ECOLOGICAL FEASIBILITY OF EURASIAN LYNX REINTRODUCTION TO BRITAIN

Lifescape Project Report
December 2023

the **Lifescape** project

ECOLOGICAL FEASIBILITY OF EURASIAN LYNX REINTRODUCTION TO BRITAIN
Lifescape Project Report December 2023

This report provides an extended summary of the original technical report by Joe Premier, Deborah Brady, Hugh Robinson, Adam Eagle, Julian Oeser, Stephanie Kramer-Schadt and Marco Heurich, "Ecological feasibility of Eurasian lynx reintroduction to Britain" that is currently being prepared for submission to a peer-reviewed scientific journal.

A glossary of key terms that appear in this report (terms formatted in **bold**) is also available.

For queries and reproduction contact: josephpremier@lifescapeproject.org, deborah.brady@lifescapeproject.org, and adam.eagle@lifescapeproject.org

EXECUTIVE SUMMARY

Eurasian lynx ('lynx') have likely been absent from Britain for at least 800 years, and by the middle of the 20th century, lynx was also extirpated in Western and Central Europe. Reintroductions in Europe started in the 1970s and have since reinstated many subpopulations. These reintroductions provide a blueprint for a potential reintroduction of lynx to Britain.

A reintroduced population in Britain could be an additional remote population within the European metapopulation and have ecological benefits locally. However, before this could be practically pursued the ecological feasibility must be thoroughly examined.

Previous predictions of lynx population dynamics in Britain have relied on expert knowledge and rule-based habitat maps which are useful but have limitations. Instead, spatially explicit individual-based population modelling is a method that can simulate interactions between lynx and the mapped landscape, which can help us better understand the potential viability of a reintroduced population.

Using an empirically derived habitat suitability map and a spatially explicit individual-based model, we simulated various release locations, timings, sex-ratios, and founder population sizes, under different mortality scenarios drawn from monitored wild European lynx populations to test the likelihood of reintroduction success. We also simulated how well reintroductions fared when combinations of release locations were used, and under "green" future scenarios in which habitat conditions are better for lynx, to understand the effects on population development.

Our results show that lynx could survive in Britain. Of the ten potential habitat patches tested, three locations were predicted to provide low extinction probabilities and successful population expansion, namely the Cairngorms, Galloway, and Kielder Forest, as well as combinations thereof. These locations were predicted to produce low extinction probabilities providing successful population expansion under diverse conditions and supported the largest populations and genetic diversity.

If only two sites were selected as focus areas for lynx reintroductions the best combination would be a release in the Highlands (Cairngorms) and Northern England (Kielder Forest). Each of these was also predicted to be successful independently. The results suggest a successful approach to restoring lynx to Britain would be a release project in the Highlands or Northern England, or ideally both.

Our approach indicates the ecological feasibility of a well-planned lynx reintroduction in Britain provided there is appropriate acceptance of such plans by stakeholders.

CONTENTS

1. INTRODUCTION

1.1. Brief history of Eurasian lynx in Britain

The Eurasian lynx (*Lynx lynx*, Linnaeus, 1758; hereafter 'lynx') was formerly native to Britain but was likely extirpated sometime during the last 800 to 1500 years. This date period is based on the reported radiocarbon date of the youngest lynx remains (circa 1550 C_{14}YBP)[1], and the linguistic and written evidence of lynx potentially still being present in the landscape in the medieval period (1066-1485 AD)[2], or perhaps even later[3].

The remains of lynx at various cave sites across Britain nevertheless reveal the species' existence on these shores before and well into the Holocene epoch. The cause of their eventual extinction from Britain is generally accepted to be the result of anthropogenic factors, comprising widescale deforestation, dwindling numbers of deer, and direct persecution driven by subsistence farmers protecting their livestock. Since the cause of lynx extinction from Britain was human activity, and the species has no natural ability to return of its own accord, it has been considered that the lynx qualifies as a candidate for reintroduction[2]. Here we do not seek to address whether lynx *should* be reintroduced to Britain; there are excellent commentaries on this matter elsewhere[2].

This report documents our detailed assessment of the ecological feasibility of lynx reintroduction to Britain. Using a combination of empirical data and predictive computer models we examine whether reintroduced lynx would survive and persist as a viable population in Britain, and what the most effective release strategies might look like.

1.2. Status of Eurasian lynx in Europe

Long since their local extinction, large predators like lynx have begun to resettle many areas of Europe[4]. This was possible due to support from the public, legal protections, and reintroductions. Lynx reintroductions have taken place since the 1970s in numerous European countries[5,6,7], with projects still ongoing[8].

Although the conservation status of the Scandinavian, Karelian, and Baltic populations are 'favourable', according to the Natura 2000 Habitats Directive, many Central European populations remain 'unfavourable-bad' or 'unfavourable-inadequate'[9]. This is due to **the distribution of lynx** in mainly small and isolated populations[5]. The anthropogenic influence of European landscapes puts populations of lynx under strain. Fragmentation of natural landscape features by roads and settlements reduces the connectivity between patches and means populations are less able to disperse[10]. Furthermore, historic preconceptions about large predators and conflicts between stakeholder wishes mean that maintained effort is necessary to ensure their conservation and survival[11,12,13,14,15].

