their provisioning of essential functions such as carbon sequestration, soil fertility, and pollination (Daily, 1997). Further, physical and psychological connections to nature nurture a sense of place (Hausmann et al., 2016) and have positive effects on human well-being (Bratman et al., 2019).

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Proper ecosystem functioning depends on biodiversity (Tilman et al., 2014), which is being eroded. Therefore, the international community has made maintaining biodiversity and ecosystem services key policy goals (IPBES, 2019). Protecting intact ecosystems might not be sufficient to achieve these goals, not least because natural ecosystems are disappearing in many areas (e.g., Potapov et al., 2017). Ecosystem restoration could help nature to recover and thereby revitalise ecosystems' functioning (Rey Benayas et al., 2009). Hence, the United Nations declared 2020 to 2030 "the decade of Ecological Restoration", intending to foster a restorative culture between humans and nature to combat climate change and biodiversity loss (United Nations Environment Agency, 2019). Reintroductions are an important consideration for ecosystem restoration, especially when key functional roles are missing (Lipsey et al., 2007).

Apex predators, like large carnivores, play an important role in healthy and resilient ecosystems by regulating prey populations (Ripple et al., 2014). Following local extinctions, large carnivores are reoccupying parts of their former ranges (Ripple et al., 2014). In Europe, this is attributed to public support, legal protection, and reintroductions (Chapron et al., 2014). Reintroductions are variously viewed as a moral duty to reverse the human-caused extirpations (Bavin et al., 2023), a legal obligation (Rees, 2001), or an opportunity to reconnect humans to nature (Palacios-Pacheco et al., 2024). Indeed, large carnivores are charismatic species, symbolic of ecosystem restoration, that can attract attention and support for conservation and restoration of nature more broadly (Meffe and Carroll, 1997; Lipsey et al., 2007). Large carnivore reintroduction is, therefore, a logical consideration to expediate ecological restoration.

While wolves (*Canis lupus*) have naturally recolonised swathes of Europe's human-dominated landscapes (e.g., Fabbri et al., 2007), Eurasian lynx (*Lynx lynx*, hereafter lynx) require translocations (Linnell et al., 2009). Lynx reintroductions have taken place across Europe from the 1970s (Linnell et al., 2009) to the present (Lynx Thuringia, 2024; Project RELynx, 2024). While lynx could theoretically recolonise continental Europe naturally, reestablishing a lynx population in the islands of Great Britain and Ireland is only possible with human intervention.

The UK and Scottish governments recently set targets to improve the poor status of habitats and biodiversity in Great Britain (Department for Environment, Food & Rural Affairs, 2018; Scottish Government, 2020), including habitat creation and species recovery. However, missing species and trophic levels precludes realisation of intact, functioning ecosystems (Hudson et al., 2017; Burns et al., 2023). Species reintroductions could be a step toward restoration of ecosystems in Great Britain (e.g., Hooker et al., 2024), especially for the absent functional roles of terrestrial carnivores, such as lynx. This has made potential lynx reintroductions in Great Britain an increasingly salient topic of discussion (Hawkins et al., 2020; Wilson and Campera, 2024) and ecological research.

Several viability assessments of potential lynx reintroduction in Great Britain have been put forward. First, population size estimates were made based on occurrence of lynx's main prey in Europe, roe deer (*Capreolus capreolus*) (Kitchener, 2001). Subsequently, the relationship between lynx and prey density from European lynx populations was used to estimate potential lynx densities (Hetherington and Gorman, 2007). However, these estimates did not consider habitat suitability for lynx nor demography. Habitat suitability and landscape connectivity was considered later using a rule-based approach. Hetherington et al. (2008) identified two habitat networks: one in the Scottish Highlands and a second in the Southern Uplands of Scotland and Kielder in northern England, but the connectivity between them was poor due to the densely populated area in Central Scotland. Later, Johnson and Greenwood (2020) used a comparable approach for England, Wales, and southern Scotland. However, these investigations relied on expert knowledge to assess habitat suitability, which may not capture important nuances in landscape composition, and did not consider how the spatial arrangement of habitat can affect lynx behaviour and demographics (Kramer-Schadt et al., 2005).

Ovenden et al. (2019) used a spatially explicit individual-based model (seIBM) to investigate the viability of lynx reintroductions in Scotland. seIBMs can incorporate demographics with spatial behaviour and life history by modelling the processes at an individual level (Grimm and Railsback, 2013). Thereby, population dynamics (e.g., population size, growth rate) emerge from individual-level decision-making (DeAngelis and Grimm, 2014). Ovenden et al. (2019) found a reintroduction was only viable with simultaneous releases in Kintyre and Aberdeenshire. However, they also used a rule-based habitat map. Furthermore, all the existing investigations were limited spatially by political boundaries, and none considered the relationship between genetic diversity and long-term population viability, nor specifics of lynx's spatial behaviour (e.g., movement, territorialism), which can impact the assessments (detailed commentary, Appendix A).

Habitat modelling techniques have developed beyond those used in earlier assessments; therefore, a data-driven habitat suitability map would be a valuable step to improve the understanding of potential reintroduction success. Recently, an extensive GPS and VHF tracking dataset was used to develop a Europe-wide habitat suitability map that addresses this gap (Oeser et al., 2023a). Further, a lynx-specific spatially explicit individual-based model (seIBM) developed to answer conservation questions (Kramer-Schadt et al., 2005) was extended to include inheritance of neutral genetic markers (Premier et al., 2020), thereby allowing investigation of both demographic and genetic (i.e., demogenetic) dynamics (e.g., population size, allelic richness), which are crucial for the viability of real populations. Using this demogenetic seIBM in conjunction with the objective habitat suitability map would improve insights into potential lynx reintroduction in Great Britain.

Our research was framed by the question, what is the ecological feasibility of lynx reintroduction in Great Britain? We hypothesised that demographics, behavioural responses in habitat selection, and management choices could affect reintroduction success. Additionally, we hypothesised that reintroduction may not be currently viable in some regions due to unsuitable habitat conditions. By exploring the drivers of reintroduction success, using a lynx-specific seIBM and based on up to date methods and data, we aimed to provide objective evidence on the most important ecological and practical conditions needed for lynx reintroduction to succeed, which can support engagement with diverse stakeholders.

2. Methods

2.1. Research framework

Our research framework (Fig. 1) was developed to answer the question: what is the ecological feasibility of lynx reintroduction in Great Britain? Based on the hypothesised drivers, we predicted different demographic rates (P1: reproductive rates and cause-specific mortality rates – section 2.2.1), habitat selection behaviours (P2: territory size and suitability – section 2.2.2), and release conditions (P3: sites, timing, number, sex ratio, and source population genetics – section 2.2.3), would alter the likelihood a population of sufficient size and genetic diversity would persist 100 years after release. Additionally, we predicted that reintroduction success may not be viable in some regions under current habitat conditions but might be possible if national habitat creation goals are achieved (P4 – section 2.2.2.3). No empirical data exists for lynx in Great Britain, therefore, we selected ranges (including low, medium, and high values) from datasets collected in European populations to test our predictions (Table 1).

We tested these predictions by simulating scenarios composed of combinations of their respective values using a lynx-specific seIBM (section 2.3). Scenarios were divided into three sets, namely: set A – exploration of demographic (P1) and habitat response (P2) parameter space for single release sites, set B – focussed on the comparison of status quo and green future habitat scenarios for single release sites (P4), and

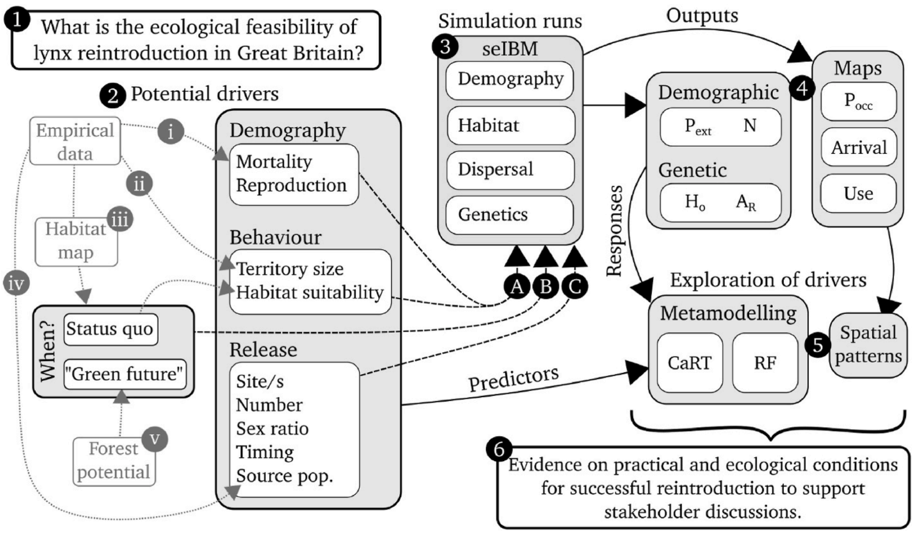

Fig. 1. Research framework diagram. (1) Main research question. (2) potential drivers of success including demographic parameters (P1, section 2.2.1), behavioural responses in habitat selection (P2, section 2.2.2), habitat conditions today (status quo) and an alternative following habitat creation ("green future") (P4, section 2.2.2.3), and management choices for release (P3, section 2.2.3). (3) The potential drivers were used as scenarios divided into three sets (A, B, C – section 2.1) for simulation runs using a lynx-specific seIBM (section 2.3). (4) Simulation outputs included demographic and genetic parameters, as well as spatially explicit metrics to aid interpretation (section 2.4). (5) The simulation inputs and outputs were analysed in metamodels to explore the drivers of reintroduction success and contextualised with the mapped metrics (section 2.5). (6) The results were synthesised to fulfil our research goal (sections 3–5). Empirical data were used in: (i) demographic rates, (ii) territory sizes, (iii) habitat suitability map fitting, and (iv) source population genotypes. Spatially explicit afforestation predictions (v) were used to inform the green future scenario.

set C – focussed on the exploration of management strategies (P3) in single and multiple release sites for a subset of release sites (identified after set A), and understanding genetic outcomes. We derived demographic (extinction probability, population size) and genetic (heterozygosity, allelic richness) metrics from simulation output to define reintroduction success and used maps of occupation, arrival time, and usage to interpret the distribution of lynx (section 2.4). Finally, we explored the parameter space to answer our research question using metamodeling (section 2.5).

2.2. *Parameter ranges for potential drivers*

2.2.1. *Demographics*

In simulation set A, we varied mortality and reproductive rates across a range of values to test our prediction (P1). This included initial combinations with all the mortality rates and all the reproductive rates grouped (nine combinations) and subsequent combinations where each mortality rate was varied while reproductive rates were fixed (81 combinations), and vice versa (27 combinations). These subsets allowed us first to assess the combined effects of demographic parameters before retrieving the effects of each parameter individually. In simulation sets B and C we used the medium demographic rates (Table 1).

We considered lynx's most important mortality causes in protected populations (Premier et al., 2025). Specifically, baseline (natural and unknown causes), vehicle collision (road and rail traffic causes), and added (poaching and other causes) mortalities. Baseline and vehicle collision mortalities depended on lynx status, i.e., resident or disperser. Baseline and added mortality rates were not spatially explicit, while vehicle collision mortality was. Vehicle collision rates for dispersers and residents were varied separately, while baseline and added mortalities were expected to affect residents and dispersers at the same level.

Vehicle collision mortality was included via two maps of relative risk (Heurich et al., 2018), one for resident and one for dispersing lynx (Appendix C: Fig. 3), due to their different spatial behaviours and mortality risks (Kramer-Schadt et al., 2004). We used OpenStreetMap (© OpenStreetMap Contributors) highways and railways for both resident and dispersing animals, as well as river width from GRWD (Allen and Pavelsky, 2018) for dispersing animals only. The relative risk of the different road classes, railways, and rivers is not available for lynx in Great Britain, so we defined their relative risk based on deer-vehicle collision rates. Considering the entire UK road network, deer-vehicle collision rates per km of major and minor roads are around 0.1 and 0.01 per year, respectively (Langbein, 2007). We assigned railways a lower relative risk based on lower rates of railway mortalities found across Europe (Premier et al., 2025). Motorways typically represent considerable barriers to lynx dispersal (Zimmermann et al., 2005), due to traffic speed, density, size, noise, and structure (Seiler and Helldin, 2006). For this reason, we included motorways as barrier in the habitat map such that lynx can only cross where the road passed underground or over bridges (section 2.2.2). The emergent resident and disperser road mortality rates were then inversely fitted (e.g., Heurich et al., 2018) to the target rates (Table 1, Appendix C: Linear features).

We took reproductive rates from published literature across lynx's European distribution to produce a range of values (Table 1). The rates were: birth probability (likelihood of reproduction given female-male co-occurrence), litter size (number of kittens born), and recruitment probability (number of kittens that survive to independence).

2.2.2. *Behavioural responses in habitat selection*

Habitat selection is a key behaviour which emerges as a response to the landscape. The availability of habitats and resources will drive territory size and habitat selection of residents and dispersers, which will affect species abundance and density. Hence, we predicted (P2) it could affect reintroduction success and considered different scenarios to explore their potential impacts on reintroduction success particularly in simulation set A.

2.2.2.1. *Territory size and population density.* Lynx territory size, and therefore density, is determined primarily by prey availability (Herfindal et al., 2005). We simulated a range of density values that did not exceed lynx densities reported in Central and Northern Europe (e.g., Palmero et al., 2021; Gimenez et al., 2019; Pesenti and Zimmermann, 2013; Duľa et al., 2021). We assumed that colonisation of habitats would not be limited by prey availability but affect population density

Table 1

Overview of simulation scenarios, including set A – broad exploration of parameter space for single release sites, set B – focus on status quo vs green future habitat, and set C – focus on release conditions including single vs multiple release sites.

Set	Release scenarios						Response scenarios			Demographic scenarios							N sims
	Release site/s	N lynx	Sex-ratio (m:f)	Timing	Genetics	Habitat	Habitat suitability	Territory size Φ		Mortalities				Reproduction			
								Minimum female territory (km^2)	Max added (km^2)	Baseline ■ resident (per year)/ disperser (per day)	Vehicle collision▲ resident (correction factor)	Vehicle collision▲ disperser (correction factor)	Added (per year)	Birth prob.°	Recruit prob. Δ	Litter size ☐	
A	Single sites	40	1:3	i	–	Status quo	Global, local	128, 82, 59	64, 41, 29	0.033, 0.046, 0.178[a]/ 0.00038, 0.00068, 0.00082[a]	0.01, 0.02, 0.03[a] (2013, 975, 655*)	0.06, 0.13[a], 0.25[b] (200500, 76500, 27250*)	0.038, 0.068, 0.172[a]	0.75[c], 0.78, 0.81[d,e]	0.41[f], 0.45 0.5[g,h]	2.16[i], 2.73, 3.3[c]	540
										0.033, 0.046, 0.178[a]/ 0.00038, 0.00068, 0.00082[a]	0.01, 0.02, 0.03[a] (2013, 975, 655*)	0.06, 0.13[a], 0.25[b] (200500, 76500, 27250*)	0.038, 0.068, 0.172[a]	0.78	0.45	2.73	4860
										0.046[a]/ 0.00068[a]	0.02[a] (975*)	0.13[a] (76500*)	0.068[a]	0.75[c], 0.78, 0.81[d,e]	0.41[f], 0.45 0.5[g,h]	2.16[i], 2.73, 3.3[c]	1620
B	Single sites	10, 20, 40	1:3	i	–	Status quo, future	Global, local	82	41	0.046[a]/ 0.00068[a]	0.02[a] (975*)	0.13[a] (76500*)	0.068[a]	0.78	0.45	2.73	120
C	Combinations of focal sites	20, 40	1:1, 1:3	i, ii, iii	Single, multiple	Status quo	Global, local	82	41	0.046[a]/ 0.00068[a]	0.02[a] (975*)	0.13[a] (76500*)	0.068[a]	0.78	0.45	2.73	336

Single release sites: Aberdeenshire●, Galloway, Kielder Forest, Kintyre●, New Forest, North Wales, North York Moors, Peak District, Southeast England, South Wales. Focal release sites: Aberdeenshire●, Galloway, Kielder Forest. Φ – density scenarios with targets 0.83, 1.30, and 1.80 lynx/100 km^2 corresponding to 160.64, 102.56, and 74.07 km^2 average female territories, ● – release sites after Ovenden et al. (2019), * – values fixed during inverse fitting of road/rail mortality rates, ■ – baseline mortality = natural + unknown mortalities, ▲ – vehicle collision mortality = rail + road mortalities, ° – probability a resident female (overlapping a male) gives birth, Δ – probability a kitten survives until independent (subadult disperser), ☐ – given birth, mean number of kittens in litter. Timing: i) first two years, ii) first three years, and iii) first six years, with the fraction of lynx released per year: i) 50 (50, 50)%, ii) 33.33 (34, 33, 33)%, and iii) 16.66 (17, 17, 17, 17, 16, 16)%.

a: Premier et al., (2025), b: Kramer-Schadt et al. (2004), c: Jędrzejewski et al. (1996), d: López-Bao et al. (2019), e: Breitenmoser-Würsten et al. (2007), f: Boutros et al. (2007), g: Kaczensky (1991), h: Breitenmoser et al. (1993), i: Gaillard et al. (2014).

(Appendix C: Prey availability). Since lynx density is an emergent parameter of the demogenetic model, we altered instead the distribution of female territory sizes to test our prediction (P2). We based this on the assumed maximum sex-ratio of three females to one male (Kramer-Schadt et al., 2005) and the target density scenarios (Table 1). We used the medium territory size in simulation sets B and C.

2.2.2.2. Habitat suitability mapping

2.2.2.2. Habitat suitability mapping. We ran the simulations on categorical habitat maps comprising: barrier, matrix, dispersal, and breeding habitats. Barrier describes habitats impermeable for lynx movements, matrix is unsuitable habitat that can be selected for a limited duration, while suitable habitats are used for dispersal and breeding (Kramer-Schadt et al., 2005).

Suitable and unsuitable habitat types were derived from the Europe-

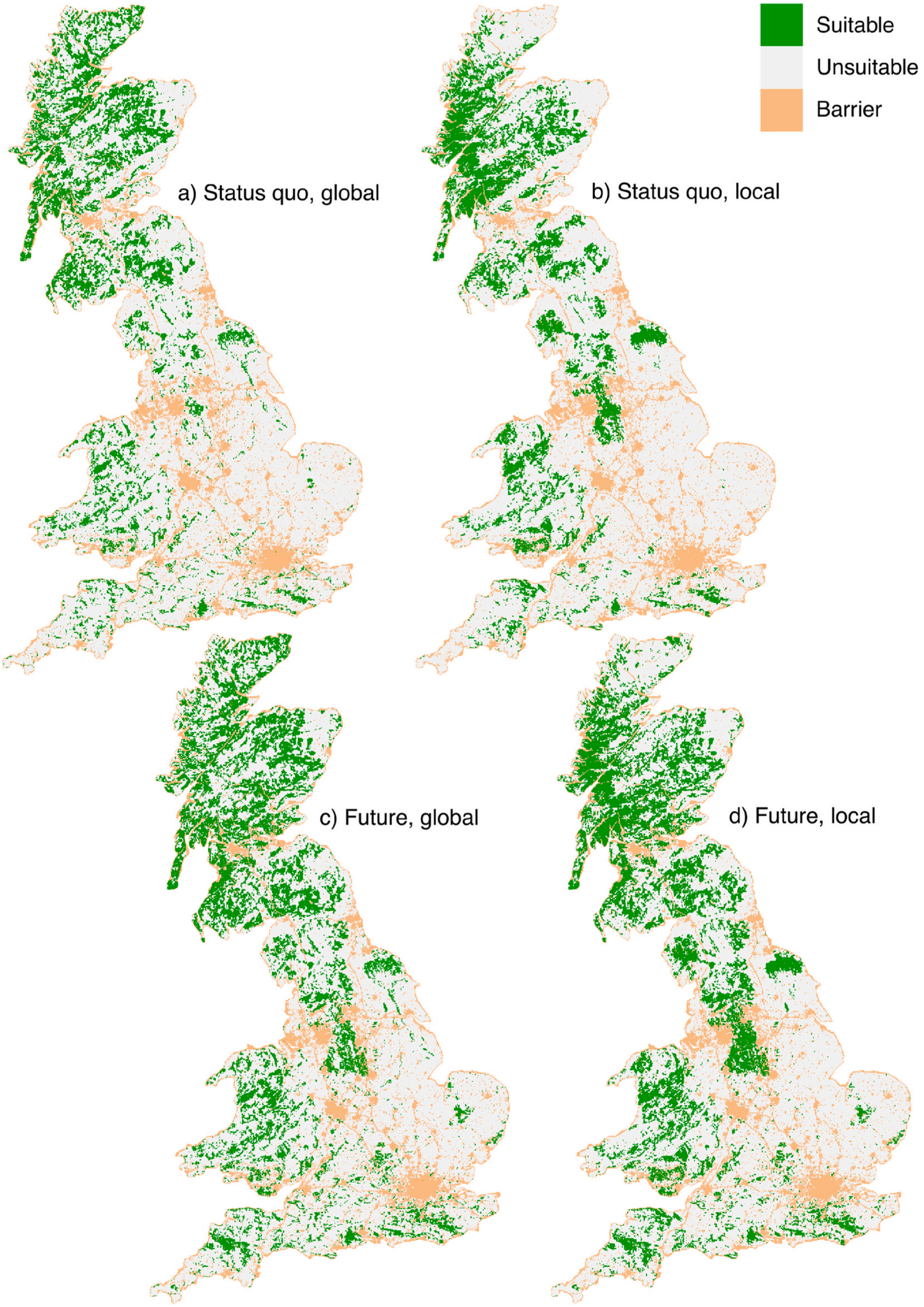

Fig. 2. Habitat maps based on predictions of the global model (a, c), local model (b, d), for status quo (a, b) and green future (c, d) scenarios (section 2.2.2). Habitat classifications comprised 24.1 % barrier, a) 60.9 %, b) 60.9 %, c) 55.3 %, and d) 55.1 % unsuitable, and a) 15.0 %, b) 15.0 %, c) 20.6 %, and d) 20.8 % suitable raster cells, respectively. Only the mainland was considered.

wide habitat suitability map of Oeser et al. (2023a) that was based on telemetry data of ~500 lynx throughout Europe and provides the most detailed information available on lynx. Oeser et al. (2023a) used two methods to fit and predict habitat suitability models, namely; "global" and "local" methods (Appendix C: Fig. 1). The former combined all data into one model and the latter comprised several models fitted with data subsets from different regions and recombined after prediction with weighting based on the environmental similarity of these regions to each location (Appendix C: Habitat models). We simulated all scenarios with both habitat models (Table 1). We used this to test our prediction (P2) about the potential behavioural responses lynx might have to the novel landscape.