The small size of populations puts them at a higher risk of extinction due to random events[16] and the probability that **genetic diversity** is lost is higher due to genetic drift and inbreeding[17]. The latter can negatively affect individual[18] and population health[19], which can at worst lead to population collapse[20]. The long isolation of many small Central European populations is already reflected in their low genetic diversity[21,22]. This will require action to maintain these populations over the long-term. The creation of a **metapopulation** of Central European lynx that enables exchange between all reintroduced and autochthonous populations, whether naturally or artificially, would improve their long-term viability[23,24]. This is currently being pursued strategically by collaborating institutions and projects in the region[25].

1.3. History of assessing the potential for a lynx population in Britain

The first assessment of the viability of lynx in Britain[26] used the spatial presence of their main prey, roe deer (*Capreolus capreolus*), to directly estimate the size of potential lynx populations. Assuming a minimum viable population of 250 lynx (see[27]), 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 (in south-southwest England and in East Anglia, respectively).

The first analyses of **habitat suitability** and population viability focused on Scotland[28,29]. Using the relationship between lynx and prey density from data published on four European lynx populations, they estimated potential lynx densities suggesting a potential population of 394 (+/- 51) in the Highlands and 51 (=+/- 19) in the Southern Uplands[2]. The results were never meant to be interpreted as the biological **carrying capacities** as the predictions were extrapolated from European data where human effects were suppressing populations (via hunting, poaching and road deaths).

Subsequently a "**rule-based modelling**" approach was used to investigate habitat suitability and connectivity[28]. The authors focused on Scotland, but also included areas of Kielder Forest contiguous with border forest. They identified 30 patches totalling 20,678 km^2 of suitable habitat, with a further 817 km^2 in the Kielder Forest area, and their rough assessment of the lynx population size that could be supported by these habitat patches agreed with previous density assessments[29]. However, the Highlands and the Southern Uplands lacked connectivity, suggesting that colonisation of the latter from the former was unlikely.

The rule-based modelling method used for Scotland[28,29] was recently applied to investigate habitat suitability and population viability in England with overlap into the Southern Uplands[30]. It allowed direct comparison to the Scotland results[28] and although the population estimates were similar where they overlapped in space, the later study suggested 36% less habitat in the Kielder Forest and Southern Uplands Scottish complex compared to the earlier work.

1.4. Modelling habitat suitability for lynx

Species distribution models (SDMs) have been widely used to predict where conditions are suitable for species and how many individuals of that species the given habitats might support[31,32]. The non-statistical 'rule-based' approach to this has been widely used in conservation planning to predict areas of potential habitat for a species[33] as it allows expert opinion and empirical knowledge to be included. However, a more objective approach is to use statistical models of species distributions, these are based on the characteristics of locations where the species is present and absent[34]. The resulting model can then predict the suitability of a new area for the species. Given the rapid developments in habitat modelling techniques, a statistically derived habitat selection map for lynx was considered to be a valuable step in investigating their potential viability in Britain.

Recently, a European-wide research collaboration on lynx was founded to better understand the species throughout its range[35]. The collaboration maintains an extensive lynx location dataset from GPS and VHF tracked animals, which, combined with various satellite derived environmental variables, has enabled the creation of models to map habitat suitability in areas where lynx are not currently present, including Britain[36].

1.5. Population viability analysis

For potential reintroductions not only must habitat suitability be assessed, the long-term viability of a population must also be considered. This is known as population viability analysis[37]. The probability of extinction within 100 years is often used as the benchmark for viability[38]. Population growth is modelled with **demographic** parameters (e.g. birth and survival rates), which are applied to a starting population size (e.g. estimated carrying capacity for the species in a given landscape, drawn from comparable real populations). This type of viability assessment is non-spatial, or not spatially explicit, i.e. the physical space that the animal is living in is not simulated. This type of approach had been used to investigate the viability of potential lynx populations in England and Wales[30].

In contrast, spatially explicit **individual-based models** (IBMs) incorporate demographic parameters of a species along with their spatial behaviour and **life history** stages[39]. The simulated individuals can move in a virtual landscape with demographic processes (i.e. survival, mortality, and reproduction) occurring whilst they interact with other individuals and the environment (e.g. through habitat selection). Such modelling is frequently employed to explore complex ecological systems where population-level dynamics (e.g. population size, growth rate) emerge from individual level decision-making (e.g. movement or habitat choices). A key advantage is that these models make fewer assumptions than those that operate at the population level[40]. Other influences on population persistence can also be incorporated into an IBM, such as prey availability, and the presence of roads or humans[41].

A spatially explicit IBM has formerly been used to investigate the population viability of lynx in Scotland[42] following the rule-based habitat approach[28] and density assumption[29]. The authors tested population persistence after reintroductions using different founder numbers and locations. Three proposed release locations were tested, with 83% survival after a Kintyre release, 35% after an Aberdeenshire release, and 21% after a Kielder Forest release, respectively. The only scenario to achieve 95% survival was a dual reintroduction of 32 lynx in Kintyre and Aberdeen. The modelled scenarios were consistent with the earlier expectation[28] that dispersal between the north and south of Scotland would be unlikely. The lynx released in northern Scotland (above the M8 urban belt) did not reliably expand into the Southern Uplands or vice versa.

Another use of an IBM[43], in this case just of lynx dispersal movements, explored post-release movements in Scotland based on published parameters[44]. It suggested a release in Dumfries and Galloway was best since it would support the most exploration of suitable habitat. However, the study was limited to just the release year and no demographic processes.

To-date, all previous assessments of the viability of potential lynx reintroduction in Britain indicate potentially viable populations only under certain scenarios. However, the research completed so far has been restricted in geographic scope, has only applied rule-based habitat modelling, and none have considered genetic diversity following release. Therefore, an IBM based on an empirically derived habitat selection map is critical for a more objective investigation of long-term lynx population viability and would allow us to pose the essential questions for planning any future reintroduction.

1.6. Development of the lynx-specific individual-based model

An IBM has already been specifically developed for lynx[10]. The IBM was developed incrementally as required to answer specific research questions. Initially, the focus was on assessing European landscapes to find suitable habitat patches for lynx[33,45], followed by investigating movement

behaviour and parameterising the movement model[44]. The habitat and movement modules were then joined by a demographic module allowing population viability analysis. The IBM has since been used to predict the viability of lynx reintroductions in Germany[10], the effects of perceptual range on connectivity[46], the effects of stepping-stones on patch colonisation[47], the colonisation probability of the Black Forest in Germany[48], and estimation of unknown mortality rates in the Bavarian-Bohemian-Austrian population13. Most recently, inheritance of neutral genetic markers was added to the model to further increase its applicability as a **demogenetic population model**[49].

Demogenetic models include the assignment of neutral genetic markers to individuals' properties. Their empirical counterparts, e.g. microsatellite loci, are used to monitor population genetics (e.g., drift and inbreeding) and for studying genetic diversity and differentiation[50]. These models are then appropriate for simulating demogenetic responses like population size and allelic richness[51]. For these reasons we have utilised this demogenetic model in our assessment of the ecological feasibility of lynx reintroduction into Britain.

1.7. Research objectives

The goal of this research was to test whether a lynx population of sufficient size and genetic diversity could persist 100 years post-release under all combinations of different scenarios and therefore provide information on the ecological conditions under which reintroduction is likely to be successful. The scenarios are as follows.

- Release conditions. We varied the following parameters to understand their effects on reintroduction success: i) release locations, ii) timing of releases (lynx per unit time), iii) sex-ratio of released individuals, iv) number of released individuals, v) genetic diversity of released population.
- Mortality scenarios. Based on the mortality rates observed in the lynx populations of mainland Europe we tested the cause-specific rates of natural, road, poaching and unknown mortalities across low, medium, and high scenarios.
- Habitat scenarios. Based on the Europe-wide habitat modelling[36] we considered two habitat selection models to understand whether reintroduction success depends on potentially emerging habitat selection behaviour. We also examined reintroduction success under a future scenario of increased woodland cover throughout Britain, based on existing domestic policy commitments to create more habitat, including woodland, and improve the connectivity of existing woodland patches[52,53].

2. METHODS

2.1. Demogenetic simulation model

The lynx demogenetic model[49] is flexible and capable of simulating demographic and genetic development under diverse conditions. It is an individual-based spatially explicit model, which means population processes emerge as the result of individual habitat and home-range selection, and movement decisions. Furthermore, it can simulate many starting conditions since the sex, genotype, release location and time of all released lynx are defined a priori. In addition, it can simulate spatially and temporally defined mortality scenarios, e.g., where lynx may be at greater risk from human activity.

The model comprises different submodules, namely: a dispersal module, including territory searching, that links the demographic processes onto the habitat map, a demographic module that considers territory occupation, reproduction, and mortality, and a genetic module that handles inheritance of neutral genetic markers. The habitat map provides the landscape where all processes take place and exhibits categorical levels that reflect dispersal and territorial behavioural modes. This is supplemented by maps describing mortality risk due to other sources, namely: linear features for residents and linear features for dispersers.

2.2. Prey availability assumptions

Considering **lynx's diet**, which comprises over 50 documented prey species[54,55,56], it is evident they are adaptable predators. Across their distribution, lynx's diet ranges from almost exclusively small mammals, to predominantly ungulates. In the mid-latitudes of Europe and Scandinavia lynx mostly predate ungulates, especially roe deer ($\gtrsim$ 70%) [54,55,57,58,59]. It has been shown that home range size of lynx is determined primarily by resource availability[60] meaning in turn that the population density arising from a reintroduction would depend greatly on the availability of prey.

In Britain there are currently six deer species present, namely: roe, red (*Cervus elaphus*), fallow (*Dama dama*), sika (*Cervus nippon*), water (*Hydropotes inermis*) and muntjac (*Muntiacus reevesi*)[61]. These would likely be lynx's main prey where their distributions coincide. These would be supplemented by smaller wild prey, including rabbits, hares, foxes, martens, squirrels, and some birds. Although the current evidence from Europe suggests livestock are not frequently targeted by lynx, it is possible that smaller livestock, such as sheep, might be predated in areas directly adjacent to woodland[62], in habitats suitable for deer[63], and where wild prey species are of lower abundance[64].