We aggregated the 100 m resolution habitat suitability maps using bilinear interpolation to reach 1 km resolution. We converted the habitat suitability maps from continuous values to binary unsuitable-suitable maps based on the threshold above which the distribution of predicted habitat suitability values at selected locations (i.e., "use") exceeded the distribution as expected by random selection (i.e., "availability") (Liu et al., 2005; Magg et al., 2016). We specifically chose to calculate the thresholds based on reintroduced European populations, taking the median of their individual thresholds. These populations are found in habitat patches with similar contexts to Great Britain, namely, embedded in human dominated and fragmented landscapes. This ensures the availability of unsuitable habitats in the vicinity to delineate the threshold of use and availability. The area required for a territory, and therefore breeding, was emergent based on habitat configuration and territory size distributions (Table 1). Cells that had habitat suitability below the respective thresholds were defined as matrix.

After suitable habitat classes, we included 'barrier' features impermeable to lynx movements, such as motorways, which are considerable barriers to lynx dispersal (Zimmermann et al., 2005). Barriers were defined using Corine land cover (CLC) 2018 (European Environmental Agency, 2020a,b), Global River Widths from Landsat (GRWL) Database (Allen and Pavelsky, 2018), and OpenStreetMap (OSM) road maps (© OpenStreetMap Contributors). The CLC raster was resampled to 1 km resolution using the nearest-neighbour approach. OSM motorways and GRWL rivers were rasterized from vector formats to 1 km resolution. We considered CLC classes with urban characteristics and large water bodies (Appendix C: Table 1), GRWL river sections with width >100 m, and OSM highways of class motorways as barriers (Kramer-Schadt et al., 2004; Heurich et al., 2018). Raster cells containing sections of motorways that passed underground or over bridges were not considered barriers. Finally, the suitable habitat classes (breeding and dispersal), matrix, and barrier were combined, giving precedence to barrier to produce the categorical habitat maps (Fig. 2a and b).

2.2.2.3. "Green future" habitat scenario

We predicted some reintroduction scenarios would be unsuccessful under current habitat conditions but might be possible if governmental habitat creation goals are achieved (P4). Therefore, in simulation set B (Table 1), we included a "green future" scenario that modelled increases in woodland extent and connectivity proposed by the UK (England and Wales; Department for Environment, Food & Rural Affairs, 2018) and devolved Scottish (Scottish Government, 2020) governments. Since no explicit plans have been provided, we used a forest potential map that maintained soil carbon sequestration (Bradfer-Lawrence et al., 2021) to estimate potential changes. Combining forest potential fraction with the existing tree cover fraction (European Environmental Agency, 2020a,b), we reclassified matrix grid cells exceeding 50 % forest as suitable (Schadt et al., 2002; Niedziałkowska et al., 2006). This resulted in two additional habitat classification maps that describe the landscape in a "green future" scenario under global and local model frameworks (Fig. 2c and d).

2.2.3. Management choices for release

The strategy of a reintroduction project has a significant role in its overall success (Wilson, 2018), therefore we predicted release conditions would affect population persistence and genetic diversity (P3). We varied several release parameters (sites, timing, number, sex ratio, and source population genetics) to understand their importance in determining reintroduction success. We used the most robust single release sites revealed in simulation set A as the focal release sites in set C to explore the other release parameters.

2.2.3.1. Release sites

We selected a manageable number of release sites in two ways. First, for England and Wales we identified areas where the two status quo habitat maps (global and local) both predicted suitable contiguous habitat greater than 130 km^2 (Appendix C: Fig. 2). Although this area alone would be insufficient for a lynx population, it allowed the same release sites to be simulated with both habitat maps. The release sites in England and Wales were: Kielder Forest, New Forest, North Wales, North York Moors, Peak District, Southeast England, and South Wales (Appendix C: Fig. 2). Release sites were divided among several patches of comparable size in North and South Wales (Appendix C: Fig. 2). Second, for Scotland, which had numerous suitable patches, we used sites in Aberdeenshire and Kintyre from Ovenden et al. (2019), and we added Galloway. Release coordinates were chosen within the largest bulk of the agreed suitable patches as hypothetical release sites representative for the patch but with no consideration for social or practical aspects. The contiguous habitat patch of Kielder Forest extended into Scotland, but the release coordinates were within England. Reintroductions were simulated for all release sites individually (sets A and B) before selecting focal sites, with low extinction probabilities, to test our prediction (P3) regarding management strategies by simulating combinations of release sites and other release conditions under medium demographic and territory conditions (set C).

2.2.3.2. Number of individuals, sex-ratio, and timing

The number of individuals released can affect reintroduction success, with more individuals providing demographic (Sanderson et al., 2014) and genetic (Wilson, 2018) benefits. We simulated a range of release population sizes to explore the effect on population development. For simulation set A we used 40 lynx, for set B we tested 10, 20, and 40 lynx, while for set C (single and multiple release sites) we tested 20 and 40 lynx. For scenarios with three release sites, the number of individuals could not be divided evenly among sites and the remaining individual was released in the largest suitable patch.

Sex-ratios of territorial lynx can be female-biased (Schmidt et al., 1997; Breitenmoser-Würsten et al., 2007), as such we allowed a maximum of three female lynx territories per male territory in simulations (Kramer-Schadt et al., 2005). In simulation sets A and B we used a female-biased ratio (1:3). To test the prediction (P3), in set C we simulated scenarios with equal (1:1) and female-biased (1:3) ratios, because the released lynx sex-ratio could affect population establishment.

Release timing is expected to affect success (P3). Therefore, in simulation set C, we simulated three possibilities for timing of releases, based on releases across consecutive years: i) first two years (50 % per year), ii) first three years (approx. 33 % per year), and iii) first six years (approx. 16 % per year). In simulation sets A and B we used release timing i).

2.2.3.3. Source population genetics

The final management choice we tested with our prediction (P3) regarded founder genetics. We therefore simulated neutral genetic markers (i.e., not associated with adaptive traits) using the demogenetic model. Neutral markers allow interpretation of changes in genetic diversity over time as products of landscape and demographic effects, rather than selection (Holderegger et al., 2006).

We applied two scenarios (single and multiple source populations) to simulate neutral genetic diversity for the focal release sites only (set C). For the multiple source population, we sampled genotypes from three populations (Scandinavian, Baltic, Harz Mountains), while for the single source case we sampled genotypes from one population (Carpathian). These two scenarios simulate sourcing strategies, where single source was the main choice until the end of the 20th century, and multiple sources reflects contemporary projects that release individuals from different wild and captive populations. Genotypes were randomly sampled from microsatellite data (Gajdárová et al., 2021), without replacement, until the number of released individuals was reached for each given simulation replicate. After simulations, we computed population heterozygosity and allelic richness as indicators of genetic diversity. Heterozygosity was calculated as the mean heterozygosity across all individuals, and allelic richness was calculated and averaged for each locus across all individuals. On average, the release population heterozygosity and allelic richness were 0.56 and 6.6 for multiple and 0.59 and 4.2 for single source populations, respectively. These scenarios represent levels of genetic diversity in modern reintroduction projects, which is typically much higher than reintroductions carried out four decades prior (Bull et al., 2016; Mueller et al., 2022).

2.3. *Demogenetic simulation model*

The lynx demogenetic model (Premier et al., 2020) can simulate demographic and genetic development under diverse conditions. Population processes are the result of individual habitat and territory selection, and movement decisions. Simulation starting conditions, such as the sex, genotype, and site of all released lynx (i.e., reintroduction and reinforcement), are defined a priori. The model comprises different submodels, namely: a dispersal module, including territory searching, that links demographic processes onto a habitat map, a demographic module that considers territory occupation, reproduction, and mortality, and a genetic module that handles inheritance of neutral genetic markers (Appendix B: ODD protocol). The habitat map provides the landscape where all processes take place (sections 2.2.2.2 and 2.2.2.3). This was supplemented by maps describing mortality risk due to road and rail infrastructure for resident and dispersing individuals (section 2.2.1).

2.4. *Measures of reintroduction success*

We simulated 7476 scenarios (i.e., combinations of input parameters) and each scenario was replicated 100 times. We defined reintroduction success as the probability of population extinction ≤ 5 % after 100 years (i.e. number of replicates that failed to reach 100 years). We calculated mean population size, heterozygosity, and allelic richness across replicates to compare scenarios. Higher values of each were considered more successful. To understand the spatial development, we mapped the probability of patch occupancy after 100 years (i.e., number of replicates occupying each patch after 100 years), the mean year of first occupancy (i.e., average first year across replicates where at least one female was territorial per patch), and the emergent use surface (i.e., inverse of resistance surface) to understand landscape connectivity. Patches were defined as contiguous suitable areas and calculated individually for each habitat map (sections 2.2.2.2 and 2.2.2.3).

2.5. *Metamodelling*

A metamodel is a model that is fitted using the inputs and outputs of an underlying model, in our case the demogenetic simulation model, to help understand the complex and highly dimensional results produced (Kleunen, 1979). We used metamodels to explore the measures of reintroduction success and thereby understand which of the hypothesised drivers were most important. We fitted ‘tree’ based metamodels, with simulation input parameters as predictors and simulation outputs as responses. The responses measuring success or failure were extinction probability ≤ 5 % (binary), population size, and, for the focal release site simulations, heterozygosity and allelic richness (all continuous). We used randomForest models (Breiman, 2001) to rank parameters by their importance in predicting reintroduction success and we used Classification and Regression Trees (CaRT; Breiman et al., 2017) to visualise the relationships between inputs and outputs as decision trees, whereby parameter space is divided into partitions that describe decreasing amounts of variability in the given simulation response. From randomForest models we retrieved the variable importance measures for classification and regressions, respectively; mean decrease in accuracy and percentage increase in mean squared error (%IncMSE), where higher values indicate greater importance. Both metamodelling frameworks we used are appropriate for exploration of simulation results (De’ath and Fabricius, 2000).

2.6. *Software*

We used the demogenetic model described by Kramer-Schadt et al. (2005) and Premier et al. (2020) (2.3, Appendix B: ODD protocol). We conducted all other data handling in “R” (R Core Team, 2020) and the packages: “dplyr” (Wickham et al., 2022), “ggplot2” (Wickham, 2016), “hierfstat” (Goudet, 2005), “rpart” (Therneau and Atkinson, 2019), “rpart.plot” (Milborrow, 2020), “randomForest” (Liaw and Wiener, 2002), “terra” (Hijmans, 2022), and “sf” (Pebesma, 2018).

3. Results

3.1. *Demographics*

In the initial simulations in set A, i.e., when mortality and reproductive rates were grouped, we found mortality was the most important parameter for predicting extinction probability (Appendix D: Fig. 1a). When all mortality rates were high, reintroductions were unlikely to succeed (extinction probability >5 %) irrespective of release site (Appendix D: Fig. 1b). Reproductive rates had little bearing on extinction probability compared to the other parameters. Population size was primarily driven by mortality, though reproduction had some predictive value in this case (Appendix D: Fig. 1c). Although for specific release sites and territory sizes the higher reproductive rates could result in two or three times the number of lynx, mortality rates were decisive in allowing population growth (Appendix D: Fig. 1d).

When we varied each cause-specific mortality rate individually, with reproductive rates fixed, we found baseline and added mortalities were the most important mortality rates in terms of extinction probability (Fig. 3) and population size (Appendix D: Fig. 2a). Road mortality rates for residents and dispersers did not affect the extinction probability strongly, though disperser road mortality was more important for population size. Under specific circumstances, for example for releases in Aberdeenshire and Kintyre, 1.5 times more lynx were found if road mortality was medium or low for dispersers (Appendix D: Fig. 2b).

Varying the reproductive rates individually, with mortality rates fixed, showed that litter size was the most important reproductive parameter for both extinction probability and population size, while recruitment and birth probabilities were ranked lowest overall (Appendix D: Fig. 3a–c). The smallest litter size pushed extinction probability above 5 %, but only when territories were largest, a situation only affecting the more robust release sites when considering the more important parameters (Appendix D: Fig. 3b). Population size was only affected by litter size when territory size was medium or small (Appendix D: Fig. 3d).

The results of simulation set A showed demographic parameters affected reintroduction success, consistent with P1. We found baseline and added mortalities were the key demographic parameters behind reintroduction success. The other mortality causes and reproductive rates affected population size but were less important compared to the other parameters included.

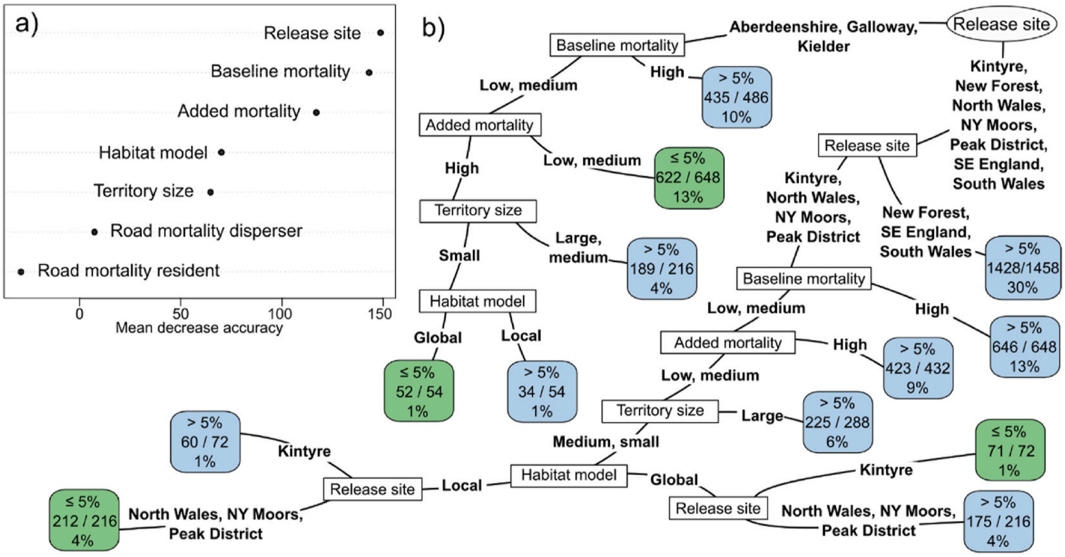

Fig. 3. Reintroduction success evaluated by extinction probability ≤5 % 100 years after release for combinations of mortality rates in simulation set A (Table 1), with a) variable importance and b) decision-tree based on binary response (success/failure) randomForest and CaRT metamodels, respectively. At each decision-tree node (first node oval box and subsequently rectangular boxes), the data are split based on the parameter in the node and its values on the branches. At the terminal nodes, the predicted extinction probability is indicated with the binary classification (success in green "≤ 5 %", failure in blue "> 5 %"), the fraction of the simulation subset in agreement with the classification, and the percentage of all simulations within the subset.

3.2. Behavioural responses in habitat selection

In simulation set A, we found habitat model tended to have greater importance for extinction probability compared to territory size, while the opposite was true for population size (Appendix D: Fig. 1–3, Fig. 3). For some release sites a specific habitat model, global or local (Fig. 4a), and medium or small territory sizes were needed for success. In more robust sites, small territories could double or triple the number of lynx compared to medium and large territories (Appendix D: Fig. 2).

Habitat model and territory size were less important for success than some mortality rates and the release site (Fig. 3). This meant the behavioural responses had a strong interplay with the other parameters in terms of emergent population size. Habitat model was still of some importance for population size in sets B (Appendix D: Fig. 5a) and C (Fig. 5a), with an up to 20 lynx difference in population size after 100 years between habitat models (Fig. 5c). Further, the habitat model was also of some importance for population genetics (Fig. 6a, Appendix D: Fig. 7a). Specifically, the local habitat model tended to result in lower heterozygosity (Appendix D: Fig. 7) and allelic richness (Fig. 6) than the global model. Consistent with our prediction (P2), the results showed

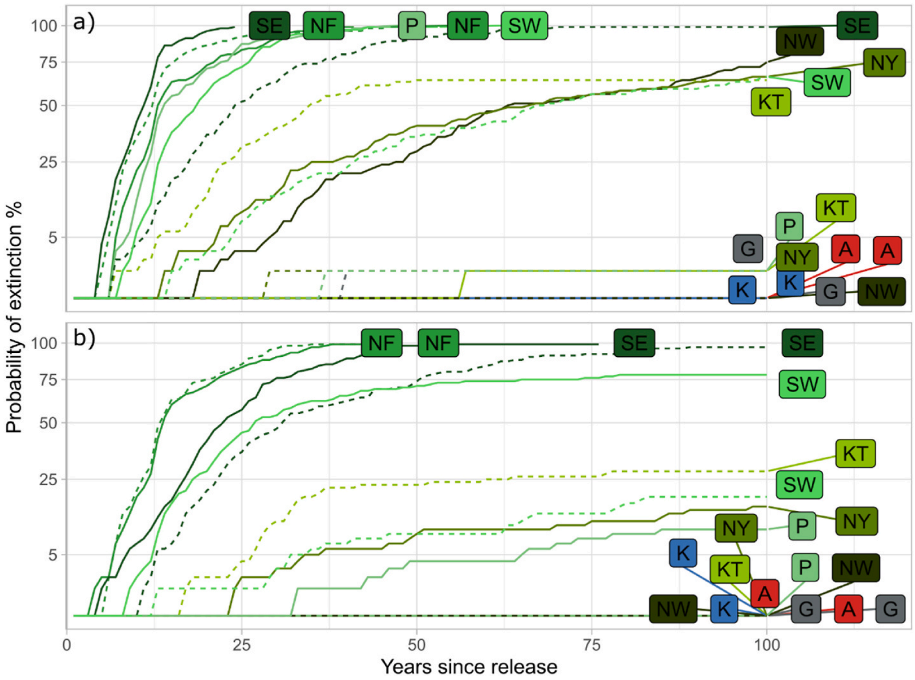

Fig. 4. Extinction probability over time for different single release sites under: a) status quo and b) green future habitat scenarios and medium simulation parameters. Solid line – global and dashed line – local habitat models. Release sites are indicated with the names: A - Aberdeenshire, G - Galloway, K – Kielder Forest, KT - Kintyre, NF - New Forest, NW - North Wales, NY - North York Moors, P - Peak District, SE - Southeast England, SW - South Wales.

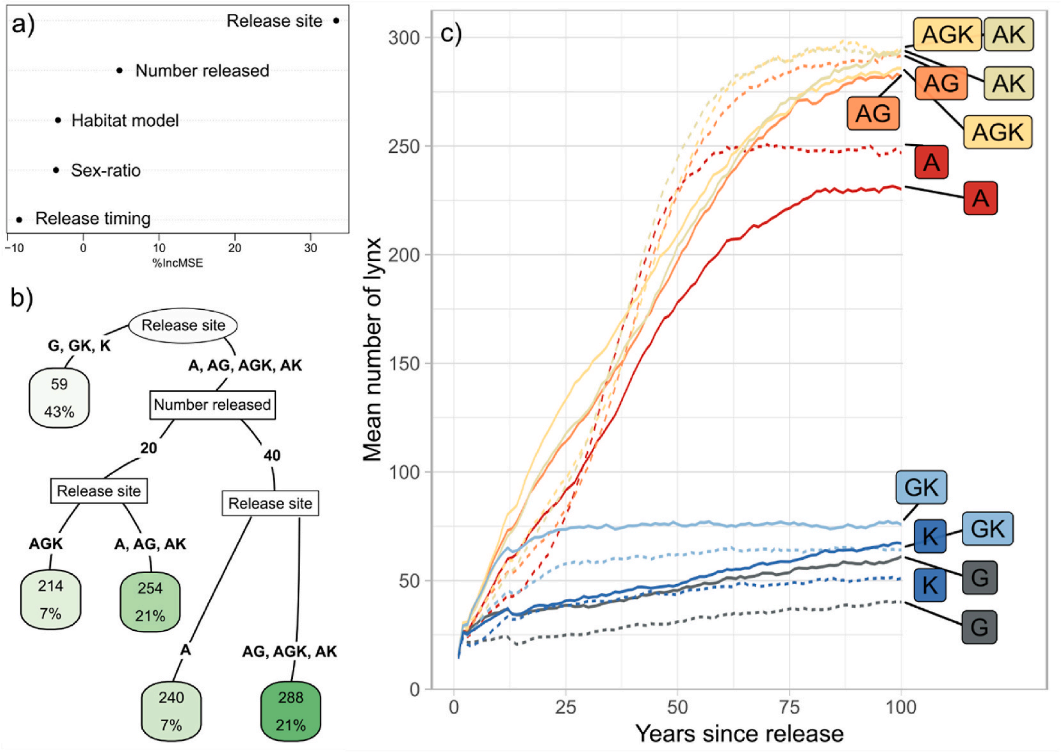

Fig. 5. Reintroduction success evaluated by population size 100 years after release for simulation set C (Table 1): single and multiple release site combinations of the focal release sites: A - Aberdeenshire, G - Galloway, and K – Kielder Forest. Panels: a) variable importance from randomForest metamodel, b) decision-tree from CaRT metamodel, and c) population size under different focal release site combinations under medium parameter and ideal release conditions. At decision-tree nodes (first node oval box and subsequently rectangular boxes) the data are split based on the parameter in the node and its values on the branches, at the terminal nodes the mean predicted population size and the percentage of the entire dataset within the subset are given. Larger populations indicated by darker green terminal nodes. Solid line – global and dashed line – local habitat models (c).

behavioural responses in habitat selection indeed affected reintroduction success.

3.3. Management choices for release

3.3.1. Release sites

In simulation set A, we found release site was of critical importance for extinction probability and population size for a single site reintroduction (Fig. 3, Appendix D: Figs. 1–3). Indeed, releases in the New Forest, Southeast England, and South Wales exceeded 5 % extinction probability under virtually all conditions (Fig. 3, Appendix D: Fig. 3). Under medium demographic and territory conditions, these sites all exceeded 5 % extinction probability within 30 years (Fig. 4a). The release sites in North Wales, North York Moors, Peak District, and Kintyre performed better but were only successful with low or medium added and baseline mortality, and small or medium territory sizes (Fig. 3). The success of these release sites depended also on the habitat model: Kintyre was only under the 5 % extinction threshold with the global map, while North Wales, North York Moors, and Peak District were only under the threshold with the local map. The release sites in Aberdeenshire, Galloway, and Kielder Forest were those with consistently low extinction probabilities, unless the baseline or added mortality rates were high (Fig. 3, Appendix D: Figs. 1 and 3).

The release sites in Aberdeenshire and Kintyre tended to develop the largest lynx populations after 100 years, with an average of approx. 250 independent individuals expected under medium simulation conditions (Appendix D: Fig. 4a), ranging from two to around 600 individuals at the extremes of demographic and territory parameters (Appendix D: Fig. 1). The release sites in Galloway and Kielder Forest each developed populations around 25 to 50 independent lynx for medium conditions (Appendix D: Fig. 4a), here ranging from 0 (no extant population) up to 300 lynx for the most advantageous conditions (Appendix D: Fig. 1). All the other release sites achieved populations under 10 lynx on average for medium conditions (Appendix D: Fig. 2). The population growth after release was steepest in Aberdeenshire, followed by Kielder Forest and Galloway, for around 25–30 years, before being overtaken by the release in Kintyre (Appendix D: Fig. 4a). However, population growth did not plateau for the Kielder Forest and Galloway scenarios.

Based on their consistently low extinction probabilities when simulated individually, the release sites Aberdeenshire, Galloway, and Kielder Forest were chosen as the “focal” sites to explore single site and multiple site reintroductions (Table 1: Set C). When comparing single and multiple site release, the release site was the most important predictor for population size but less so for extinction probability because all the focal sites were robust as standalone sites (Fig. 5a and Appendix D: Fig. 6a).

The highest extinction probabilities (still under 5 %) were found with the local habitat model when 20 lynx were released from the combinations: Aberdeenshire-Galloway-Kielder Forest, or Aberdeenshire-Kielder Forest, or Kielder Forest alone. Multiple releases, including the sites Galloway and Kielder Forest were expected to reach a population size of around 60 independent individuals (Fig. 5b). Larger populations emerged from release site combinations that included Aberdeenshire, between 214 and 288 independent individuals. Indeed, releasing lynx at multiple sites was expected to increase the population growth rates compared to single sites (Fig. 5c). For example, dividing released lynx among Galloway and Kielder Forest meant the population size reached a plateau after just 25 years, something not achieved by each separately after 100 years. The overall largest populations (approx. 280) were achieved after releases in Aberdeenshire and at least one of Galloway or Kielder Forest, while single site releases in Aberdeenshire grew at a similar rate but plateaued with 30–50 fewer individuals (i.e., 230 to

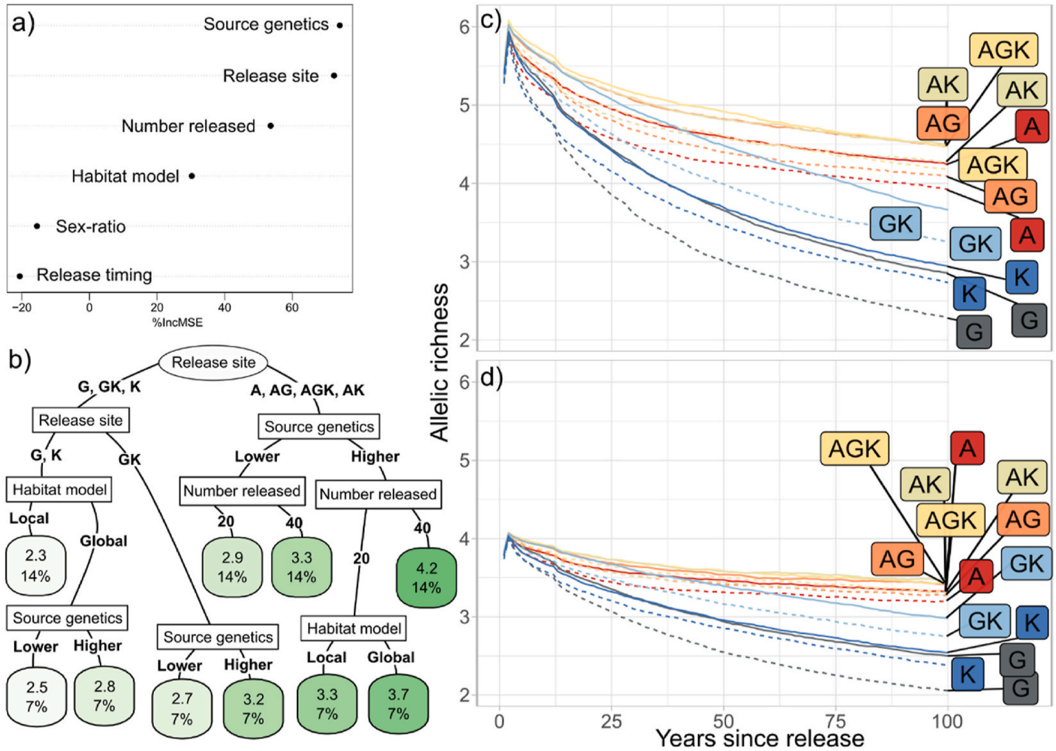

Fig. 6. Reintroduction success evaluated by allelic richness 100 years after release for simulation set C (Table 1): single and multiple release site combinations of the focal release sites: A - Aberdeenshire, G - Galloway, and K – Kielder Forest. Panels: a) variable importance from randomForest metamodel, b) decision-tree from CaRT metamodel, and allelic richness with higher (c) and lower (d) source population genetic diversity after different focal release site combinations under medium parameter and ideal release conditions. At decision-tree nodes (b) first node oval box and subsequently rectangular boxes) the data are split based on the parameter in the node and its values on the branches, at the terminal nodes the mean predicted allelic richness and the percentage of all simulations within the subset are given. Higher allelic richness indicated by darker green terminal nodes. Solid line – global and dashed line – local habitat models (c, d).

250).

Release site was also important for heterozygosity and allelic richness (Fig. 6a and Appendix D: Fig. 7a). The highest heterozygosity and allelic richness were found by releasing in Aberdeenshire or multiple site releases that included Aberdeenshire (Fig. 6b and Appendix D: Fig. 7b). Standalone releases in Galloway tended to have the lowest heterozygosity and allelic richness on average (Fig. 6c and d, Appendix D: Fig. 7c and d).

3.3.2. *Number of individuals, sex-ratio, and timing*

In simulation set B, we found that releasing 10 lynx was not sufficient to keep the extinction probability under 5 %, even for the focal release sites (Appendix D: Fig. 5). In simulation set C, considering only the focal release sites, the number of individuals released was an important parameter for extinction probability (Appendix D: Fig. 6a). The extinction probability was lowest when 40 lynx were released, although it was below 2.5 % on average for all conditions (Appendix D: Fig. 6b). When lynx were divided among three release locations, the number of lynx after 100 years was higher when 40 were released compared to 20 (Fig. 5b). The number of lynx released was the most important parameter for heterozygosity and important for allelic richness (Fig. 6a and Appendix D: Fig. 7). Releasing more individuals helped preserve greater heterozygosity and allelic richness over 100 years. For example, releasing 20 lynx in a multiple site release including Aberdeenshire resulted in an allelic richness between 2.9 and 3.7 on average, while releasing 40 lynx increased this to between 3.3 and 4.2 (Fig. 6b).

Compared to the other parameters in set C, sex ratio was of little importance for predicting extinction probability (Appendix D: Fig. 6a), population size (Fig. 5a), heterozygosity (Appendix D: Fig. 7a), and allelic richness (Fig. 6a). Release timing was also of similarly low importance for population size, heterozygosity, and allelic richness but had some relevance for extinction probability (Appendix D: Fig. 6a). For a release of 20 lynx in the sites Aberdeenshire-Galloway-Kielder Forest, or Aberdeenshire-Kielder Forest, or Kielder Forest alone, the intermediate release timing (over three years) reduced the low extinction probability from 2.3 to 1.6 % on average (Appendix D: Fig. 6b).

3.3.3. *Source population genetics*

In simulation set C we tested the effect of source population genetics on the development of heterozygosity and allelic richness. We found that the source population (multiple vs single source populations) was of high importance for heterozygosity and allelic richness (Fig. 6a and Appendix D: Fig. 7a). Releasing individuals from multiple source populations created higher heterozygosity and allelic richness that was still higher after 100 years. For simulations with multiple source populations, heterozygosity increased to 0.6 between 5 and 10 years, while the single source population releases immediately decreased from 0.6 (Appendix D: Fig. 7c and d). Subsequently, heterozygosity declined to values between 0.48 and 0.25, as expected, due to drift. The results for allelic richness were comparable (Fig. 6c and d). Allelic richness increased rapidly to ~6.0 with multiple source populations, while with a single source population allelic richness increased slightly to ~4.0. Over time allelic richness decreased to between 2.3 - 4.5 and 2.0–3.5 for multiple and single source populations, respectively.

The results concerning release strategy mostly consistent with our prediction (P3). Especially release sites, number, and source population genetics affected the different measures of reintroduction success, while timing and sex-ratio were less pivotal.

3.4. *Status quo vs green future*

In simulation set B, we found that the release site was of far greater

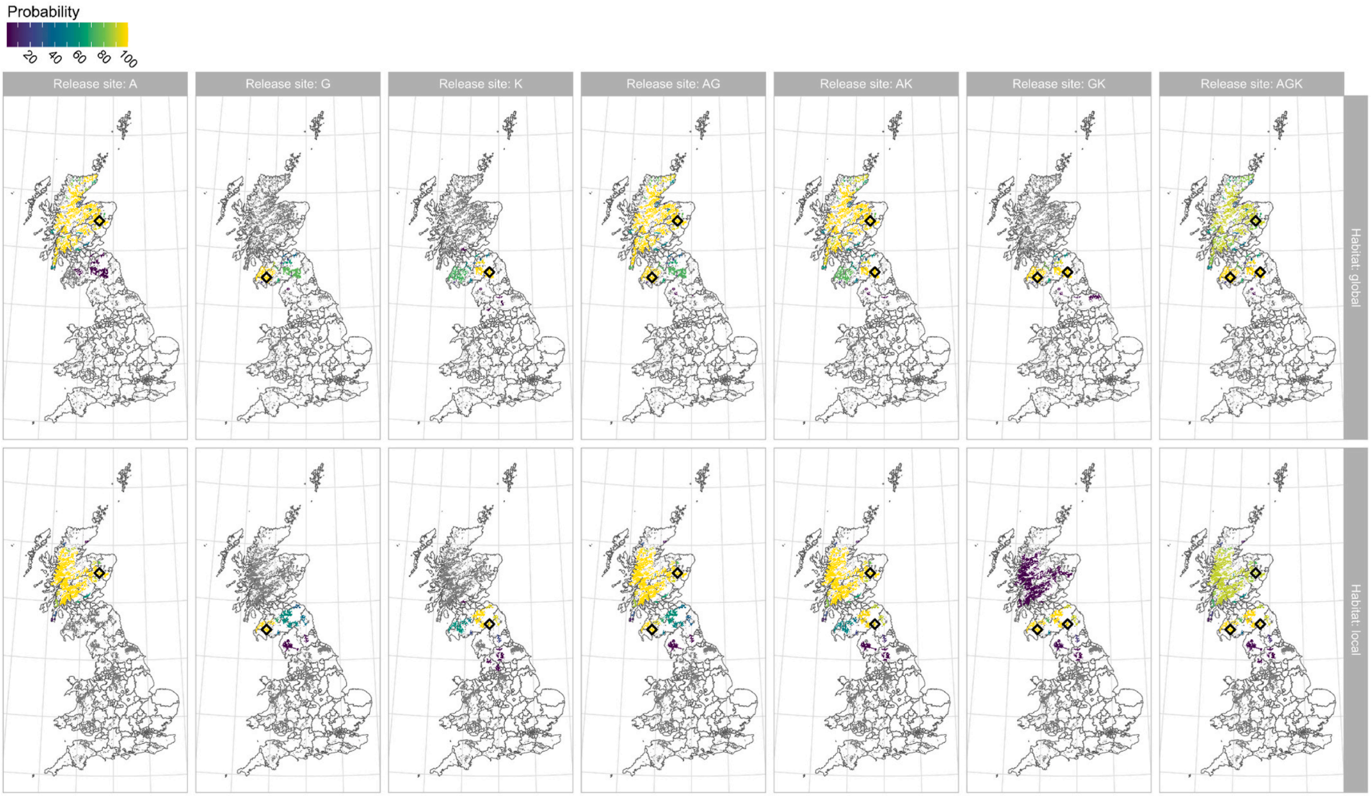

Fig. 7. Probability of occupancy after 100 years based on combinations of focal release sites. Release sites are indicated by diamonds, and with the names: A - Aberdeenshire, G - Galloway, K – Kielder Forest, and combinations thereof. Occupancy probability increases with the colour gradient from indigo to yellow, with brighter colours showing higher likelihood of occupancy. Grey lines indicate county borders.

importance for predicting extinction probability and population size than the habitat scenario (Appendix D: Fig. 3) and there were no great differences between the habitat scenarios (Fig. 4). In other words, the release sites with high extinction probabilities under status quo conditions, were still unfavourable under future conditions, while those that had low extinction probabilities (i.e., focal sites) improved mostly in terms of population size (Appendix D: Results 1). While these results are consistent with the prediction (P4) for some areas of Great Britain, the green future habitat improvements had, overall, a relatively minor positive effect on reintroduction success.

3.5. Spatial distribution

The spatial distributions depended, a priori, on the available habitat. For example, lynx distribution was wider in areas of northernmost Scotland with the global compared to the local habitat model (Fig. 7). From all release sites, it took decades for lynx to occupy all patches that were possible within the simulation period (Appendix D: Figs. 10–12). The Central Belt (densely populated and human modified region of central Scotland) reduced the connectivity between habitat patches in northern Scotland with those in southern Scotland and northern England (Fig. 8). Although dispersal was possible across this region, from north or south, it was unlikely this would lead to colonisation (Fig. 7). For both habitat models, connectivity between northern and southern Scotland emerged mostly in a dispersal corridor between Glasgow and Edinburgh, to the east of the M74 motorway. This seemed more easily reached from the Kielder Forest patch and the eastern part of the Southern Uplands. Under green future conditions, connectivity was improved northward via the same corridor and another narrow corridor west of Glasgow, but patch occupancy probabilities were still low (around 5 %). Populations released within southern Scotland and northern England expanded well in the region, even though the main suitable patches were bisected by the M74 motorway that reduced connectivity, though the green future scenario did improve matters (Figs. 7 and 8). Occupancy of patches further south than Kielder Forest or Galloway had probabilities less than 5 %, partly caused by the same motorway reducing connectivity with Cumbria in northwest England.

Compared to single site releases, multiple site releases comprising at least two release sites increased the extent of occupied patches (Fig. 7), accelerated the occupation of more patches (Appendix D: Fig. 9), and promoted the widest exploration of the landscape by dispersing individuals (Fig. 8). The spatial patterns following multiple site releases were, broadly speaking, superimpositions of the single site releases.

The spatial distributions emergent from the remaining six release sites revealed low occupancy probabilities (<50 %) under status quo conditions for at least one habitat model, or there was a large disparity in the predictions from the two habitat models (Appendix D: Fig. 9). Specific details for the remaining release sites, and combinations, are provided in Appendix D: Results 2.

4. Discussion

Using a demogenetic simulation model developed for Eurasian lynx in combination with empirical data we aimed to answer the question, what is the ecological feasibility of lynx reintroduction in Great Britain? We hypothesised the drivers, including controllable parameters considered by practitioners, as well as ecological and human aspects that cannot be controlled and are unknown in Great Britain due to lynx's nearly 800-year absence (Hetherington et al., 2006; Raye, 2017). Consistent with our predictions, the results showed: P1) demographic parameters, P2) behavioural responses in habitat selection, and P3) management strategies, affected reintroduction success. Added and baseline mortalities were key drivers of extinction probability and population size. Habitat model affected extinction probability,

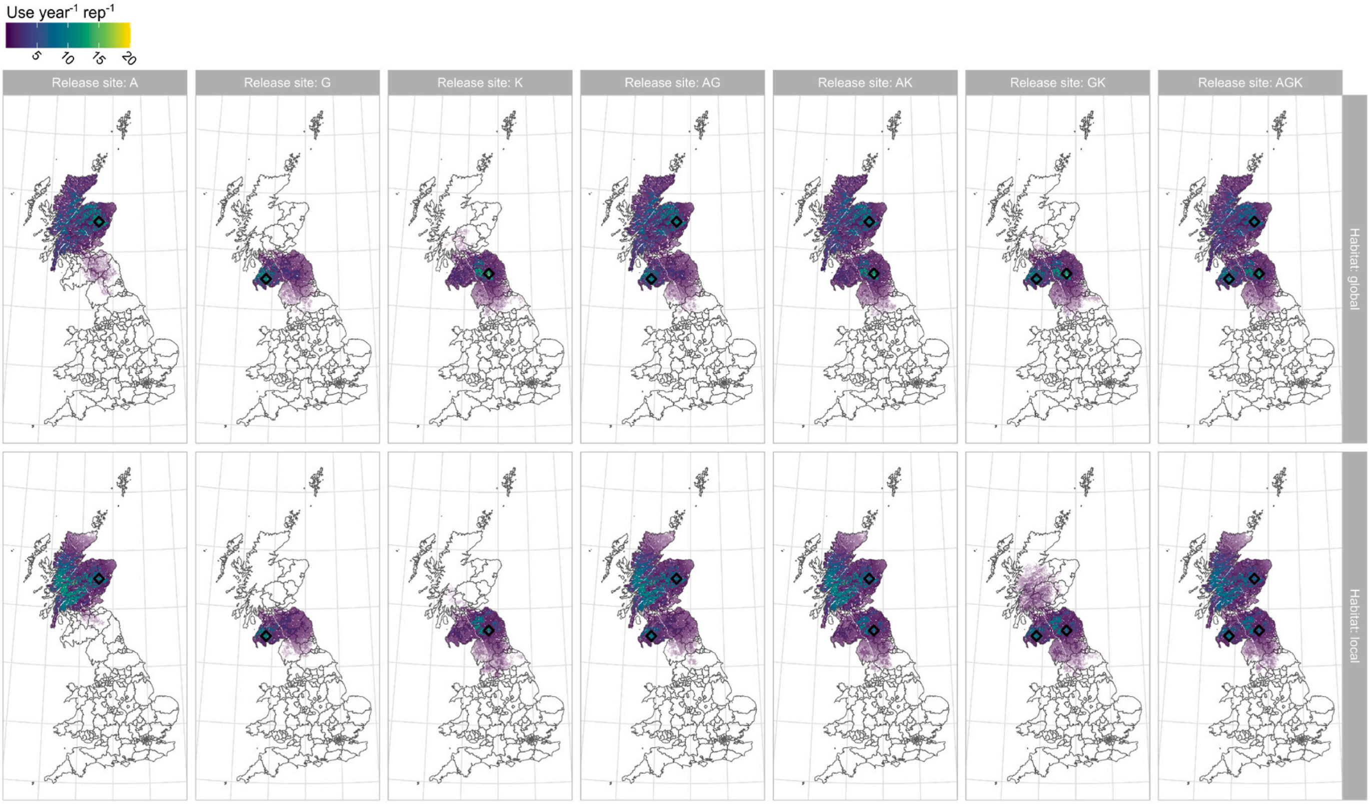

Fig. 8. Use surface (i.e., inverse of resistance surface) based on combinations of focal release sites. Release sites are indicated by diamonds, and with the names: A - Aberdeenshire, G - Galloway, K – Kielder Forest, and combinations thereof. Amount of use increases with the transparency and colour gradient from transparent indigo to opaque yellow, with opaque brighter colours showing higher usage. Grey lines indicate county borders.

population size, and genetic diversity, while territory size was relevant for population size. Management strategy was vital for reintroduction success. Selection of a suitable release site could minimise extinction probability and maximise population size and genetic diversity. Release sites in Aberdeenshire, Galloway, and Kielder Forest had the highest probabilities of success across diverse conditions (with medium parameters <5 % extinction and approx. 240, 60, and 60 lynx after 100 years, respectively). Further, releasing more lynx in multiple sites was the most effective way of founding a large lynx population in Great Britain. If sourced correctly, a reintroduced lynx population was expected to retain adequate genetic diversity for many decades after release, especially when compared to older lynx reintroductions (e.g., Bull et al., 2016; Mueller et al., 2022). Finally, our results suggested that poor release sites under today's habitat conditions would not be vastly improved under the "green future" scenario. This scenario increased population sizes and improved landscape connectivity, consistent with our prediction (P4), but these improvements were not necessary for a reintroduction to be successful in the focal release sites we identified. Without habitat improvements, connectivity between Kielder Forest and Galloway was possible, while connectivity between the Southern Uplands and Kielder Forest region and northern Scotland was more difficult. Considering all our results, we suggest an ideal lynx reintroduction project in Great Britain would release lynx both north and south of the Central Belt (e.g., Aberdeenshire and Kielder Forest).