There is a lack of broad scale monitoring of deer densities across Britain, which has been highlighted as a crucial knowledge gap when considering viability of reintroduced lynx[65]. However, there are population estimates and presence maps[66] as well as occurrence probability maps[61]. In relation to the potential future distribution of lynx, it most likely that prey availability will not directly limit their colonisation of suitable habitats since there are suitable potential wild prey species available across most of mainland Britain (e.g. deer and lagomorphs[61,66,67]). However, prey availability could affect the lynx's eventual population density.

Lynx population densities vary depending on local conditions and estimation methods but typically fall between 0.27 to 4.20 per 100 km^2 [68,69,70,71,72]. Considering the unknown range of potential lynx densities following a reintroduction in Britain, we propose a conservative range of values (Table 1) that do not exceed the stated densities found in Central and Northern Europe, and the lower estimates consistent with previous studies[29]. Since density is not an input parameter of the

demogenetic model, we estimated instead the range of female territory sizes, based on the assumed maximum sex-ratio of 3 females to 1 male[10] and the target density scenario.

2.3. Parameter ranges

The reintroduction viability analysis is a sensitivity analysis based on the empirically derived ranges for various demographic parameters and behavioural responses (Table 1). By simulating a range of values for the parameters we can explore the reintroduction viability under many possible conditions. For example, mortality rates are key parameters in demography. We based mortality scenarios on the mortality rates observed in lynx populations in mainland Europe, including low, medium, and high scenarios for natural mortality, road mortality as well as added (e.g., poaching) and other unknown mortalities.

2.4. Spatial data preparation

2.4.1. Habitat maps

Habitat maps provide the basic landscape upon which the simulated lynx individuals base their individual movements and territorial decisions. Landscape connectivity and population dynamics are, thereby, properties that emerge from the interaction between individual decisions and habitats. The simulations were based on maps of categorical habitat preference comprising the categories: barrier, matrix, dispersal, and breeding habitats. Barrier describes habitats that are impermeable for lynx movements, matrix is unsuitable habitat that can be selected for a limited duration, while dispersal and breeding describe suitable habitats that are preferred. The latter three categories were based on a European-wide habitat map[36]. The authors' mapping was based on GPS and VHF telemetry data of around 500 lynx throughout Europe, which makes it possible to predict habitat suitability in Britain based on empirical data.

2.4.1.1. Habitat suitability map description

Two methods were used to fit and predict habitat suitability models[36], described in brief here. First, a "global" approach in which all data from all populations were combined to fit one habitat suitability model. Second, a "local" metamodel approach[73], whereby a habitat suitability model was fitted locally, i.e., for each population, and their predictions across Europe were combined via weights defined by the ecological similarity of training regions to that found at each predicted pixel. The resultant prediction map provides continuous values that indicate relative suitability of habitat across Britain. The global and local approaches provide relatively similar habitat suitability predictions for Britain (Figure 1), but they are distinct and deliver different patterns of suitable and unsuitable areas.

The global model is trained on all the data from lynx populations across Europe simultaneously, thus minimising extrapolation outside of training data. The local metamodel is based on various models fitted for individual populations that when taken individually are not trained on such a wide range of environmental conditions resulting in improved local predictions from similar environmental conditions, yet a tendency to extrapolate beyond the range of the global model. We therefore tested reintroductions under both habitat models. Employing this range of habitat suitability scenarios acts as sensitivity testing of the potential lynx behavioural responses to the British landscape.

Table 1. Overview of simulation scenarios, including parameter values (low, medium, high).

Set	Release scenarios						Response scenarios				Demographic scenarios							
	Release location/s	N lynx	Sex-ratio (m:f)	Timing	Genetics	Habitat	Habitat suitability	Territory size Φ			Mortalities					Reproduction		
								Minimum female territory (km²)	Max added (km²)	Max female overlap	Baseline ■ resident (per year)	Baseline ■ 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 locations: Cairngorms●, Galloway, Kielder Forest, Kintyre●, New Forest, North Wales, North York Moors, Peak District, Southeast England, South Wales.	10, 20, 40	1:1, 1:3	i	-	Status quo	Global, local	128, 82, 59	64, 41, 29	3[74,75]	0.033, 0.046, 0.178[76]	0.00038, 0.00068, 0.00082[76]	0.01, 0.02, 0.03[76] (2013, 975, 655*)	0.06, 0.13[76], 0.25[44] (200500, 76500, 27250)	0.038, 0.068, 0.172[76]	0.75[77], 0.81[75,78]	0.41[79], 0.48[77], 0.5[80,74]	2.16[81], 2.34[78], 3.3[77]
B	Single locations: Cairngorms●, Galloway, Kielder Forest, Kintyre●, New Forest, North Wales, North York Moors, Peak District, Southeast England, South Wales.	10, 20, 40	1:1, 1:3	i	-	Status quo, future	Global, local	82	41	3[74,75]	0.046[76]	0.00068[76]	0.02[76] (975*)	0.13[76] (76500)	0.068[76]	0.75[77], 0.81[75,78]	0.48[77]	2.34[78]
C	Combinations of focal locations: (Cairngorms●, Galloway, Kielder Forest)	20, 40	1:1, 1:3	i, ii, iii	Low, high	Status quo	Global, local	82	41	3[74, 75]	0.046[76]	0.00068[76]	0.02[76] (975*)	0.13[76] (76500)	0.068[76]	0.75[77], 0.81[75,78]	0.48[77]	2.34[78]