4.1. Demographics

We tested mortality and reproductive rates and found that variability in the latter would be unlikely to compromise reintroduction success. Mortality rates were, however, decisive. We found that high added (~17 % per year) and baseline (resident ~ 18 % per year, disperser ~ 30 % per year) mortality made it difficult for otherwise viable release sites to persist for 100 years. To understand the potential effects of these mortality causes, we chose the maximum range of their rates in Europe (Premier et al., 2025). The highest values for natural mortality and illegal killing were from the Harz Mountains and Białowieża Forest, respectively. The Harz Mountains is considered a population with high survival rates, due to the low rates of illegal killing, but with high incidence of sarcoptic mange (Anders and Sacher, 2005; Mueller et al., 2020). Combining this with the small sample of individuals (n = 9) suggests the natural mortality rate may not be representative of the entire population. In the Białowieża Forest, the high rate of illegal killing of ~17 % annually was real but the result of a particular period of high persecution, which has since been reduced (Kowalczyk et al., 2015). Therefore, exposure to such high rates would be an extreme circumstance which, expectedly, exacerbated Allee effects (Armstrong and Wittmer, 2011), further challenging the establishment of an inherently low density and reproduction rate species.

Natural mortality could be minimized if the reintroduction is well-managed, with animals carefully health-screened prior to release (Ryser-Degiorgis et al., 2021) and the risk of local wildlife diseases assessed. Other natural mortality factors are rare (Premier et al., 2025). Therefore, the medium rates we simulated (baseline: resident ~ 5 % per year, disperser = 25 % per year) offers a more reasonable expectation of population development since it represents the mean for all the available European data (Premier et al., 2025). Added mortality, which includes poaching, is more uncertain (4.6).

Roads are a significant source of mortality for lynx, especially for dispersing individuals (Kramer-Schadt et al., 2004). Overall, our results showed road mortality would not be a limiting factor for population persistence in the focal patches. However, apart from Galloway and Kielder Forest, the connectivity among larger patches was extremely weak. This was also hindered by the mortality of dispersing individuals crossing roads to reach other patches (Appendix D: Fig. 15). Our results showed that improving habitat or reducing road mortality would both improve connectivity and increase population sizes.

We modelled lynx-vehicle collision risk based on the relative risk posed by different road types for deer (Langbein, 2007). In the absence of empirical data for lynx, we believe basing this on deer data is adequate (e.g., Heurich et al., 2018). Collision rates for deer reflect the risk of different road classes since these are correlated to traffic density and speed, which would also be the main factors for lynx. Given the wide distribution of the six deer species in Great Britain (Croft et al., 2019), their road kills should be representative of the relative risks posed by the different road types. Furthermore, deer are lynx's main prey, so we might expect their road mortality risk, like their occurrence, to be well correlated (Müller et al., 2014).

4.2. Habitat selection and prey availability

The population densities of lynx's prey species in Great Britain are poorly quantified at a national scale. Due to their hunting efficiency, lynx can occur in low resource areas, with low prey availability (Schmidt, 2008; Nilsen et al., 2009). Therefore, prey availability is unlikely to be a limiting factor for lynx in Great Britain, but it could affect their densities. Further, habitat selection can vary depending on the availability of different habitats (Oeser et al., 2023b; Čonč et al., 2024), which means the response lynx would have to the landscape in Great Britain is uncertain.

We predicted these unknowns would affect reintroduction success (P3) and therefore used different habitat suitability models (Oeser et al., 2023a) and territory sizes to allow the emergence of a range of lynx population densities typical in Europe (i.e. 0.83 to 1.8 lynx per 100 km^2). These parameters did drive differences in all measures of reintroduction success, for example some release sites were only successful with one habitat model, but these could be circumvented by choosing an appropriate release strategy (4.3).

Previous analyses (Hetherington et al., 2008; Johnson and Greenwood, 2020), which defined densities using a relationship between prey density and lynx density (Hetherington and Gorman, 2007), applied uncommonly high lynx densities, e.g., per 100 km^2: 2.63 in the Highlands (Hetherington and Gorman, 2007), 3.75 in Southeast England, and 5.57 in Thetford (Johnson and Greenwood, 2020). This is despite the estimates excluding lagomorphs and interactions with human disturbances. Our approach was more conservative since we instead altered the possible distribution of territory sizes (three distributions simulated), whereby density emerged as a function of individual habitat and territory selection, as well as demographic processes. We then determined which release sites offered high probabilities of reintroduction success under a range of emergent population properties. Specifically, the focal release sites have good potential for reintroduction success despite the different spatial distributions of lynx that emerged. Our conservative assumptions could be investigated empirically before a reintroduction to determine whether prey resources are available to support lynx predation rates observed in European populations (Oliveira et al., 2025).

Finally, it is recommended to consider the phylogenetic origins of reintroduced animals (Houde et al., 2015), so that species traits are well-suited (Crandall et al., 2000). This may also affect lynx (Bonn Expert Group, 2021) and, although not covered explicitly in our work, the different habitat and spatial scenarios we tested have indirectly shown that various traits (i.e., home range size, home range and within home range habitat selection) could be suited for release in Great Britain.

4.3. Management choices for release

4.3.1. Release site

Release site assessment is an established aspect of reintroduction biology, necessary to select an appropriate site and understand the potential population development (Seddon et al., 2007; Kramer-Schadt et al., 2005). Consistent with our prediction (P3), we found reintroduction success was heavily dependent on the release site. Among our ten candidate release sites in Great Britain, we identified three that were found to be potentially viable independently; Aberdeenshire, Galloway (both in Scotland), and Kielder Forest (England). Reintroductions in the North York Moors, Peak District, North Wales, or South Wales had high uncertainty regarding success, while the New Forest and Southeast England were unsuccessful for 99 % of their respective simulations (see also Appendix D: Discussion 1).

Reintroductions comprising multiple release sites could improve success by reducing the risk of extinction due to stochastic events (Maschinski, 2006), which might be beneficial for lynx in fragmented landscapes (Zimmermann et al., 2007) and help create a larger population that can preserve more genetic diversity (Hewitt, 1999). For this reason, we also included multiple site releases in our prediction. Our results indeed showed that combinations of the three individually viable sites could have an even higher likelihood of success, particularly in terms of population size and genetic diversity. This echoes the result of Ovenden et al. (2019), who found a multiple site release of lynx in Scotland had a higher chance of demographic success compared to single-site releases.

We only explicitly tested a subset of potential release sites, but others in Scotland could even be more successful. Therefore, it would be important for reintroduction practitioners to test the viability of specific releases before a project is underway.

4.3.2. Number of individuals, sex-ratio, and timing

Releasing sufficient individuals for species reintroductions is important (Tracy et al., 2011), especially for lynx (Kramer-Schadt et al., 2005). Past lynx reintroductions were based on very few individuals (Breitenmoser-Würsten and Obexer-Ruff, 2003), but since the 21st century, reintroductions have released at least 20 individuals. For example, the Harz Mountains population was founded with 20 captive-bred individuals (Mueller et al., 2020), the Palatinate Forest with 20 wild-caught individuals from Switzerland and Slovakia (Idelberger et al., 2021), and West Pomerania with 61 captive-bred individuals (Tracz et al., 2021). As such, we predicted the number of lynx released would affect reintroduction success (P3). Indeed, our simulations showed that releasing 10 lynx would only suffice demographically with the most advantageous conditions, whereas 20 lynx would be sufficient in the focal release sites for both demographic and genetic viability. Releasing 40 lynx was best, especially when dividing individuals among different release sites.

Although lynx's territorial behaviour leads to a higher density of resident females than males (e.g., Schmidt et al., 1997), we found in contrast to our prediction that the released sex-ratio, whether even or female biased, was of little importance for reintroduction success. Also release timing was only relevant when releasing fewer individuals among multiple release sites, in which case releasing 40 lynx circumvented any adverse negative effect on extinction probability and improved genetic diversity.

4.3.3. Source population genetics

Even with an ideal start, genetic drift is inevitable in isolated populations, which causes a decline in genetic diversity, and can eventually affect demographics due to inbreeding depression (Keller and Waller, 2002). This is also the case for the lynx populations in Europe (Mueller et al., 2022), and hence we predicted that the source population would affect population genetics. Our simulations showed that releasing lynx of diverse origins is important to maximise long term genetic diversity. Our results showed that a lynx reintroduction in Great Britain could have the potential to retain a similar level of genetic diversity after 100 years as that of large autochthone populations (allelic richness ≅ 4.5; Bull et al., 2016).

4.4. Habitat creation

The habitats in Great Britain are in a poor state (Burns et al., 2023) and the governments of Great Britain have set habitat recovery targets to counter this (Department for Environment, Food & Rural Affairs, 2018; Scottish Government, 2020). We predicted that habitat improvements could make some release sites viable that would not be today (P4). However, we found that our green future scenario did not dramatically change the extinction probability for sites that were not viable under today's habitat conditions. That said, population sizes and connectivity were improved for release sites with already low extinction probabilities.

Considering the uncertain policy delivery, our green future scenario might seem an optimistic. However, we were conservative by selecting a scenario in line with national carbon reduction goals (Bradfer-Lawrence et al., 2021), using a high threshold for forest cover, and we did not consider any other improvements to connectivity, such as green infrastructure. Further, there are many factors, such as socioeconomics, politics, or climate change, that could drive land use and land cover change in the future. These could have significant impacts on reintroduced lynx but were out of the scope of our current research. If large landscape changes do occur it would be important to consider their potential impacts in future viability assessments.

4.5. Potential reintroduction success in Great Britain

Releases in Kielder Forest had low extinction probabilities for both habitat models, even with the largest territory sizes (lowest lynx density). Only when baseline or added mortality were at their highest values did extinction probabilities exceed 5 %, which is an unlikely situation (4.1, 4.6). Reintroduction in Kielder Forest resulted in 50–60 independent individuals for status quo and 130 to 140 for the green future habitat conditions, respectively, under medium parameters, and the population development had not yet plateaued at 100 years. Kielder Forest and the connected Southern Uplands was previously identified as a suitable patch, with estimates between 50 and 55 individuals based on densities between 0.83 (Hetherington et al., 2008), 1.33 (Johnson and Greenwood, 2020) and 2.63 (Ovenden et al., 2019) lynx per 100 km^2. Despite the varying density figures, or territory sizes, these population estimates, and our own, are quite consistent.

Compared to England and Wales, more research attention has hitherto been focused on a potential Scottish lynx population (Hetherington and Gorman, 2007; Hetherington et al., 2008; Ovenden et al., 2019; Philips, 2020), including population estimates between 235 and 450 lynx. Our estimates are towards the lower end, at around 290 individuals (based on a simultaneous Aberdeenshire and Galloway release). Ovenden et al. (2019) did not consider the ecologically connected patches that crossed the English border, and Kintyre had the lowest extinction probability of the release sites they tested, whereas we found Kintyre performed worse than Aberdeenshire and Galloway, depending on the habitat model we used. According to our work, the connectivity of Kintyre to the bulk of Northern Scotland depends strongly on lynx habitat selection. For this reason, our results point to Aberdeenshire as a more reliable release site, due to the low extinction risk and good connectivity with the rest of northern Scotland, which promoted population growth.

We only tested multiple site releases using release sites that we found had low extinction probabilities individually, therefore extinction risk was not greatly reduced with a multiple site reintroduction. We did, however, find that population expansion was faster when the same number of released individuals was divided among two or three sites as opposed to one. Further, the total population size after 100 years was larger with multiple release sites, partly due to the low connectivity between the key patches of suitable habitat (i.e. southern Scotland and Kielder Forest, and northern Scotland).

Releasing 40 individuals across two or three sites conserved allelic richness better than a single site, while heterozygosity did not differ between Aberdeenshire and a multiple site release. Since allelic richness is more appropriate for understanding the adaptability and evolutionary potential of species (Allendorf, 1986; Caballero and García-Dorado, 2013), this measure is of utmost importance for reintroduced populations. It is still crucial for multiple site reintroductions to release sufficient individuals to avoid founder effects on genetic diversity or local extinction.

Although the multiple site releases Aberdeenshire-Galloway and Aberdeenshire-Kielder Forest were broadly comparable, the latter combination gave a higher allelic richness than the former when using the local habitat model. This was also reflected in single site releases at either Galloway or Kielder Forest, where Kielder Forest returned higher allelic richness than Galloway with either habitat model. Further, the most promising connectivity corridor between northern and southern Scotland lay between Glasgow and Edinburgh to the east of the M74. This seems more accessible from the east, i.e. from Kielder Forest, than from the west, i.e. Galloway. However, the low connectivity between the suitable habitats north and south of Scotland's Central Belt means colonisation of all suitable patches from a single site release is unlikely. The sex-biased dispersal of lynx (Zimmermann et al., 2005) could lead to these patches being occupied by males only, precluding colonisation - a phenomenon observed elsewhere in Europe (Herdtfelder, 2014). This supports the idea of releasing lynx into more than one site to maximise success. Given releases in patches north and south of the Central Belt (e.g. Kielder Forest and Aberdeenshire), it is possible that genetic exchange via infrequent male dispersal events will be sufficient for long-term gene flow. However, this question was outside the scope of the current work.

In this study we tended to focus on the best possible conditions for reintroduction. In practise these may not be achievable (e.g. timing, sex-ratio, number released, source population genetics). It can be assumed that reintroduction planning is constrained by management, logistical, and stakeholder concerns that do not always allow an optimal strategy to be implemented. That said, we measured success over 100 years as a standalone population within Great Britain, without subsequent management actions. Ideally, natural dispersal events would provide sufficient connectivity and genetic exchange between subpopulations (Gajdárová et al., 2021), yet, in continental Europe, habitat fragmentation means lynx populations are isolated (Kramer-Schadt et al., 2005). The success of a potential European metapopulation might depend on artificial methods (Premier et al., 2021). Indeed, translocations for genetic rescue (Pazhenkova et al., 2025) and to strengthen metapopulation structures (Molinari et al., 2021; Krebühl et al., 2021; Lynx Thuringia, 2024) have become integral for conserving reintroduced lynx populations. It is apparent that a reintroduction is not the final intervention, and, in this respect, we set unfairly high expectations to assess reintroduction viability. Interventions to create artificial connectivity would no doubt provide the best viability beyond the population establishment phase, but quantifying the specific parameters required for these interventions (e.g., number of lynx, frequency of releases, sex-ratio, locations) was outside the scope of the current work.

4.6. The human dimension

Currently, human-nature relations are unbalanced. Human activities cause climate change, biodiversity loss, and ecosystem destruction (Sage, 2020), while simultaneously human well-being depends on nature's provisioning of services (Daily, 1997). Solutions to these problems seem to depend on redressing the balance in human-nature dynamics, for example for mitigating climate change (Griscom et al., 2017) or epidemics (i.e., “one health”; Gibbs, 2014). Reconnecting humans to nature could help nurture a sense of place that would be pivotal in ecosystem restoration (Hausmann et al., 2016).

Conservation biology aims to provide practical information that can help protect biodiversity in the face of threats (Soulé, 1985), such as global change. While protecting natural or intact ecosystems that are rich in biodiversity is ideal, ecosystems are often already perturbed. Restoring the functioning of perturbed ecosystems can also help bring humans and nature back into balance. It is in this context that the United Nations declared this "the Decade of Ecological Restoration" (2020–2030), underlining ecosystem restoration as a key ingredient to reach diverse environmental goals (United Nations Environment Agency, 2019).

Great Britain's ecosystems are some of the most perturbed in Europe (Burns et al., 2023). The governments of Great Britain recognised this and in line with international treaties have made species and habitat recovery, including reintroductions, a goal (Department for Environment, Food & Rural Affairs, 2018; Scottish Government, 2020). Reintroducing species with key functional roles should be a priority in restoration (Lipsey et al., 2007). The missing trophic level of apex predators in Great Britain, and their ecosystem roles (Ripple et al., 2014), makes them an obvious target to restore naturalness. Further, such flagship species may ignite interest in conservation and ecosystem restoration (Meffe and Carroll, 1997) and help reconnect the public to nature (Palacios-Pacheco et al., 2024).

Lynx is an elusive species that poses no physical threat to humans. Despite this, it has not escaped controversy (Lüchtrath and Schraml, 2015; Červený et al., 2019; Kirkland et al., 2021). Indeed, their reintroduction could be contentious with some stakeholders (Wilson, 2004; Hawkins et al., 2020; Wilson and Campera, 2024; Whiley and Tzanopoulos, 2024). The illegal release of four lynx in Scotland in January 2025 could lead to mistrust and conflict among stakeholders (Whitehead, 2025), which is wholly counterproductive to ecosystem restoration goals (Coz and Young, 2020).

In Europe, illegal killing is the leading cause of mortality of lynx (Andrén et al., 2006; Sindičić et al., 2016). Our results showed that with medium illegal killing rates (added ~ 7 % per year, based on European mean) a reintroduction may succeed, however higher rates are unlikely to be reconciled. Reintroduction success depends on the harmonious coexistence of lynx with local stakeholders, which begins with dialogue and trust among involved parties (Liukkonen et al., 2009). If social aspects of a potential reintroduction are carefully managed, persecution could fall below the European average. Understanding the socioeconomic drivers of acceptance locally is a crucial next step to help design appropriate public engagement. Consultations must be integrated into the decision-making process to mediate an acceptable relationship between stakeholders and lynx well before reintroduction begins (Drouilly and O'Riain, 2021; Marino et al., 2024).

5. Conclusions

Ecosystem restoration provides us an opportunity to mitigate impacts of human activities on nature. Species reintroductions, especially of missing functional roles, could play an important part in restoration. Therefore, in this study we explored the ecological feasibility of lynx reintroduction in Great Britain, informing our simulations with empirically derived data.

Reintroductions in our focal sites; Aberdeenshire, Galloway, and Kielder Forest, were the most likely to succeed under diverse scenarios, including different demographic, habitat selection, and release conditions. Despite fragmented habitat across Great Britain, populations could persist in some patches, although connectivity between suitable areas was poor. We mapped landscape usage that indicates the potential dispersal corridors and where connectivity might be protected or improved.

Based on our findings, the key components in a reintroduction strategy would consist of: 1) a multiple site release in two or more of the three focal sites, 2) a total of 40 released individuals (although a release of 20 in any one focal release site was sufficient), 3) diverse founder genetics in order to provide the best protection against genetic drift and inbreeding, 4) appropriate health screening of released animals to ensure natural mortality is minimized, and 5) key stakeholder and public acceptance is critical to ensure average, or lower, mortality related to persecution.

At this stage, considering predecessor studies and our own results, we believe the ecological understanding of lynx's reintroduction potential in Great Britain can only be improved with a carefully designed and monitored release. However, it is imperative that this is done legally and with broad support. Our results provide the information for discussions between stakeholder groups and indicate harmonious coexistence between humans and nature is needed for a lynx reintroduction to be a success.

CRediT authorship contribution statement

Joe Premier: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Deborah Brady:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Samantha Cartwright:** Writing – review & editing, Writing – original draft, Resources, Project administration, Methodology. **Hugh Robinson:** Writing – review & editing, Resources, Methodology, Funding acquisition, Conceptualization. **Byron Weckworth:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Julian Oeser:** Writing – review & editing, Software, Resources, Methodology, Formal analysis, Data curation, Conceptualization. **Adam Eagle:** Writing – review & editing, Supervision, Project administration, Funding acquisition. **Stephanie Kramer-Schadt:** Writing – review & editing, Supervision, Software, Resources, Methodology, Investigation, Formal analysis, Conceptualization. **Marco Heurich:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Data curation, Conceptualization.

Open research statement

No data were collected for this study.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Previous lynx viability studies for Great Britain

The viability of potential lynx populations in Great Britain was first estimated using the occurrence of roe deer (*Capreolus capreolus*), the lynx's main prey in many areas (Kitchener, 2001). Assuming a minimum viable population of 250 individuals (Breitenmoser et al., 2001), three potential populations were identified, including a viable population of 885 lynx in Scotland and northern England and two others that were either marginal or not viable. Subsequently, the relationship between lynx and prey density from data published on four European lynx populations was used to estimate potential lynx densities (Hetherington and Gorman, 2007), suggesting smaller potential populations ($n \approx 394$ in the Highlands, $n \approx 51$ in the Southern Uplands). However, these numbers did not account for the availability of suitable habitats for lynx, nor the population effects of threats like hunting, poaching, and road mortality.

Habitat suitability and landscape connectivity for lynx in Great Britain was considered using a rule-based modelling approach in population viability assessments (Hetherington et al., 2008; Johnson and Greenwood, 2020). Hetherington et al. (2008) identified 30 patches totalling approx. 21,500 km^2 of suitable habitat in Scotland and northern England (Hetherington and Gorman, 2007). However, the Highlands, in northern Scotland, and the Southern Uplands, in southern Scotland, lacked connectivity, suggesting that colonisation of the latter from southern Scotland and northern England was unlikely. Johnson and Greenwood (2020) identified 63 suitable habitat patches in England, Wales, and southern Scotland, totalling 11,369 km^2, and estimated a total of 256 lynx across all habitat patches. Although Hetherington et al. (2008) focussed on Scotland and Johnson and Greenwood (2020) focussed on England and Wales, their analyses overlapped in Southern Scotland and Northern England, where they proposed similar population sizes (50 and 52 individuals, respectively). However, these investigations relied on expert knowledge to assess habitat suitability, which may not capture important nuances in landscape composition, and did not consider the spatial arrangement of habitat that can affect lynx behaviour and demographics (Kramer-Schadt et al., 2005).

Besides habitat suitability, a critical aspect for potential reintroductions is the long-term viability of a population (Beissinger and McCullough, 2002). Changes in a population over time can be modelled with demographic parameters, such as birth and survival rates, applied to a starting population size. Both Hetherington (2005) and Johnson and Greenwood (2020) used estimated carrying capacities as starting populations and demographic parameters from European lynx populations to investigate the viability of potential populations in Great Britain. However, these assessments were not spatially explicit. Spatially explicit individual-based models (seIBMs) can incorporate demographic parameters of a species with their spatial behaviour and life history stages (Grimm and Railsback, 2013). The processes of survival, mortality, and reproduction modelled at an individual level allow interactions with other individuals and their environment. This type of modelling is frequently employed to simulate complex ecological systems where population level dynamics (e.g., population size, growth rate) emerge from individual-level decision-making, with the advantage of making fewer assumptions than population-based models (DeAngelis and Grimm, 2014). Indeed, Ovenden et al. (2019) used an seIBM to investigate the viability of lynx reintroductions in Scotland. Of three proposed reintroduction sites tested, they found a reintroduction was only viable with simultaneous releases in Kintyre and Aberdeenshire. However, as for prior studies, a rule-based habitat map was used.

Appendix B. The Eurasian Lynx Dispersal, Demographic & Genetic Model

We describe the model following the ODD protocol for individual-based models (Overview, Design Concepts, Detail; Grimm et al., 2010; Grimm et al., 2006; Grimm and Railsback, 2005). This ODD protocol is based on that of Kramer-Schadt et al. (2011) and Premier et al. (2020).

Purpose

We developed an individual-based, spatially-explicit population simulation model with neutral genetic markers, or - a demogenetic population model. This was used to assess the development of genetic structure and diversity of reintroduced lynx populations in heterogeneous landscapes under scenarios of different movement syndromes and founder population sizes. The model was previously published in a number of papers where it was used for a variety of purposes, e.g. for assessing the additional impact of roads (Klar et al., 2006), perceptual range (Pe'er and Kramer-Schadt, 2008), stepping stones (Kramer-Schadt et al., 2011), unknown mortality (Heurich et al., 2018) on population connectivity and viability. Further, it has been used to understand the effects of landscape and behaviour on population genetics (Premier et al., 2020). Here, we describe the basic model from the preceding papers; specific settings, simulation experiments and changes to the model rules are described in the respective publications. Here we describe the parameters as used in the current paper.

State variables and scales

The model consists of four sub-models, 1) a demographic model of lynx considering territory occupation, reproduction, and mortality, 2) a dispersal model that links the demographic processes onto a landscape sub-model (3), and 4) a genetic sub-model that handles neutral genetic markers. Demographic parameters stem from published data of long-term field studies in fragmented landscapes in Switzerland, Poland and Spain (Ferreras et al., 1992; Jedrzejewski et al., 1996; Breitenmoser-Würsten et al., 2001; Schmidt-Posthaus et al., 2002). The original dispersal module (Kramer-Schadt et al., 2004) was calibrated with field data from dispersing lynx collected in the Swiss Jura Mountains (Breitenmoser et al., 1993).

The state variables of the lynx individuals are (1) sex, (2) age, (3) location (x-y coordinates), (4) demographic status (disperser or resident) and (5) neutral genetic markers (microsatellite loci lengths). The landscape consists of a grid of 1 km^2 cells which corresponds with the animal's perceptual range as the smallest spatial unit. Cells represent functional landscape types for lynx and are classed in (a) suitable for breeding, (b) suitable for dispersal, (c) avoided, but used occasionally, and (d) barriers (Schadt et al., 2002). Landscape borders (i.e., at the seacoast) are reflective. Time steps represent one day to capture the variability in daily dispersal distance in concert with the landscape variability. Simulation time (in years) is variable and depends on the question addressed.

Process overview and scheduling

At the beginning of each model time step (year), the number of resident and non-resident males and females on the landscape map are determined. All non-residents older than 1 year disperse and search for territories (see Dispersal Sub-model). Each day, non-resident individuals disperse a certain number of steps with the direction depending on the underlying landscape type, search for a territory and undergo a daily mortality probability. The spatially explicit processes of dispersal and territory selection in the model depend upon local habitat quality within the immediate surrounding of the animals' location. If dispersing individuals survive (probabilistic event depending on daily dispersal mortality M_{disp}), they settle or continue dispersing in the following year. At the end of each daily time step, the location of the dispersing individuals is updated. If the disperser has found and occupied a territory, the status is set to resident. Next, the demographic, and therefore also genetic, processes of the residents come into play (see Demographic Sub-model). At the end of each year, the occupied territories of the residents and the age and status of each lynx are updated (Appendix B: Fig. 1).

Design concepts

The model considers lynx demography and genetic inheritance, dispersal, territory selection and occupation and interaction of the landscape types with these ecological processes. The behavior and demography of the lynx are imposed by reaction towards the landscape types as well as by status-dependent parameters. Stochasticity is included to represent demographic and environmental noise. Allee effects are considered in the demographic sub-model: only when male and female lynx have overlapping territories is reproduction considered. Inheritance of neutral genetic markers is determined by Mendelian inheritance and is inherently stochastic. Genetic mutation during reproduction is considered in the genetic sub-model such that allele loci may mutate via a stepwise mutation model at a given rate.

Initialization

Initial population characteristics (size, age distribution, location, population genetics) are variable and are set via individuals' state variables. Each individual is attributed: sex, location (x-y coordinates), and 12 loci-pairs (i.e. 24 neutral genetic markers).

Input

The model does not include any external model or data files of driving environmental variables.

Sub-models

Demographic sub-model. — This sub-model controls the individuals with resident status. Territory occupation, reproduction, and resident mortality are processes happening on an annual level. Each resident female whose territory is overlapped by that of a male reproduces with a certain probability (P_{birth}, Appendix B: Table T1). We set the probability of having one or two cubs surviving their first year to 0.5 and the sex ratio to 1:1 Annual resident mortality (M_{res}) is also a probabilistic event. The cells belonging to a resident's territory are kept if the individual survives.

Genetic sub-model. — This sub-model handles the diploid genotypes (neutral genetic markers modelled as microsatellite loci lengths) during reproduction events. Each cub which survives their first year inherits 1 maternal and 1 paternal allele at each loci (total 12 loci allele pairs), with an even probability given to each parental allele. Genetic mutation is simulated using a stepwise mutation model (SMM). During reproduction the inherited alleles undergo mutation at a chosen rate. If mutation of an allele takes place the SMM is applied; as such an integer allele A_0 has an even probability of increasing or decreasing its value by 1, to A_0+1 or A_0-1. The lower limit is constrained as a microsatellite length of zero is not possible, hence if $A_0 = 1$ a length decreasing step is not permitted and an even probability is assumed for either increasing or keeping the allele length.

Dispersal sub-model (including territory searching behaviour). — Each day, a certain number of movement steps (*s*) is assigned, based on model calibration with field data (Appendix B: Table T1). The spatial unit of dispersal is one movement step, i.e. 1 km^2 grid cell. In each step, individuals survey their eight-cell neighbourhood and make decisions based on this information (see below). Their choice of direction is comprised of two components: the probability of leaving preferred dispersal habitat by stepping into the matrix (P_{matrix}, Appendix B: Table T1), and a correlation factor determining the probability of continuing with the same direction as their previous movement within a day (P_C, Appendix B: Table T1). The hierarchy is a preference of dispersal habitat over a persistent movement forward, with the first direction of every day chosen randomly. Within a day, the next cell is chosen based on the preference for dispersal habitat and the avoidance of matrix. If the neighbourhood of a dispersing lynx, comprising the origin cell and its 8 neighbours, contains only matrix or dispersal habitat cells, the probability of choosing one of these cells is random (i.e., 1/9). However, if the neighbourhood is a mixture of dispersal habitat and matrix, we consider the preference for dispersal habitat as follows: The number of matrix cells n_{mat} within the neighbourhood is counted. The probability of leaving dispersal habitat P_{leave} is then dependent on the number of matrix cells around the origin cell multiplied by a factor P_{matrix} (ranging from total avoidance of matrix [$P_{matrix} = 0$] to randomly choosing any surrounding cell [$P_{matrix} = 1/9$], with $P_{leave} = n_{mat} * P_{matrix}$. If an animal has stepped into the matrix, it is assigned a 'memory' of its last location in a dispersal habitat, toward which it returns should it fail to find a dispersal habitat cell within $P_{maxmatrix} = 10$ steps. A daily mortality probability is included (M_{disp}, Appendix B: Table T1). We note that the mortality probability M_{disp} is landscape-independent due to the absence of sufficient field-data regarding mortality risks in different landscape types.

We upscale the landscape in terms of territory searching behaviour, i.e., each dispersing female needs to collect a certain amount of contagious cells of non-occupied breeding habitat ($N_{HRCells}$), whereas males search for cells that are already occupied by females and can overlap up to 3 females. To include stochasticity in territory size we draw for each female a random number of cells from a uniform distribution $N_{HRCells}$ between 70 and 100 cells. The simulated female then has to use this amount of cells as her territory. Once occupied, territory cells cannot be used by other females. In unoccupied areas the female that comes first has the best chance of occupying a territory.

Table T1

Basic parameter values for the demographic and the dispersal sub-models. Values can change depending on the scenarios assessed in the respective publications (for this publication see Table 1).

Sub-model	Symbol	Parameter value or range
Demographic sub-model		
Reproduction rate (=prob. of giving birth)	P_{birth}	0.75

(*continued on next page*)

Table T1 (*continued*)

Sub-model	Symbol	Parameter value or range
Annual mortality probability of residents	M_{res}	0.1 (translates into ~13 % annual mortality rate)
Genetic sub-model		
Mutation rate		10^{-4}/locus
Dispersal sub-model		
Correlation factor	P_C	0.5
Probability of stepping into matrix	P_{matrix}	0.03
Maximum number of steps an individual stays in matrix before returning	$P_{maxmatrix}$	10
Maximum number of steps per day	s_{max}	45
Exponent of step distribution	x	11
Daily mortality probability of dispersers	M_{disp}	0.0007 (translates into ~22 % annual mortality rate)

Each day, each dispersing lynx is assigned a certain number of movement steps s based on a probability $P(s)$ using a power function with an exponent x and parameter s_{max} that determines the maximum number of steps that a dispersing lynx can cover during a single day.

$P(s) = (1 - ((s - 1)/(s_{max} - 1)))^x$.

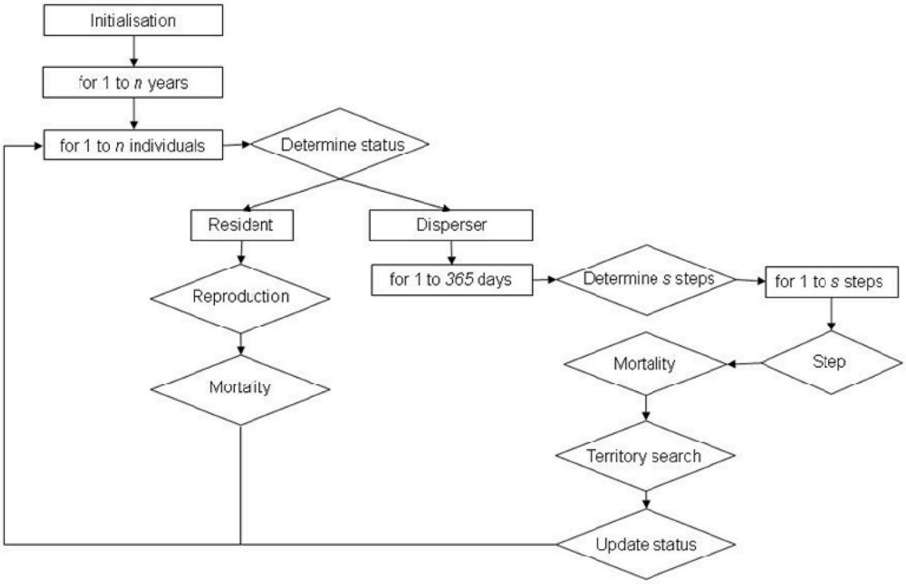


Fig. 1. Overview flow diagram of model processes.

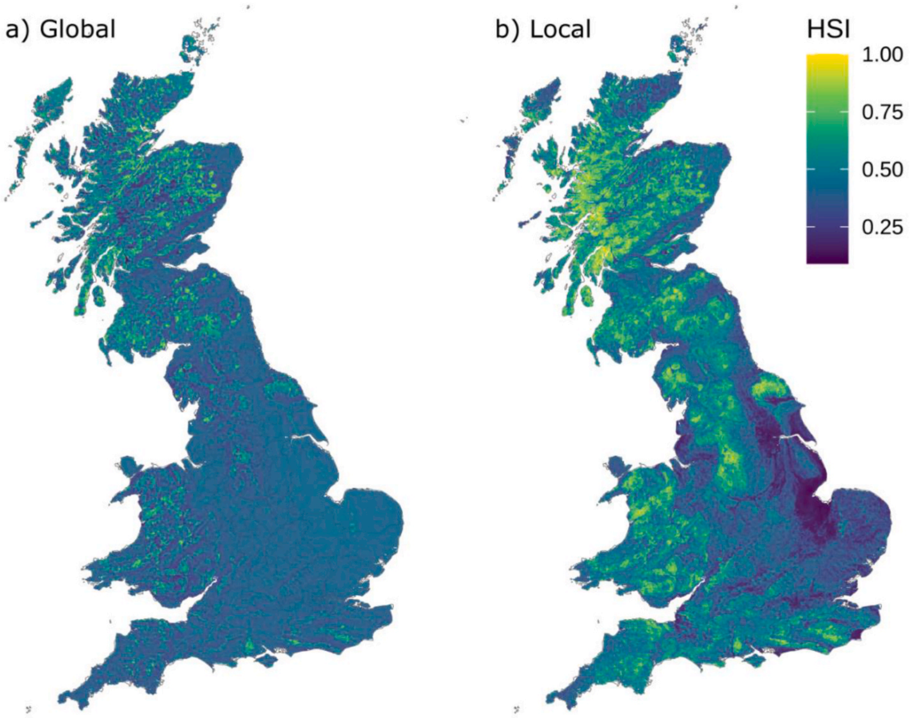
Appendix C. Methods and assumptions

Appendix C: Prey availability

There is a lack of broad-scale monitoring of deer densities across Great Britain, which various parties have highlighted as crucial knowledge gap when assessing the viability of reintroduced lynx (e.g. Milner and Irvine, 2015). In the mid-latitudes of Europe and Fenno-Scandia, lynx mostly predate ungulates, especially roe deer (*Capreolus capreolus*) (>70 %) (Jędrzejewski et al., 1993; Molinari-Jobin et al., 2007; Krofel et al., 2011; Belotti et al., 2015). In Great Britain, there are six deer species present, namely: roe, red (*Cervus elaphus*), fallow (*Dama dama*), sika (*Cervus nippon*), Chinese water (*Hydropotes inermis*) and muntjac (*Muntiacus reevesi*) (Croft et al., 2019). These would likely make up the dominant prey species of lynx where their distributions coincide. However, lynx is an adaptable predator with a diet comprising over 50 documented prey species (e.g., Belotti et al., 2015; Khorozyan and Heurich, 2023a). Therefore, their diet can be supplemented many smaller species, including, for example, rabbits (*Oryctolagus cuniculus*) and hares (*Lepus* sp.). Although the current evidence from Europe suggests lynx do not frequently target livestock, it is possible that smaller livestock, such as sheep, might be predated in areas close to suitable lynx habitats or if wild prey species are of lower abundance (Stahl et al., 2002; Odden et al., 2006, 2008; Khorozyan and Heurich, 2023b). The available population estimates and presence maps (Mathews et al., 2018) and occurrence probability maps (Croft et al., 2019) show that prey species are available across Great Britain. Therefore, prey availability is unlikely to limit lynx colonisation of suitable habitats but affect the emergent lynx densities. For this reason, we simulated a range of emergent densities as described in the main text.

Appendix C: Habitat models

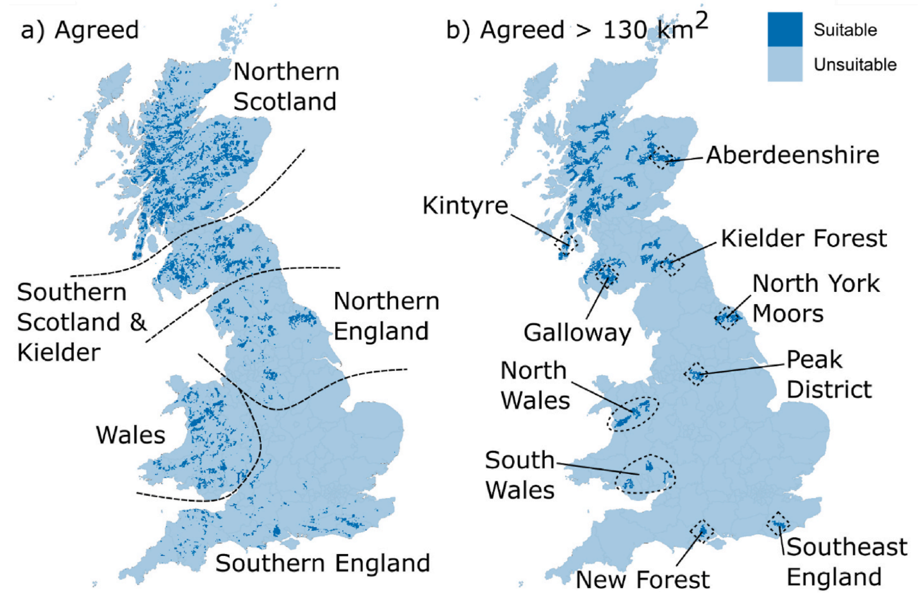
Oeser et al. (2023) used two methods to fit and predict habitat suitability models. First, a “global” approach in which all data from all populations were combined into one habitat suitability model. Second, a “local” approach, whereby habitat suitability models were fitted for each population, and predictions across Europe were combined via weights defined by the ecological similarity to training regions found in each predicted grid cell. The scale of selection for the simulation model is within home-range (Kramer-Schadt et al., 2005), also called 3rd order selection (Johnson, 1980), with the distribution of lynx (i.e., 1st order) an emergent phenomenon. The two approaches provide relatively similar habitat suitability predictions (Appendix C: Fig. 1), but their methods are distinct and deliver different spatial organisation of suitable and unsuitable areas. We therefore tested reintroductions under both habitat model scenarios, for a sensitivity analysis of the potential behavioural responses lynx might have to the British landscape.



Appendix C: Fig. 1. Predicted relative lynx habitat suitability index (HSI) for Great Britain based on a) global model, b) local metamodel (Oeser et al., 2023).

Appendix C: Table 1
Habitat classification overview. Habitat classification maps provided in main text (as Fig. 2).

Habitat classification	Data source	Original values
Barrier	Corine landcover 2018 (European Environmental Agency, 2020a,b)	Continuous urban fabric, Discontinuous urban fabric, Industrial or commercial units, Road and rail networks and associated land, Port areas, Airports, Mineral extraction sites, Dump sites, Construction sites, Green urban areas, Sport and leisure facilities, Intertidal flats, Water courses, Water bodies, Coastal lagoons, Estuaries, Sea and ocean
	Global River Widths from Landsat (GRWL) Database	River sections of width >100 m
	OpenStreetMap (© OpenStreetMap contributors) downloaded from Geofabrik (https://download.geofabrik.de/)	Highways classified as motorways
Matrix	Oeser et al. (2023)	3rd order habitat suitability (Local <0.576, Global <0.400)
Suitable habitat	Oeser et al. (2023)	3rd order habitat suitability (Local ⩾ 0.576, Global ⩾ 0.400)
Breeding habitat	Oeser et al. (2023)	3x3 moving-window focal analysis to find minimum 3 adjacent cells of suitable habitat.



Appendix C: Fig. 2. a) Patches of suitable habitat as agreed by both global and local model predictions, with the geographical nomenclature used to describe the regions provided, and b) agreed patches larger than 130 km^2 chosen arbitrarily to reduce the number of locations tested to ten with the identified release locations labelled. In North and South Wales several patches of similar size were found, therefore released lynx were divided among these.

Appendix C: Linear feature maps

The categorical habitat maps described above provide the basic landscape upon which the simulated lynx individuals base their movement and territorial decisions, and in turn constrains the spatially explicit demographic processes. The habitat, however, does not contribute to mortality of the individuals. One of the dominant mortality causes for lynx are vehicle collisions, which amount to 8 % of mortalities in European lynx populations (Premier et al., 2025). This is considered in the demogenetic simulation model via two underlying maps of risk (Heurich et al., 2018), one for resident lynx and one for dispersing lynx due to their different spatial behaviours and apparent mortality risks (Kramer-Schadt et al., 2004). It is therefore necessary to map the relative risk of each location to mortality due to the linear features by aggregating spatial data to these.

The spatial data used to create the linear features map were OpenStreetMap (© OpenStreetMap Contributors) highways and railways for both resident and dispersing animals, as well as the river width from GRWD (Allen and Pavelsky, 2018) for dispersing animals only. The true relative risk of the different road classes, railways, and rivers are not available for lynx in Great Britain. It is assumed that the risk depends on traffic density, which serves as both the source of mortality and the source of dissuasion (Seiler and Helldin, 2006). The highest collision risk would come from large busy roads (motorways), which are inherently the least likely to be crossed due to traffic density, size, noise, and structure (Seiler and Helldin, 2006). Motorways are known to be considerable barriers to dispersal of lynx (Zimmermann et al., 2005). For this reason, we included motorways as barrier in the habitat map to create a low crossing likelihood (i.e. zero unless the road passed over bridges or underground). Primary roads do not present a large barrier effect but do carry a large collision risk. These are therefore likely the most dangerous roads for lynx, as well as for many mammalian species in Great Britain, such as deer (Langbein, 2007). As was done in one simulation study on a lynx population in Germany (Heurich et al., 2018), we decided to define the relative risk of the different road classes based on the mortality rates for deer species on roads. Although various values have been reported, when the entire UK road network is considered the deer vehicle collision rates per km of major and minor roads are around 0.1 and 0.01 respectively (Langbein, 2007). We assigned railways the lower relative risk due to the low rates of railway mortalities found across Europe (Premier et al., 2025).