Φ – density scenarios with targets 0.83, 1.30, and 1.80 lynx/100 km² corresponding to 160.64, 102.56, and 74.07 km² average female territories, ● – release locations after 42, * – values fixed during inverse fitting of road/rail mortality rates10·13, ■ – 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)%.
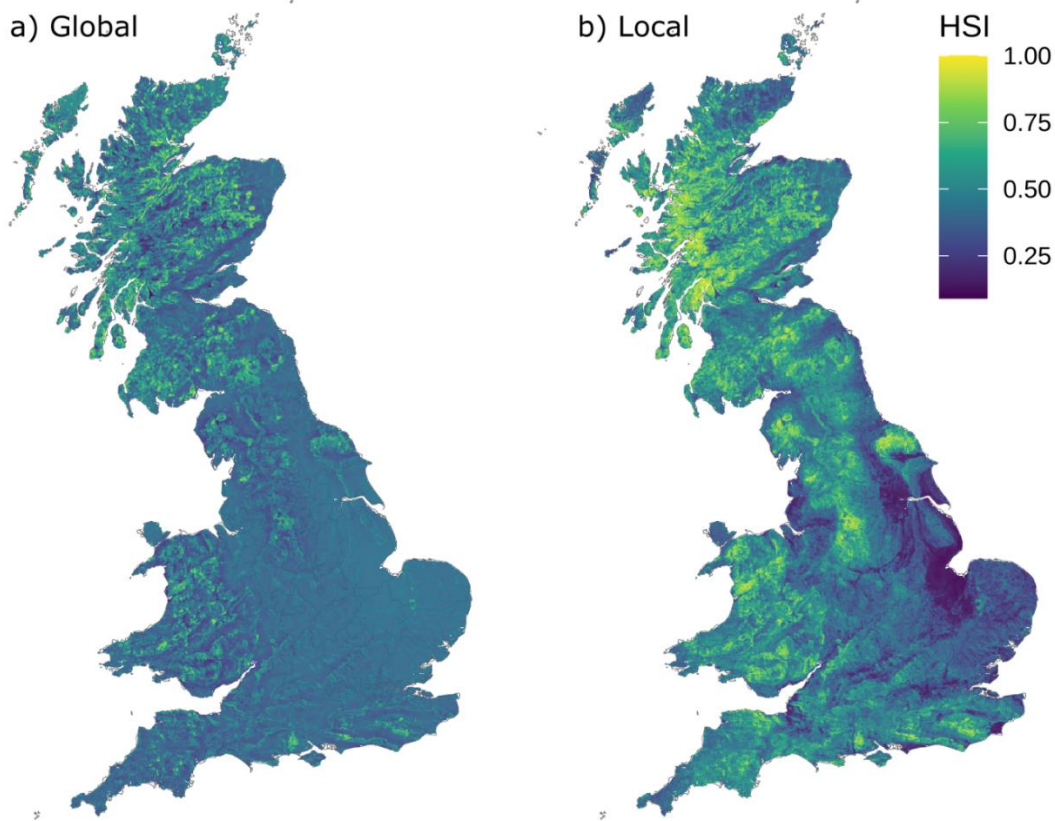
Figure 1. Relative lynx habitat suitability index (HSI) for Britain[36]. Although the local model appears to predict higher suitability, this is moderated by the higher threshold that emerged when converting the values into categories (Figure 2).

2.4.1.2. Distinguishing suitable habitats, matrix, and barriers

We converted the local and global habitat suitability maps from their continuous values to binary suitable-unsuitable maps using thresholds defined by the locations used in reintroduced lynx populations in Europe (see [82] applied in [83]). Reintroduced populations represent the best choice to determine the threshold because: i) we are simulating a reintroduction, ii) their habitat suitability distributions provide more clear differences between available and used values, iii) they are found in the more fragmented landscapes of Europe than the large autochthonous populations, which is a better corollary to the British context.

The resolution of the maps[36] was 100 m, so we aggregated these by a factor of 10 to reach the demogenetic models' 1 km resolution. From the areas of suitable habitat, we defined breeding habitat as contiguous cells of suitable habitat[84], although the actual area required for a territory was an emergent distribution constrained by the minimum female territory size and the max added parameter (Table 1). Any remaining suitable habitat, that was not part of a large breeding patch, was defined as dispersal habitat. Cells that had unsuitable habitat were defined as matrix, and included, for example, agricultural, and low-density human settlements. In this way we achieved a classification map with the classes breeding, dispersal, and matrix.