Resident linear features.

Using the OSM highways features we distinguished the classes: motorway, trunk, primary, secondary, tertiary, and unclassified roads, as well as railways. We excluded sections of roads and railways that passed over bridges or underground. For the unclassified roads, we removed those found in urban areas according to CLC (Appendix C: Table 4) to reduce overestimation of risk in residential areas. We then converted each road class into a raster layer with resolution 1 km^2 based on the length of roads per pixel (i.e., km/km^2). These road density rasters were then summed based on the relative risks for deer-vehicle collisions:

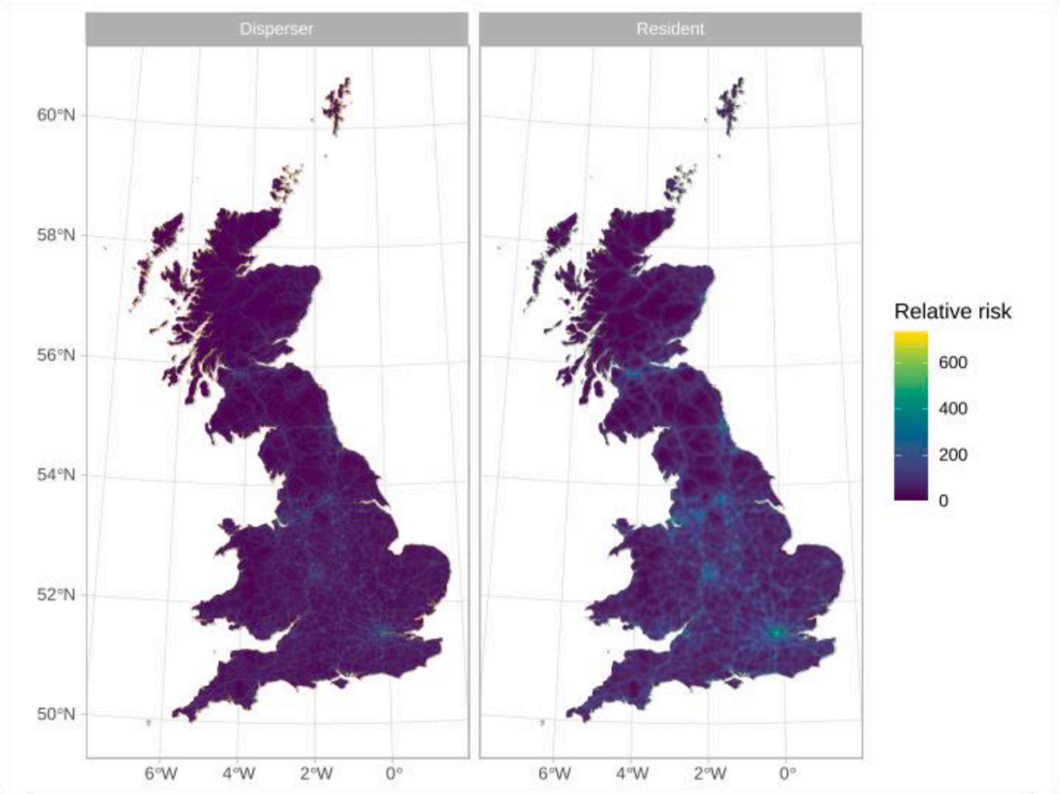
$$\begin{aligned} \mathrm{Risk}_{\mathrm{res}} &= 0.1 \times (\mathrm{Motorway} + \mathrm{Trunk} + \mathrm{Primary}) \\ &+ 0.01 \times (\mathrm{Secondary} + \mathrm{Tertiary} + \mathrm{Unclassified} + \mathrm{Railway}) \end{aligned}$$

Finally, the resident linear features risk map was smoothed spatially with a moving window of approx. 50 km^2, which is at the lowest extent of lynx home ranges (e.g. Molinari-Jobin et al., 2007), to distribute the risk as would be expected for resident lynx behaviour (Appendix C: Fig. 3).

Disperser linear features.

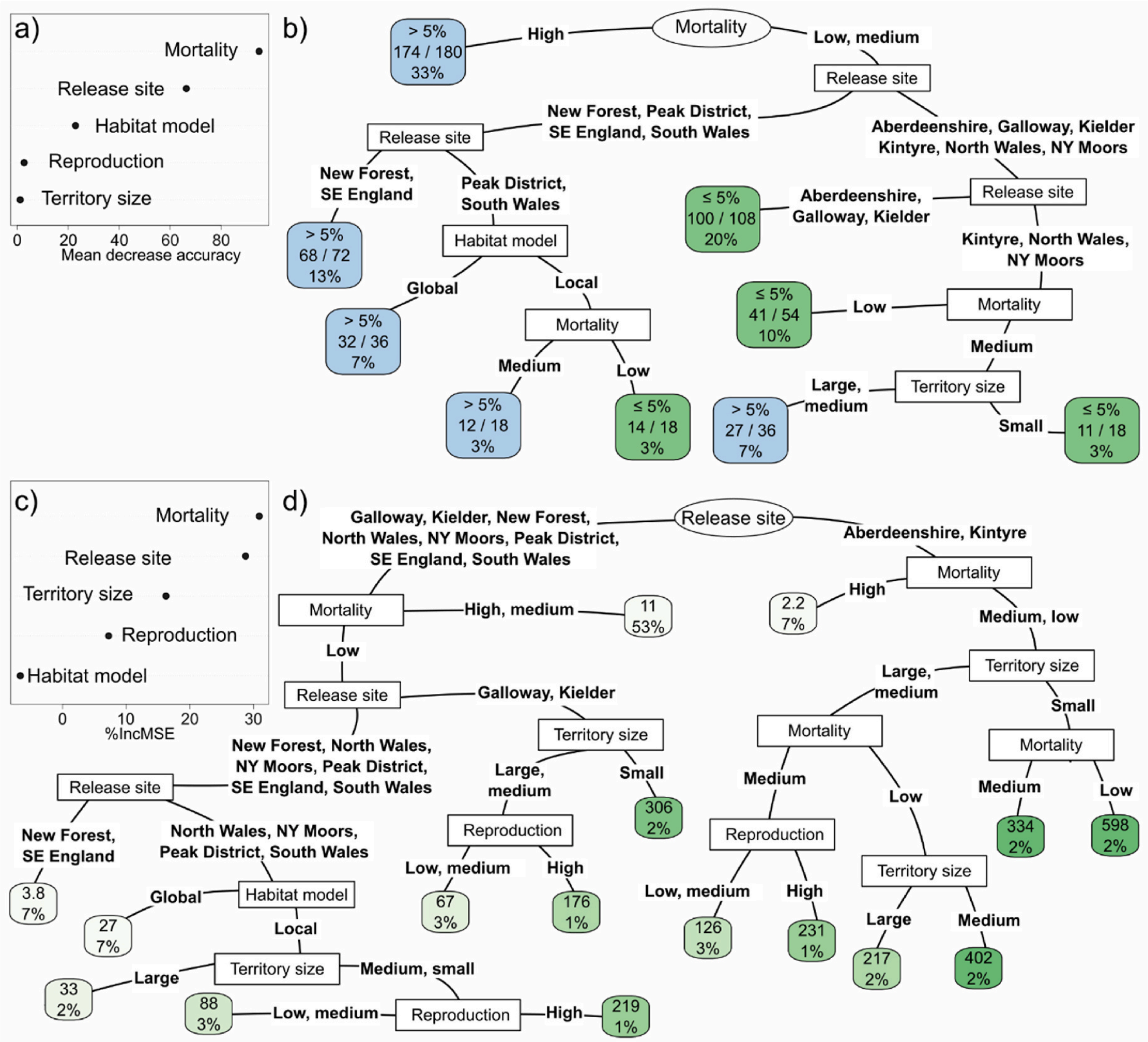
Similar to the resident linear features, we used the same classes of roads and railways. In addition, we used rivers with width >100 m. Since dispersers acquire a per step mortality probability derived from their movements through the landscape, the underlying linear features were handled slightly differently. For the unclassified roads, we removed those found in urban areas according to CLC (Appendix C: Table 1) to reduce overestimation of risk in residential areas. We removed sections of bridges and tunnels only for “minor” roads (secondary, tertiary, unclassified) and railways. Again, each category was rasterized based on its length in km/km^2. Before combining the rasters, we set the length of “major” roads (motorway, trunk, primary) that passed over bridges or through tunnels to zero km in the affected pixels. Thereby, allowing for lower risk connectivity if one or more major classes were safely avoidable in each pixel but maintaining risk due to unavoidable crossings of minor roads. Rivers of width 100 m or wider were given the higher relative risk as these were classified as barrier in the same way as motorways were for the habitat map. These were then summed with the respective weights:

$$\text{Risk}_{\text{disp}} = 0.1 \times (\text{Motorway} + \text{Trunk} + \text{Primary} + \text{Rivers}) \\ + 0.01 \times (\text{Secondary} + \text{Tertiary} + \text{Unclassified} + \text{Railway})$$

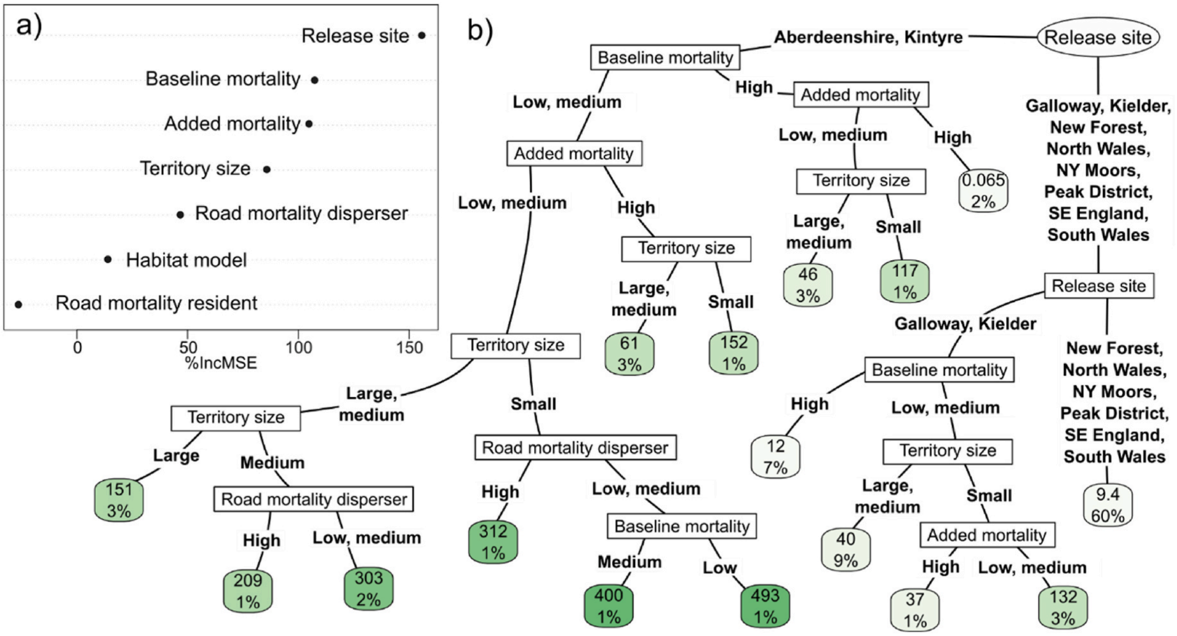


Appendix C: Fig. 3. Relative linear feature risk maps for different lynx statuses: resident and dispersing. Relative risk overlays county boundaries for spatial reference.

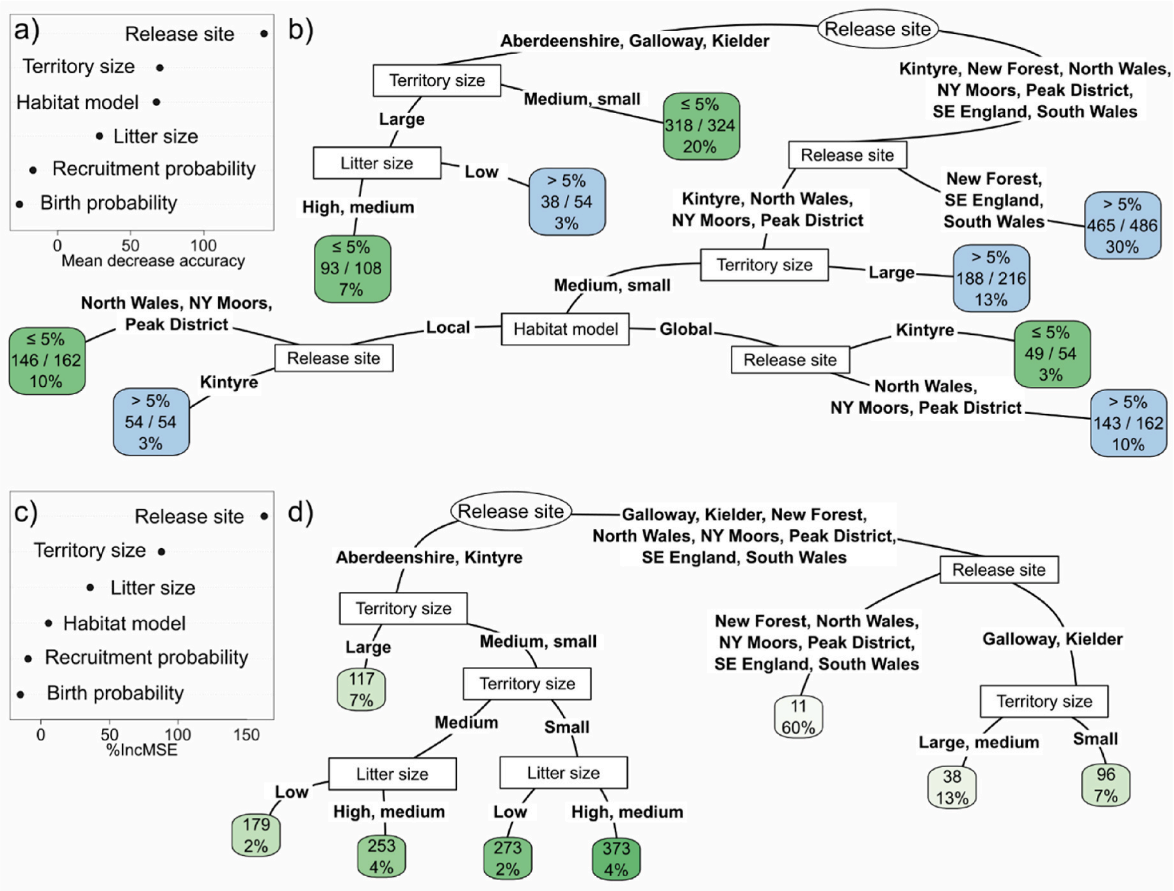
Appendix D. Results



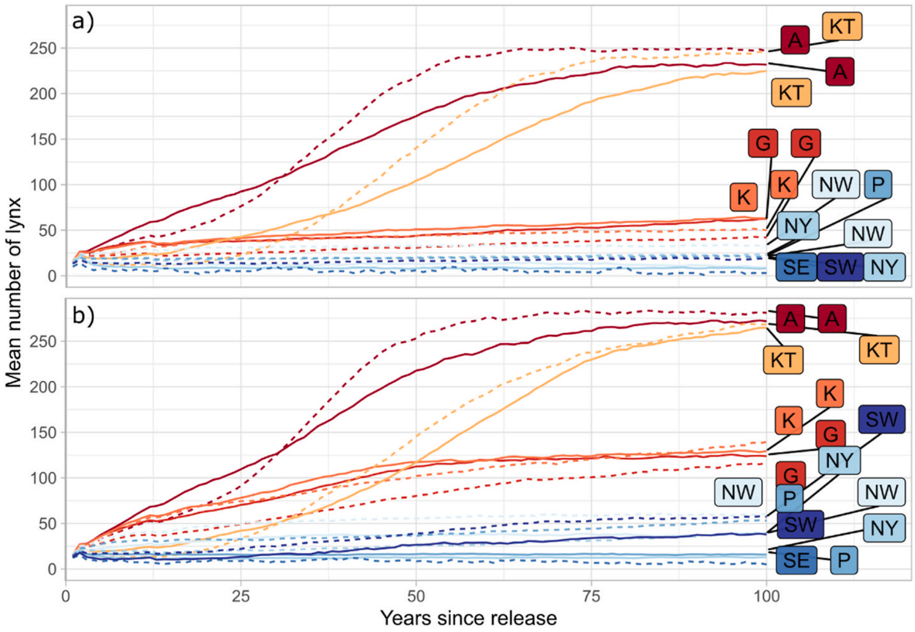
Appendix D: Fig. 1. Reintroduction success evaluated by extinction probability ≤5 % (a, b) and population size (c, d) 100 years after release when varying extreme combinations of grouped reproductive rates and mortality rates (set A, Table 1). Panels a) and c) provide variable importance from randomForest metamodels, while b) and d) show decision-trees from CaRT metamodels, respectively. At each decision-tree node (first node oval box and subsequently rectangular boxes), the data are split based on the parameter in the node and its values on the branches. At the terminal nodes, in b): the predicted extinction probability is indicated with the binary classification (success in green "≤ 5 %", failure in blue "> 5 %"), the fraction of the data subset in agreement with the classification, and the percentage of the entire dataset within the subset, and in d): the mean predicted population size and the percentage of the entire dataset within the subset are given. Larger populations indicated by darker green terminal nodes.



Appendix D: Fig. 2. Reintroduction success evaluated by population size 100 years after release when varying mortality rates individually (set A, Table 1), with a) variable importance and b) decision-tree (continuous response) randomForest and CaRT metamodels, respectively. At each decision-tree node (first node oval box and subsequently rectangular boxes) the data are split based on the parameter in the node and its values on the branches. The mean predicted population size and the percentage of the simulations within the subset are given at the terminal nodes. Larger populations indicated by darker green terminal nodes.



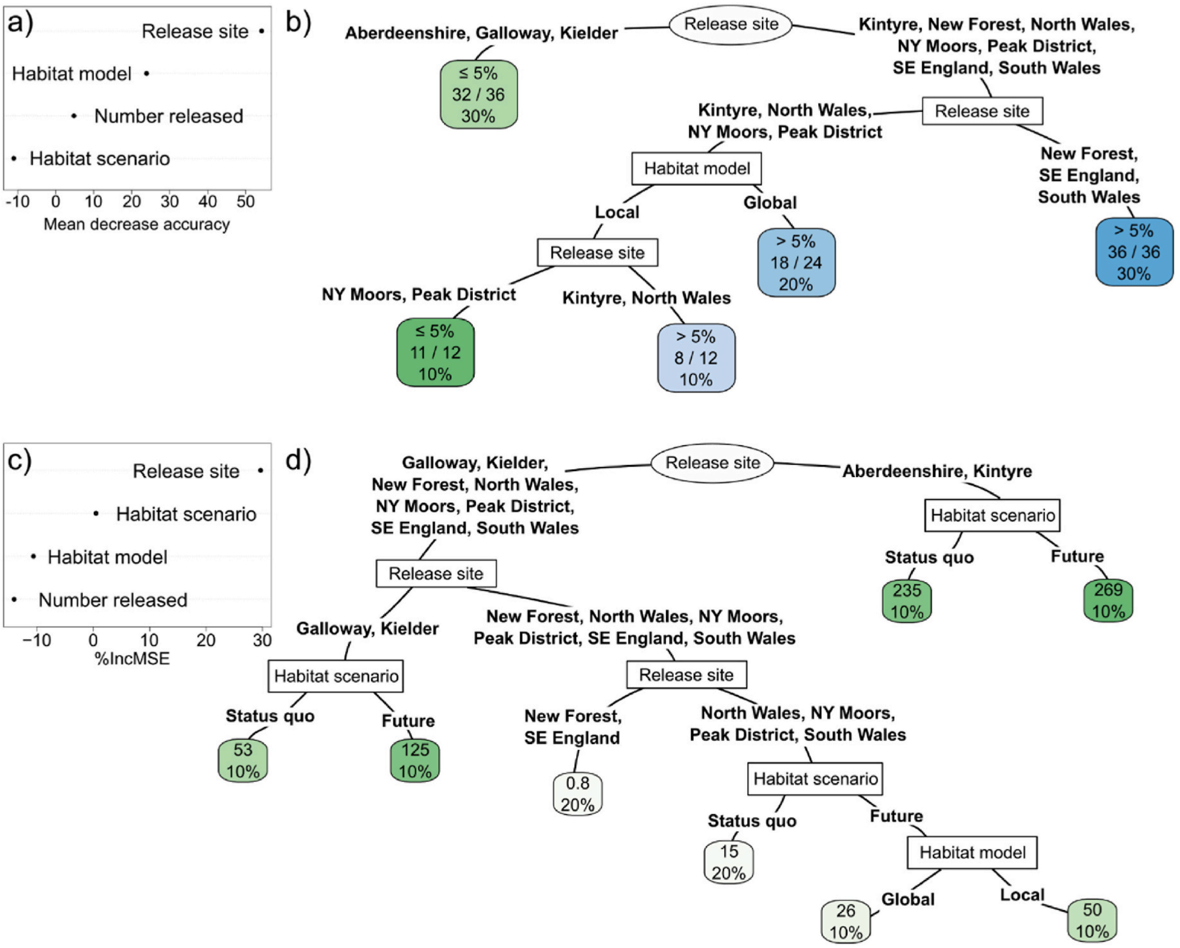
Appendix D: Fig. 3. Reintroduction success evaluated by extinction probability ≤5 % (a, b) and population size (c, d) 100 years after release when varying reproductive rates individually (set A, Table 1). Panels a) and c) provide variable importance from randomForest metamodels, while b) and d) show decision-trees from CaRT metamodels, respectively. At each decision-tree node (first node oval box and subsequently rectangular boxes), the data are split based on the parameter in the node and its values on the branches. At the terminal nodes, in b): the predicted extinction probability is indicated with the binary classification (success in green "≤ 5 %", failure in blue "> 5 %"), the fraction of the data subset in agreement with the classification, and the percentage of the entire dataset within the subset, and in d): the mean predicted population size and the percentage of the entire dataset within the subset are given. Larger populations indicated by darker green terminal nodes.



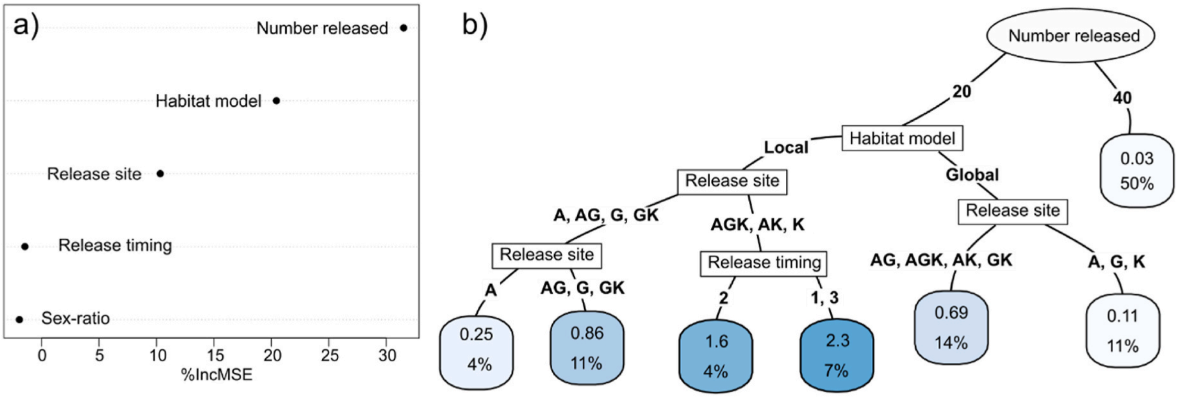
Appendix D: Fig. 4. Population size for different single release locations under: a) status quo and b) green future habitat scenarios (set B, 20 lynx). Solid line – global and dashed line – local habitat models. Release locations are indicated with the names: A - Aberdeenshire, G - Galloway, K – Kielder Forest, KT - Kintyre, NF - New Forest, NW - North Wales, NY - North York Moors, P - Peak District, SE - Southeast England, SW - South Wales. Population size only considers simulations replicates that reached 100 years, as such there are no lines for the New Forest releases.

Appendix D: Results 1. Simulation set B: Status quo vs "green future"

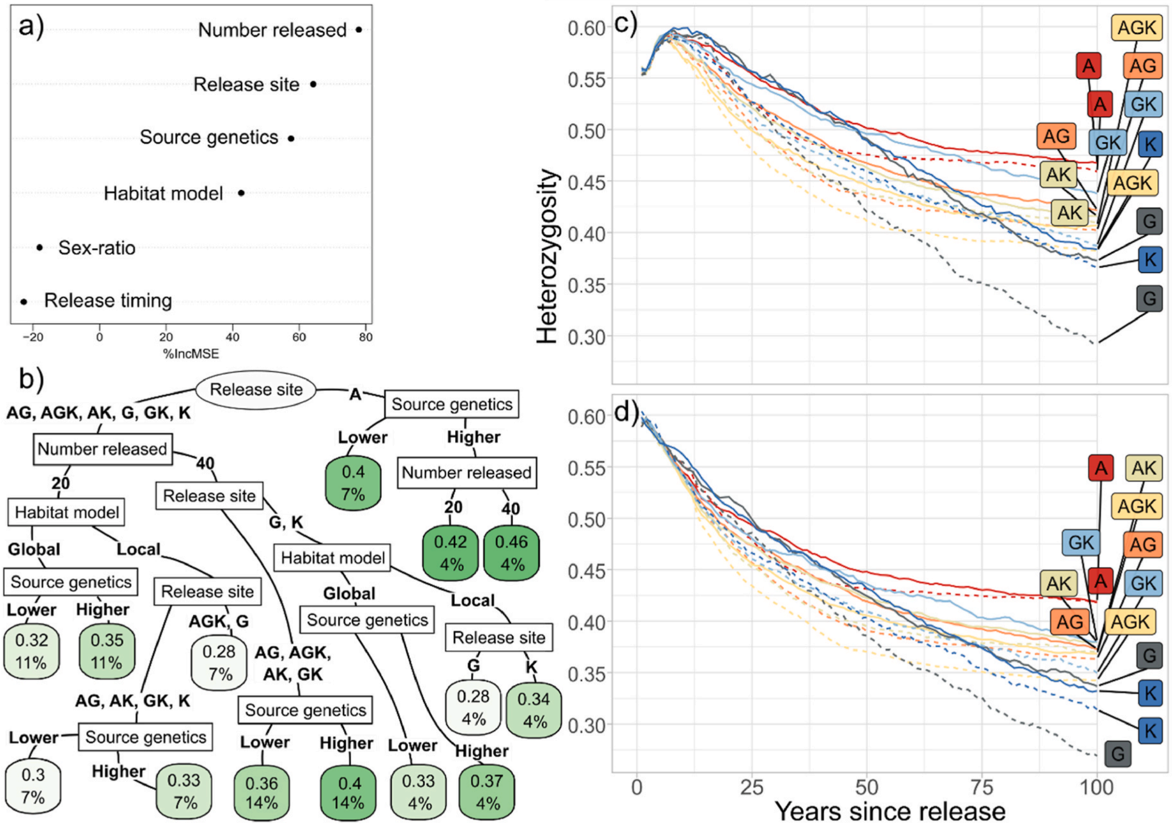
Comparing the status quo and 'green future' habitat scenarios (Table 1: Set B), we found that the release location was of far greater importance for predicting extinction probability and population size than the habitat scenario (Appendix D: Fig. 5a). The decision-tree showed that the 'green future' scenario did not improve the likelihood of extinction below the 5 % threshold (Appendix D: Fig. 5b). Releases in Southeast England and the New Forest exceeded 5 % extinction within 15 years (Fig. 4b). The habitat model (global vs local), however, was an important driver of extinction probability according to the decision-tree. For example, 'green future' releases of 40 lynx in Kintyre, North York Moors, and Peak District went over 5 % extinction within 70 years for one habitat model only. The decision-tree suggested that releasing 20 individuals would satisfy the 5 % threshold for both habitat models. However, population sizes were partitioned by the habitat scenario (Appendix D: Fig. 5d). For example, the decision-tree showed that releases in Aberdeenshire or Kintyre under the 'green future' scenario developed populations with ~30 individuals more frequently than status quo habitat. Galloway and Kielder Forest, more than doubled the number of individuals (from 54 to 124) with a much steeper growth expected in the 'green future' (Appendix D: Fig. 4b). Releases in the New Forest and Southeast England still had populations close to zero, regardless of habitat conditions.



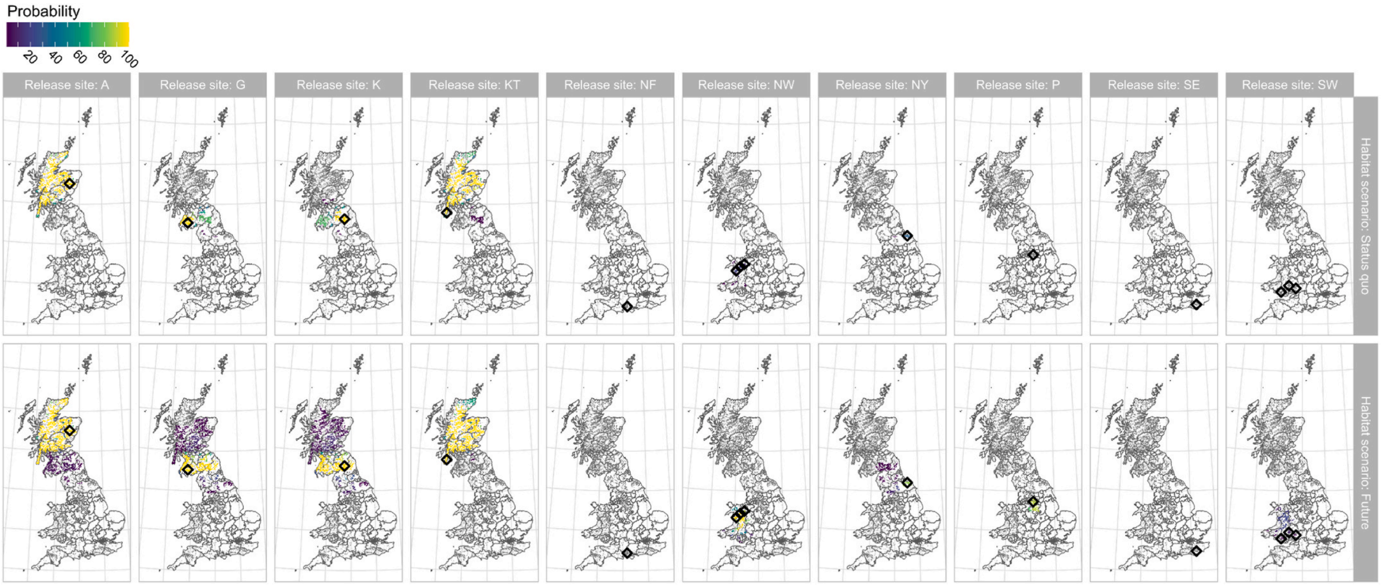
Appendix D: Fig. 5. Reintroduction success evaluated by extinction probability ≤5 % (a, b) and population size (c, d) 100 years after release for simulation set B (Table 1). Panels a) and c) provide variable importance from randomForest metamodels, while b) and d) show decision-trees from CaRT metamodels, respectively. At each decision-tree node (first node oval box and subsequently rectangular boxes), the data are split based on the parameter in the node and its values on the branches. At the terminal nodes, in b): the predicted extinction probability is indicated with the binary classification (success in green "≤ 5 %", failure in blue "> 5 %"), the fraction of the data subset in agreement with the classification, and the percentage of the entire dataset within the subset, and in d): the mean predicted population size and the percentage of the entire dataset within the subset are given. Larger populations indicated by darker green terminal nodes.



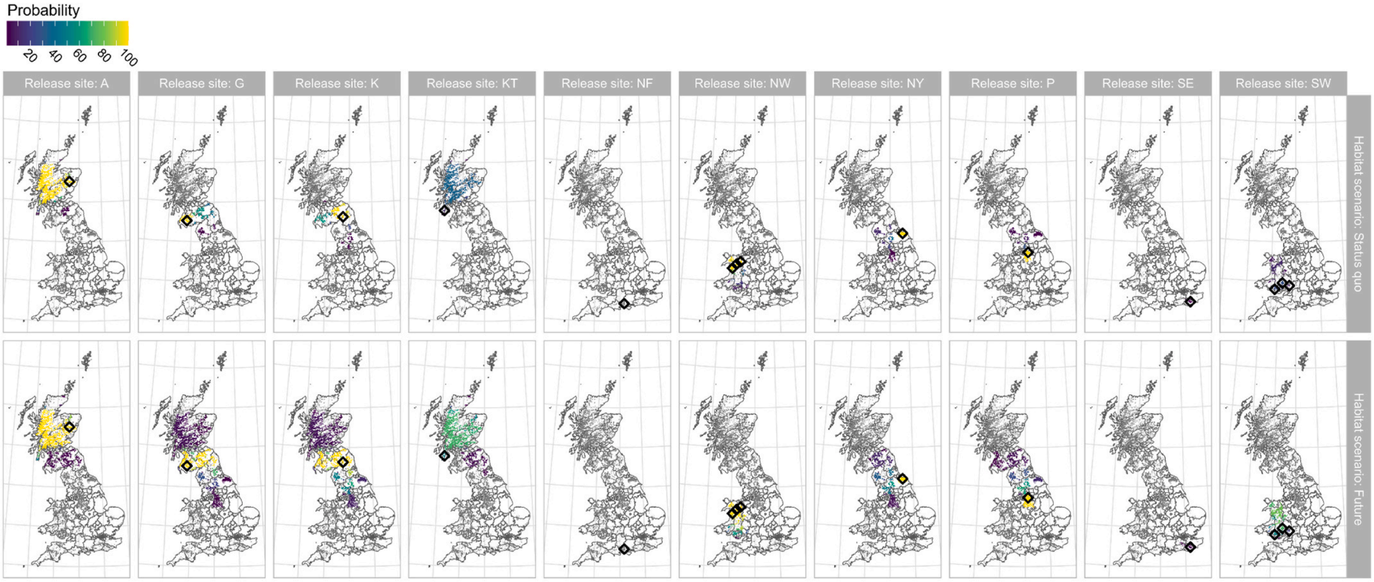
Appendix D: Fig. 6. Reintroduction success evaluated by extinction probability as a continuous response (categorical not possible since all values < 5 %) 100 years after release for simulation set C (Table 1): single and multiple release site combinations of the focal release sites: A - Aberdeenshire, G - Galloway, and K - Kielder. Panels: a) variable importance from randomForest metamodel, b) decision-tree from CaRT metamodel. At decision-tree nodes (first node oval box and subsequently rectangular boxes) the data are split based on the parameter in the node and its values on the branches, at the terminal nodes the mean predicted extinction probability (possible range: 0 to 100) and the percentage of the entire dataset within the subset are given. Higher extinction probability indicated by darker blue terminal nodes.



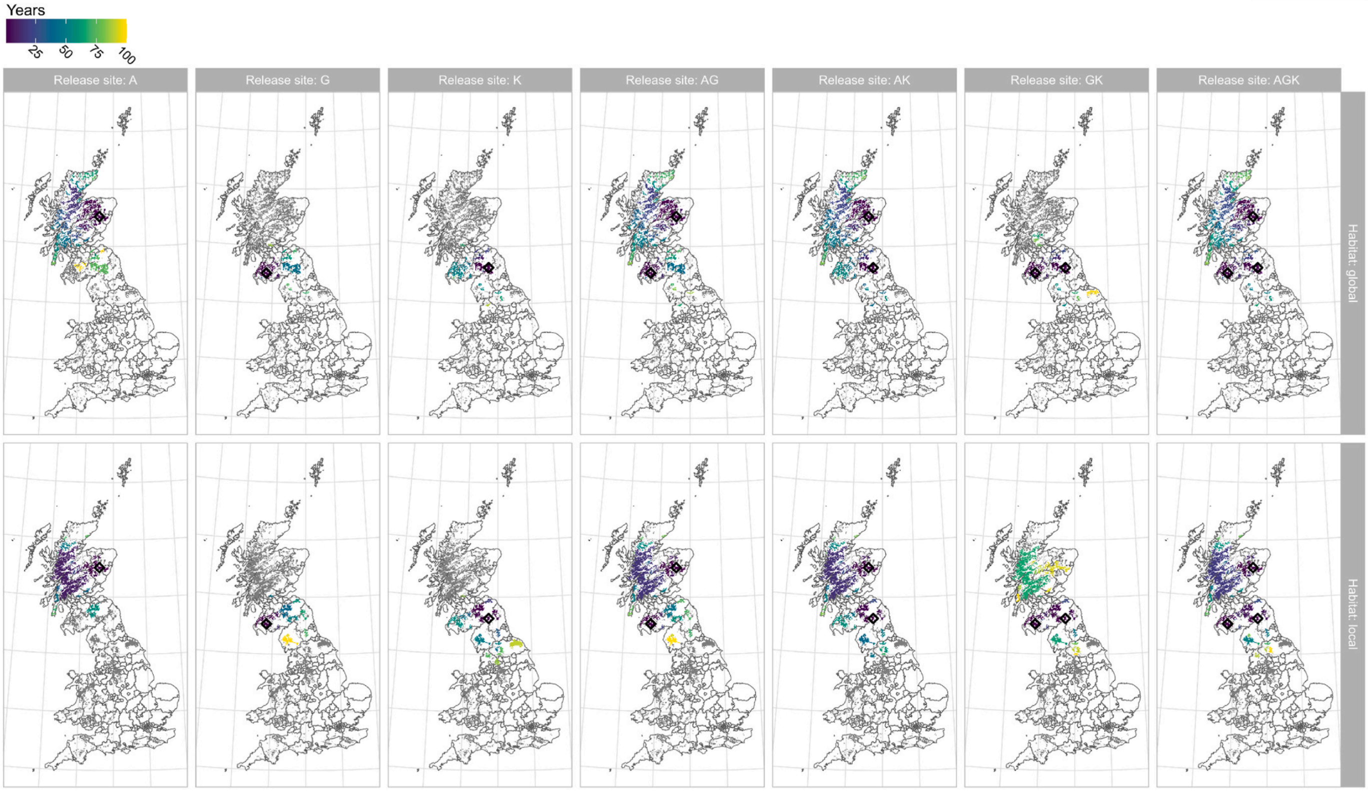
Appendix D: Fig. 7. Reintroduction success evaluated by Heterozygosity 100 years after release for simulation set C (Table 1): single and multiple release site combinations of the focal release sites: A - Aberdeenshire, G - Galloway, and K - Kielder. Panels: a) variable importance from randomForest metamodel, b) decision-tree from CaRT metamodel, and heterozygosity with higher (c) and lower (d) source genetic diversity under different focal release location combinations. At decision-tree nodes (first node oval box and subsequently rectangular boxes) the data are split based on the parameter in the node and its values on the branches, at the terminal nodes the mean predicted heterozygosity and the percentage of the entire dataset within the subset are given. Higher heterozygosity indicated by darker green terminal nodes. Solid line – global and dashed line – local habitat models (c, d).



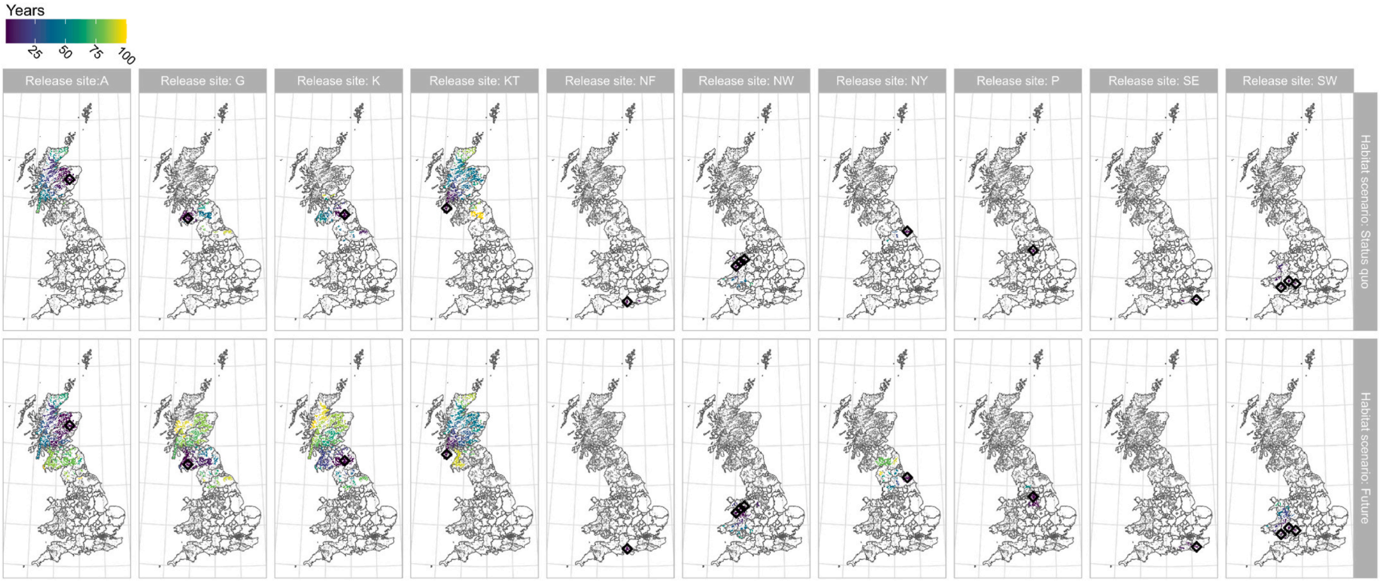
Appendix D: Fig. 8. Probability of occupancy after 100 years based on the global habitat model, single release locations, and under status quo or future habitat scenarios. Release locations are indicated by diamonds, and with the names: A - Aberdeenshire, G - Galloway, K – Kielder Forest, KT - Kintyre, NF - New Forest, NW - North Wales, NY - North York Moors, P - Peak District, SE - Southeast England, SW - South Wales. Occupancy probability increases with the colour gradient from indigo to yellow, with brighter colours showing higher likelihood of occupancy.