In addition to the suitable habitat classes, a map of 'barrier' features was included. This indicated impermeable landscapes for lynx's movements[13,44], such as motorways which are considerable barriers to lynx dispersal[85]. Barriers were defined using Corine landcover (CLC)[86], Global River Widths

from Landsat (GRWL) Database[87], and OpenStreetMap (OSM) road maps (© OpenStreetMap Contributors). We considered Corine landcover classes with urban characteristics and large water bodies, GRWL river sections with width >100 m, and OSM highways of class motorways as barriers[13,44]. Pixels containing sections of motorways tagged with bridges or tunnels in the OSM data were not considered as barriers. Finally, the suitable habitat classes (breeding and dispersal), matrix, and barrier were combined giving precedence to barrier to produce the final maps of categorical habitat preference (Figure 2).
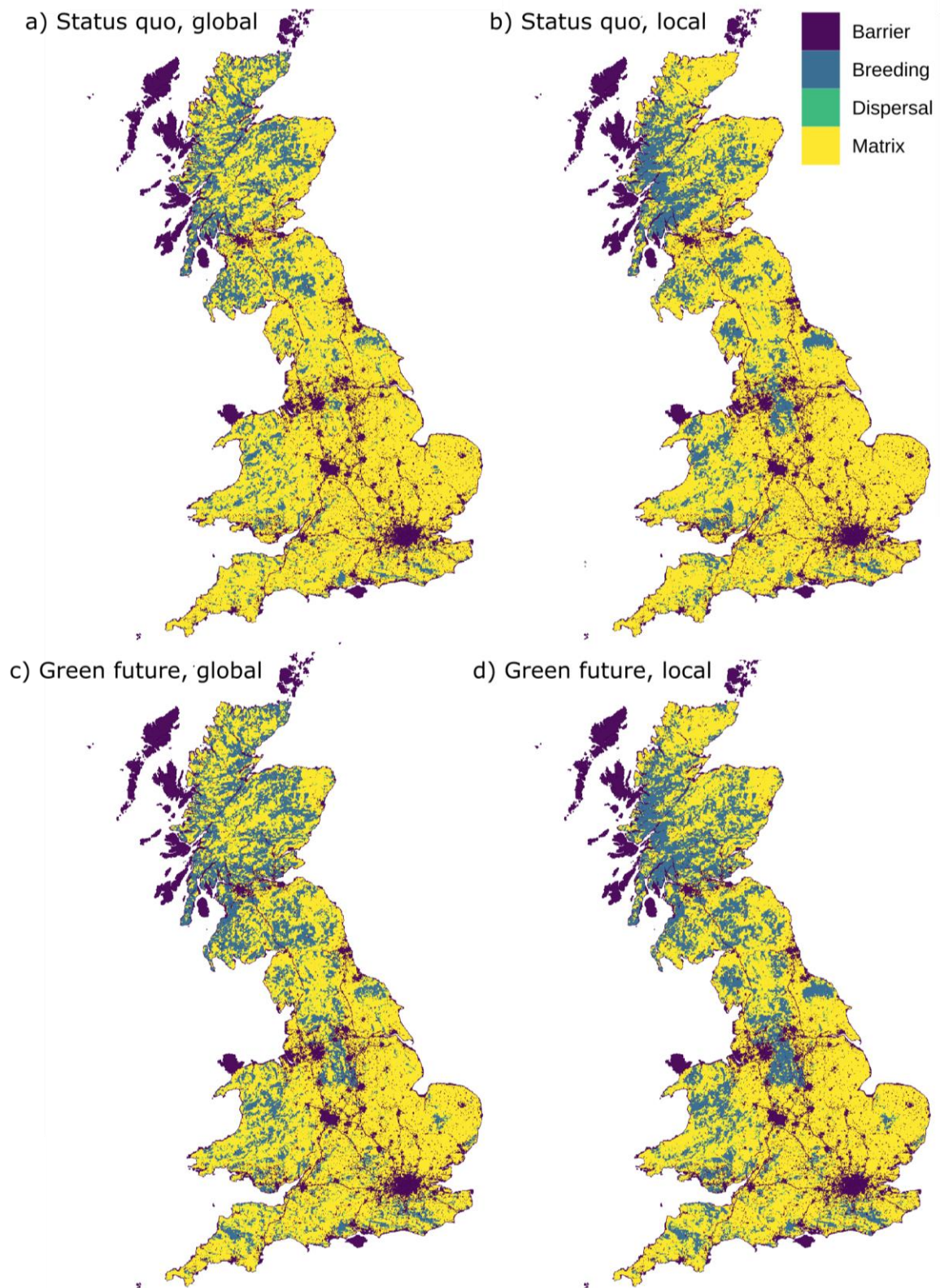
2.4.1.3. "Green future" habitat map

A further scenario we considered in our simulation modelling was the planned future increases in woodland extent and connectivity. As no explicit target areas have yet been provided, we used a forest potential map that retained the highest soil carbon sequestration as the basis for our "green future" habitat scenario[88]. Combining this potential forest creation fraction with the existing tree cover fraction[89], we reclassified matrix pixels exceeding 50% forest fraction as suitable habitat[33,90], and then reclassified dispersal and breeding habitats accordingly.