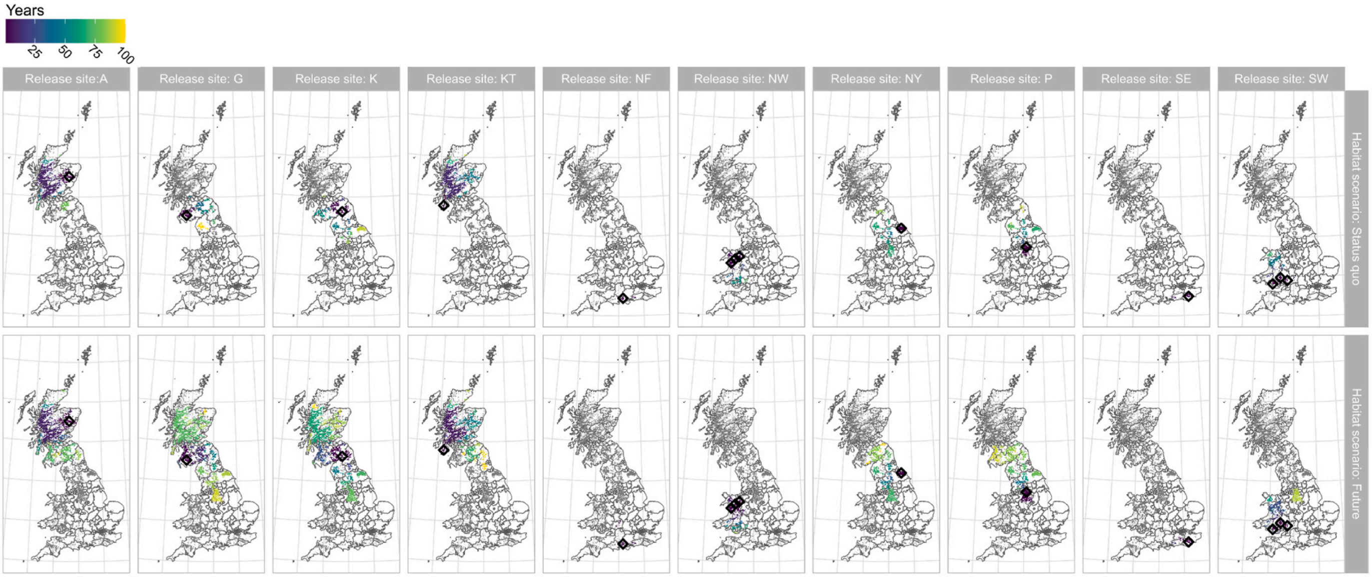
Appendix D: Fig. 9. Probability of occupancy after 100 years based on the local habitat model, single release locations, and under status quo or future habitat scenarios. Release locations are indicated by diamonds, and with the names: A - Aberdeenshire, G - Galloway, K – Kielder Forest, KT - Kintyre, NF - New Forest, NW - North Wales, NY - North York Moors, P - Peak District, SE - Southeast England, SW - South Wales. Occupancy probability increases with the colour gradient from indigo to yellow, with brighter colours showing higher likelihood of occupancy.



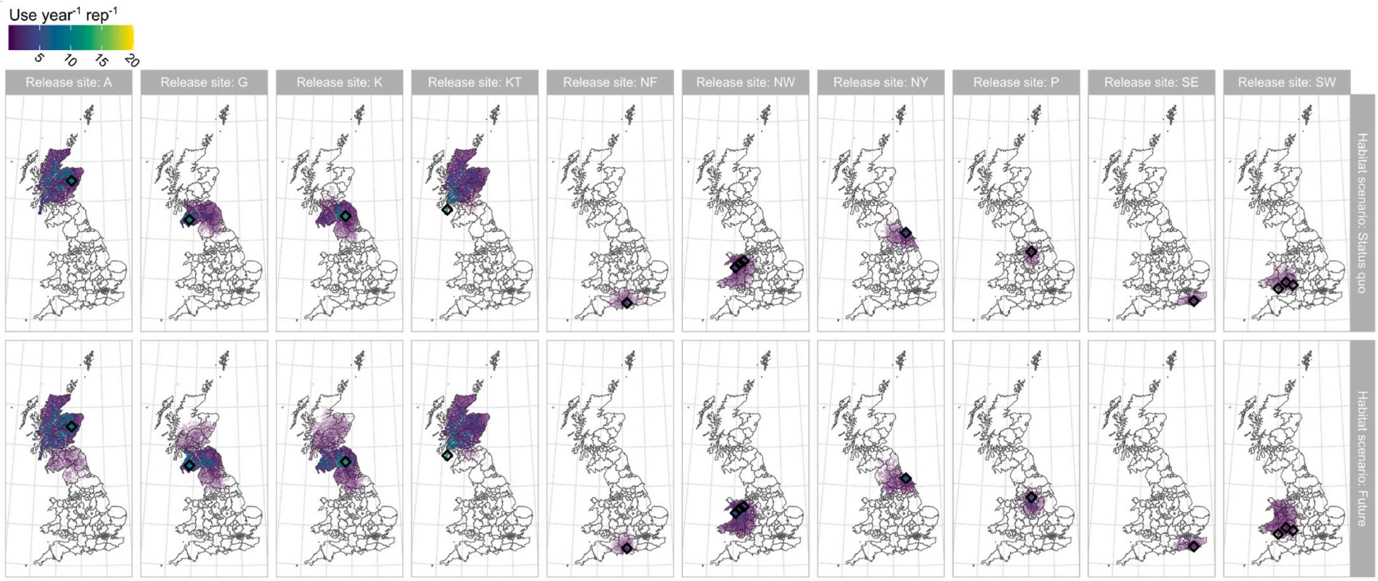
Appendix D: Fig. 10. The mean first occupancy year is based on combinations of focal release locations. Release locations are indicated by diamonds, and with the names: A - Aberdeenshire, G - Galloway, K – Kielder Forest, and combinations thereof. Only simulation repetitions with successful occupation (after 100 years) of a given patch contributed to the first occupancy year of that patch. Mean first occupancy year increases with the colour gradient from indigo to yellow, with darker colours showing faster arrival. Grey lines indicate county borders.



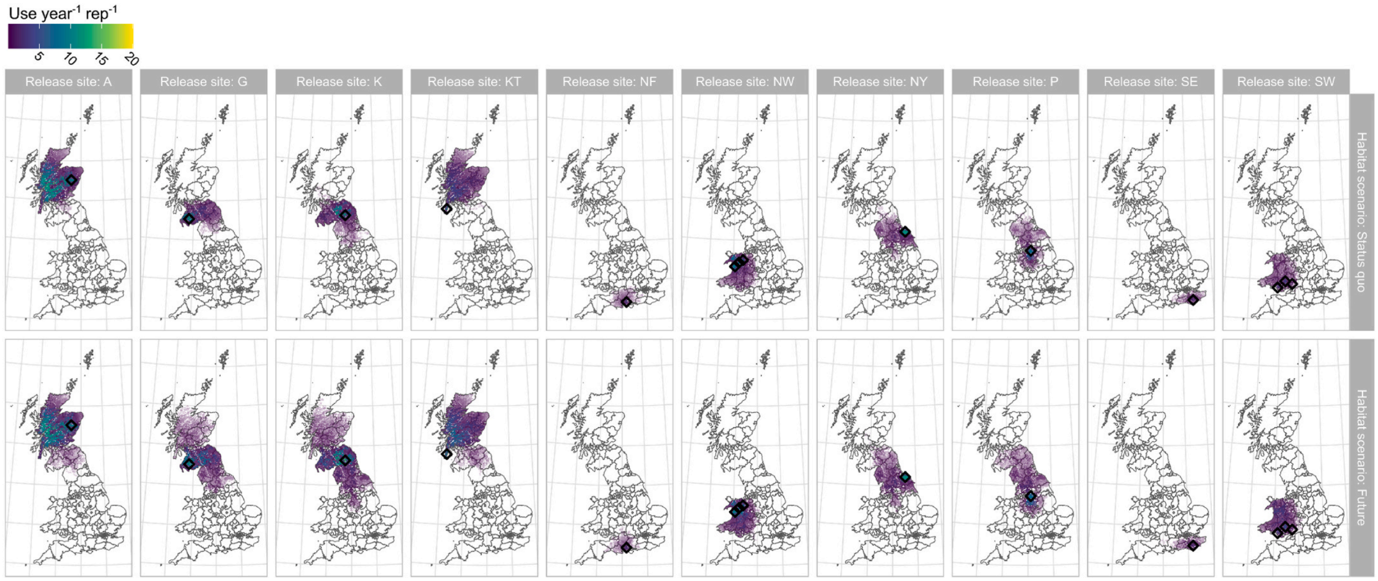
Appendix D: Fig. 11. Mean first occupancy year based on the global habitat model, single release locations, and under status quo or future habitat scenarios. Release locations are indicated by diamonds, and with the names: A - Aberdeenshire, G - Galloway, K – Kielder Forest, KT - Kintyre, NF - New Forest, NW - North Wales, NY - North York Moors, P - Peak District, SE - Southeast England, SW - South Wales. Only simulation repetitions with successful occupation (after 100 years) of a given patch contributed to the first occupancy year of that patch. Mean first occupancy year increases with the colour gradient from indigo to yellow, with darker colours showing faster arrival.



Appendix D: Fig. 12. Mean first occupancy year based on the local habitat model, single release locations s, and under status quo or future habitat scenarios. Release locations are indicated by diamonds, and with the names: A - Aberdeenshire, G - Galloway, K – Kielder Forest, KT - Kintyre, NF - New Forest, NW - North Wales, NY - North York Moors, P - Peak District, SE - Southeast England, SW - South Wales. Only simulation repetitions with successful occupation (after 100 years) of a given patch contributed to the first occupancy year of that patch. Mean first occupancy year increases with the colour gradient from indigo to yellow, with darker colours showing faster arrival.



Appendix D: Fig. 13. Use surface (i.e., inverse of resistance surface) based on the global habitat model, single release locations, and under status quo or future habitat scenarios. Release locations are indicated by diamonds, and with the names: A - Aberdeenshire, G - Galloway, K – Kielder Forest, KT - Kintyre, NF - New Forest, NW - North Wales, NY - North York Moors, P - Peak District, SE - Southeast England, SW - South Wales. The amount of use increases with the transparency and colour gradient from transparent indigo to opaque yellow, with opaque brighter colours showing higher usage.



Appendix D: Fig. 14. Use surface (i.e., inverse of resistance surface) based on the local habitat model, single release locations, and under status quo or future habitat scenarios. Release locations are indicated by diamonds, and with the names: A - Aberdeenshire, G - Galloway, K – Kielder Forest, KT - Kintyre, NF - New Forest, NW - North Wales, NY - North York Moors, P - Peak District, SE - Southeast England, SW - South Wales. The amount of use increases with the transparency and colour gradient from transparent indigo to opaque yellow, with opaque brighter colours showing higher usage.

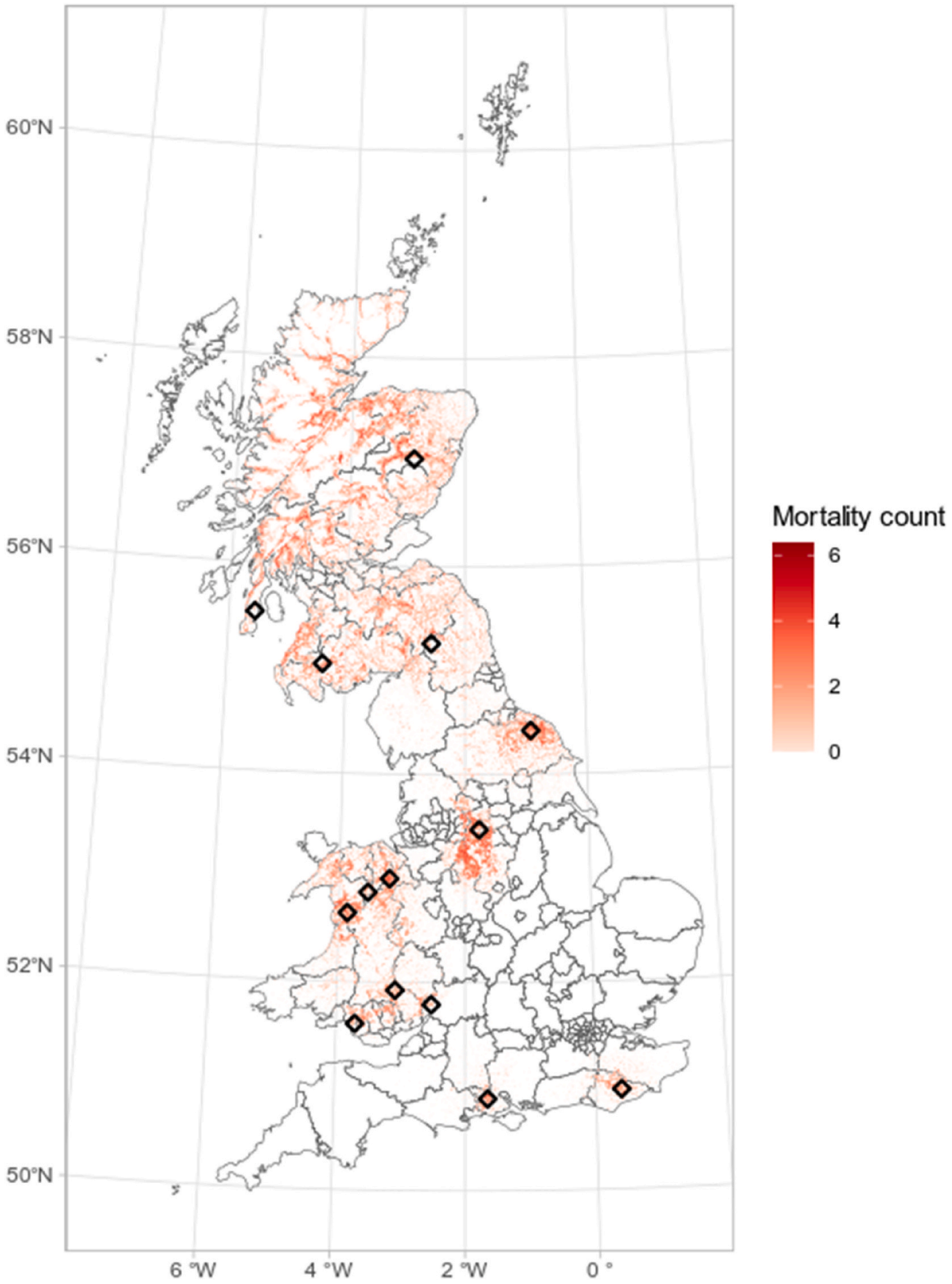
Appendix D: Results 2. Spatial distribution

After a release in Aberdeenshire there were high lynx occupancy probabilities across Northern Scotland for both habitat models (Fig. 7). Lynx reached patches beyond the Aberdeenshire release patch within a decade on average (Appendix D: Fig. 9). The available habitat limited the extent of occupied patches, resulting in a wider distribution with the global habitat model even in areas of northernmost Scotland. Patches in Kintyre and Northern Scotland took approx. 50 years to be occupied on average and the maximum extent was reached after approx. 75 years, for both habitat models. Despite some apparent barriers north of the Central Belt (densely populated and human modified region of central Scotland), dispersal was possible across this region (Fig. 8), though there was still a low probability that patches in southern Scotland, south of the Central Belt, would be occupied after 100 years. If they were reached, this happened in around 50–75 years on average. For both habitat models, the highest connectivity through the Central Belt was in the east toward Kielder Forest. This route was more reliable under the green future scenario, but the occupancy probabilities were still low (around 5 %) for patches in southern Scotland, though lynx did reach patches as far south as Yorkshire in England with the global habitat model (Appendix D: Fig. 9).

The Kintyre release location resulted in similar occupancy patterns across northern Scotland as the Aberdeenshire release location, however, with lower probabilities and later arrival times (Fig. 7, Appendix D: Figs. 8–12). Further, the emergent connectivity was very different depending on the habitat model. Specifically, the global habitat model had higher connectivity from the release location northwards towards northern Scotland than the local model, which showed overall weaker connectivity (Fig. 8, Appendix D: Figs. 13 and 14). The eastern route through the Central Belt again provided connectivity to northern Scotland.

The single location releases in either Galloway or Kielder Forest resulted in similar but opposite spatial developments. In both cases, the opposite patch had over 60 % occupancy probability after 100 years for both global and local models, with first occupancy developing within 50 years on average. These patches were bisected by a motorway, with lynx only able to connect these patches through a small number of corridors (Fig. 8). Both revealed low occupancy probabilities (<5 %) further south, partly caused by the same motorway reducing connectivity with Cumbria in northwest England. Under green future conditions occupancy of the opposite patch was more likely and reached more quickly (25 years) and, in general, more patches north and southward were occupied, including advanced expansions into northern Scotland after 75 years. Differing from releases in Galloway, releases in Kielder Forest had a non-zero probability of occupying small patches north of the Central Belt under status quo conditions, for both habitat models. Connectivity between northern Scotland and southern Scotland emerged mostly in a dispersal corridor between Glasgow and Edinburgh and to the east of the M74 motorway. This seems more easily reached from the Kielder Forest patch and the eastern part of the Southern Uplands. Under green future conditions, connectivity was improved northward via the same corridor and another narrow corridor west of Glasgow, as well as southward into England for both habitat models.

Dividing released individuals among all three locations resulted in the highest occupancy probabilities for Galloway and Kielder Forest but slightly reduced occupancy probability (approx. 90 %) for some patches in northern Scotland. The differences in occupancy based on the local and global habitat models were broadly negligible. The average first occupancy times for non-release patches were only slightly earlier for single location releases compared to when the individuals were divided for multiple location releases. For example, lynx occupied the southernmost patch of the Kintyre peninsula within 75 years whether 40 individuals were released in Aberdeenshire, or if 14 individuals were released in Aberdeenshire and 13 each in Galloway and Kielder Forest simultaneously. Consistent with the preceding spatial results, simultaneous releases in Aberdeenshire, Galloway, and Kielder Forest resulted in the most extensive spatial distribution of lynx, though only slightly greater (in a southerly direction) than paired combinations of Aberdeenshire and Galloway, or Aberdeenshire and Kielder Forest. It appeared that simultaneous releases in Galloway and Kielder Forest might slightly promote dispersal into the north of Scotland.



Appendix D: Fig. 15. Road mortality events aggregated from all simulation runs in set A under medium parameters and global and local habitat models. Values are the log transformation of the number of mortality events per pixel across all replicates divided by the number of parameter sets that had mortality events in each pixel.

Appendix D: Discussion 1. Non-focal release locations

North York Moors and Peak District.

The North York Moors and the Peak District provide less certainty for potential reintroduction projects. Firstly, under medium conditions releases in these sites were only viable (extinction probability <5 %) when simulating using the local habitat model prediction. Compared to the local habitat prediction, the global habitat model had less suitable habitat in both areas. Specifically for simulation repetitions that reached 100 years under medium conditions, in the North York Moors the population reached around 25 and 10 lynx for local and global models, while the Peak District release resulted in 20 and 0, respectively. Of the same order to our results, Johnson and Greenwood (2020) estimated 8.3 lynx for the North York Moors and did not identify a viable patch in the Peak District. Even under future habitat conditions, and still medium mortality conditions, with the global habitat model we found the North York Moors and Peak District sites exceeded the 5 % extinction threshold after 30 and 60 years, respectively.

New Forest and Southeast England.

Reintroductions in the New Forest and Southeast England were unsuccessful for 99 % of all our simulation parameter combinations. This was likely due to the small populations these regions supported, which even with small territory sizes was only around 5 individuals. This is in strong contrast to Johnson and Greenwood (2020), who estimated 107.1 lynx could occupy Southeast England and who found this patch as the most resilient sub-population in England and Wales. However, their approach was not spatially explicit in terms of road mortality and movement, and used a rule-based habitat suitability that might not have represented the selection behaviour of lynx as well as the habitat suitability predictions of Oeser et al. (2023) that we utilised. Furthermore, they based the lynx density on prey availability at 3.75 lynx per 100 km^2, which would be one of the highest across Europe, while our territory size assumptions resulted in more conservative emergent densities, up to 1.80 lynx per 100 km^2. These sites would perhaps be sufficient to serve as stepping-stones between larger patches, however just as with a stepping-stone population these sites were at high risk of extinction (Port et al., 2021).

Connectivity in England.

The release sites North York Moors and Peak District were poorly connected despite their proximity. Johnson and Greenwood's (2020) least cost path analysis also did not identify a connection between them. Using the local habitat model, we found lynx first reached the opposite patch after 75 years on average. However, using the global model, colonisation in either direction did not occur, even with the improved habitat scenario. Johnson and Greenwood (2020) did identify a corridor between Kielder and the North York Moors. This connection was apparent using the local habitat model, or the global with improved habitat, and also took 75 years on average. When Kielder was the release site, connectivity was slightly slower to the North York Moors, probably because finding a smaller target patch embedded in poorer habitat is more difficult and due to the shading effect of smaller suitable habitat patches (Kramer-Schadt et al., 2011).

Reintroduction in Wales.

We tested reintroductions with releases in North Wales or South Wales under a range of different parameters. Based on our results we can say that North Wales provides a better reintroduction success rate than South Wales. However, the North Wales site was only under the 5 % extinction probability threshold for success when simulating using the local habitat model. The analysis of Johnson and Greenwood (2020) also identified plentiful suitable habitat in Wales but estimated a Welsh population of only 3.3 lynx due to the low density (0.21 per 100 km^2) assumed due to low prey densities. With our largest territory size simulations (density $\cong$ 0.83) and medium parameters we estimated a Welsh population of 12–20 lynx for releases in South or North Wales, respectively. However, similar to Johnson and Greenwood (2020) the low-density simulations were likely to go extinct before 100 years. Deer distributions in Great Britain are likely to increase (Palmer, 2014), and so far no studies considered Lagomorph prey explicitly as dietary components. Therefore, the emergent population size will depend both on habitat selection and the true prey availability. Based on the local habitat model and a North Wales release, our estimates lie in the range of 12–60 lynx with 0.83–1.8 lynx per 100 km^2, respectively.

Connectivity between patches in Wales was mostly sufficient, with no barriers separating North and South Wales's suitable habitat patches. However, within South Wales although barriers were not necessarily impassable, the dense road network meant suitable habitat patches were highly fragmented. Our results also showed that Wales and England have very low, if any, connectivity. Johnson and Greenwood (2020) also described this low connectivity, but the authors suggested a mechanistic movement model and consideration of underpasses or bridges might affect this finding. In our work we integrated these aspects and found individuals could only breach the West Midlands on extremely rare occasions, even with improved habitat conditions. As such, colonisation of the Peak District from Wales, and vice versa, is unlikely. However, rare dispersal events could be sufficient to provide genetic exchange between these patches if they were already populated. This would need to be tested in further simulations since it was outside the scope of this work.

Data availability

Data will be made available on request.

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