This resulted in two additional habitat classification maps that describe the landscape in a "green future" scenario under 'global' and 'local' model frameworks (Figure 2). These future habitat maps represent conservative improvements to the landscape, since we have only accounted for habitat improvement where it coincides with carbon goals, we used a conservative threshold for forest cover, and we do not consider connectivity improvements that are likely to occur, such as green-infrastructure.

2.4.2. Linear feature maps

The habitat maps described do 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[76]. This is considered in the demogenetic simulation model via two underlying maps of risk[13], one for resident lynx and one for dispersing lynx. This is due to their different spatial behaviours and apparent mortality risks[44]. It is therefore necessary to map the relative mortality risk due to the linear features at each location.

We created the linear features maps using data on highways and railways (© OpenStreetMap Contributors) for both resident and dispersing animals, as well as the river width[87] for dispersing animals only. The true relative risk of the different road classes, railways, and rivers are not available for lynx in Britain. It is assumed that the risk depends on traffic density, which serves as both the source of mortality and the source of dissuasion[91]. 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. Motorways are known to be considerable barriers to dispersal of lynx[85]. For this reason, we included motorways as barrier in the habitat map to create a low crossing likelihood (i.e. zero unless there are tunnels/bridges). Primary roads do not present a large barrier effect but do carry a large collision risk and hence are not considered barriers. These are therefore likely the most dangerous roads for lynx, as they are for many mammalian species in Britain, for example for deer[92]. Following the method of [13], we defined the relative risk of the different road classes based on the mortality rates for deer species on roads. When the entire UK road network is considered the deer vehicle collision rates per kilometre of major and minor roads are around 0.1 and 0.01, respectively[92]. We assigned railways the lower relative risk due to the low rates of railway mortalities found across Europe[76].

Figure 2. Habitat maps used in the demogenetic simulation modelling. Maps were based on predictions of the global model (a, c), local metamodel (b, d), for status quo (a, b) and green future (c, d) scenarios.

2.4.2.1. 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 through tunnels. We removed unclassified roads found in urban areas according to CLC to reduce overestimation of risk in residential areas. We 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. Finally, the resident linear features risk map was smoothed spatially with a moving window of approx. 50 km^2, which is at the lowest range of lynx home ranges (e.g.[58]), to distribute the risk as would be expected for resident lynx behaviour.

2.4.2.2. Disperser linear features

For roads and railways, we used the same mapping approach as for the resident linear features. We also included rivers with width >100 m. Since dispersers acquire a per step mortality probability derived from their movements through the landscape, the relative risk of underlying linear features was handled slightly differently. We removed sections of tunnels and bridges only for "minor" roads (secondary, tertiary, unclassified) and railways. 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 kilometres 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 were given higher relative risk as these were classified as barriers akin to motorways. These were then summed with the respective weights.

2.5. Release conditions

The number of individuals translocated per time unit, the selection of individuals to translocate, and the location of releases should be considered to maximise the likelihood of population persistence. We simulated these with a range of release scenarios described in Table 1 and in detail as follows:

2.5.1. Release locations

Prior studies, especially considering Scotland[42], proposed suitable release locations, namely: Cairngorms, Galloway, and Kintyre. We complement these with locations in England and Wales based on the classified habitat suitability maps. Specifically, we selected places where the global and local models' predictions agreed there was suitable habitat exceeding a contiguous area of > 130 km^2 (Figure 3). We chose this threshold to reduce the number of release locations to 10. Release locations were therefore defined as Kielder Forest, New Forest, North Wales, North York Moors, Peak District, Southeast England and South Wales in addition to the three locations in Scotland. These names were chosen since the release locations are placed in patches that roughly correspond to these geographical areas, but see Figure 3 for the full spatial delineation of the release locations, patches, and geographic nomenclature.

The release location coordinates were placed in the largest habitat bulk within each of the agreed suitable patches. In North and South Wales numerous patches of similar size were found, therefore released lynx were divided among these. Reintroductions were initially simulated for each location individually before selecting focal locations based on those with low extinction probabilities under

diverse conditions (extinction probability ≤ 5%). The focal locations were subsequently tested under a subset of scenarios to identify the best release regimes (i.e. sex-ratio, number of individuals, timing, and founder genetics) under medium mortality and territory size conditions.
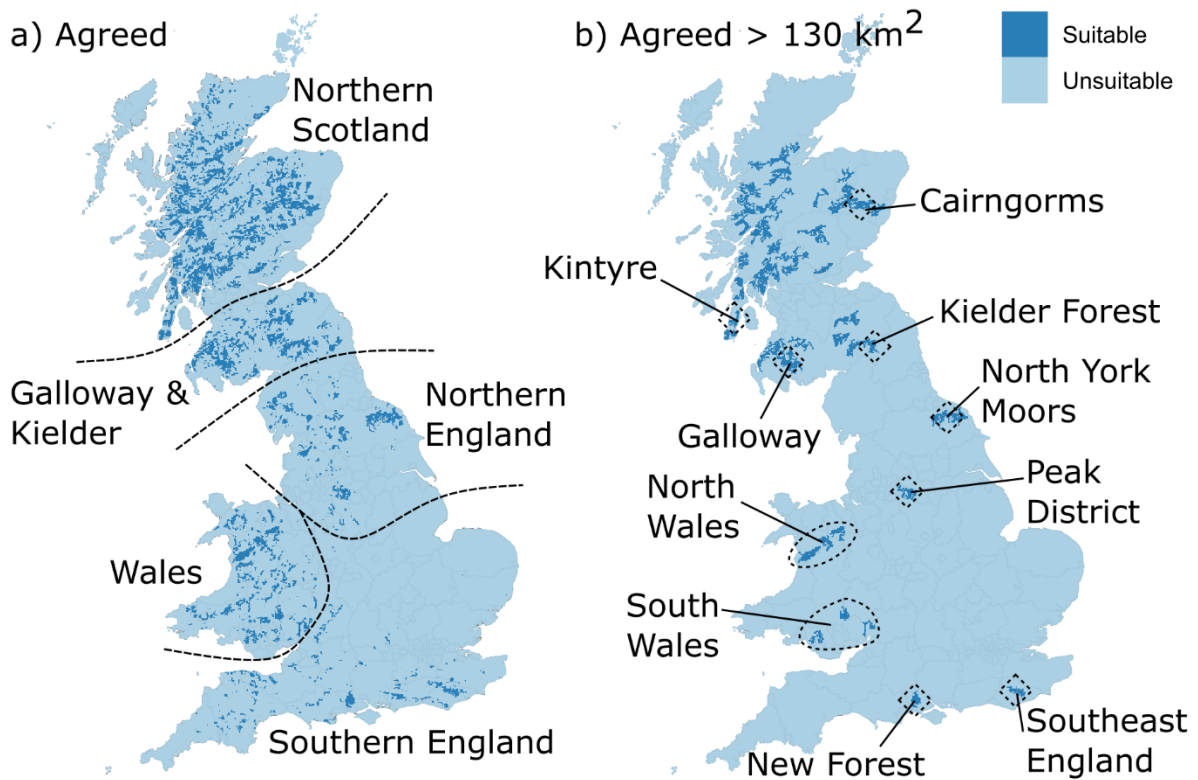

Figure 3. a) Patches of suitable habitat as *agreed* by both global and local model predictions, with the geographical nomenclature used to describe the regions provided, and b) agreed patches larger than 130 km² chosen arbitrarily to reduce the number of locations tested to ten with the identified release locations labelled. In North and South Wales numerous patches of similar size were found, therefore released lynx were divided among these.

2.5.2. Sex-ratio, number of individuals, and timing

The observed sex-ratio in lynx populations is between 1 and 6 females per male[93,94], with the simulated range between 1 and 3 female territories per male territory[10]. It is possible that the release population's sex-ratio could affect establishment in the wild because the **social-spatial organisation** depends on habitat configuration. Therefore, certain sex-ratios might be better suited to maximise population expansion. We tested two scenarios, namely 1:1 and 1:3 (male:female) ratios.

The number of individuals released affects the likelihood of successfully establishing a population. Releasing a large number of individuals can have protective benefits for demographics[16] and genetics[20]. We therefore simulated a range of release numbers in order to explore the effects on population development, as follows: for simulations that considered single release locations we

tested n = 10, 20, and 40, while for multi-release location scenarios we tested n = 20, 40. Although 40 individuals is considered rather high, it may be realistic if captive bred lynx were released[7,95]. For scenarios with 3 release locations (Table 1), the number of individuals could not be divided evenly among locations and the remaining individual was released in the location with the largest area of suitable habitat.

The timing of releases was simulated with three different possibilities, based on releases across various numbers of subsequent years: i) first two years, ii) first three years, and iii) first six years. In other words, per year the fraction of lynx released was: i) 50 (50, 50)% , ii) 33.33 (34, 33, 33)% , and iii) 16.66 (17, 17, 17, 17, 16, 16)%.

2.5.3. Source population (founder genetics)

The population genetic development of a lynx reintroduction is an important aspect of long-term population viability. Large wild populations or a captive breeding program could be considered as viable sources of lynx for release due to their high genetic diversity. We simulated two levels of population genetic diversity (high and low) for the focal locations scenarios. The genotypes of the released individuals were based on published microsatellite genotype data[24]. For the high diversity source population, we chose genotypes from a mix of the Baltic, Harz, and Scandinavian populations, while for the low diversity case we took genotypes only from the Carpathian population. For each simulation scenario we selected individuals' genotypes at random from the given dataset, without replacement. These two levels of diversity represent likely scenarios of released genetic diversity in modern reintroduction projects, which is typically much higher than reintroductions carried out four decades prior[96].

2.6. Measures of reintroduction success

We adopted several measures of reintroduction success for our simulations[10,42]. Overall reintroduction success was defined by probability of population extinction ≤ 5% after 100 years (i.e. number of simulation replicates that failed to reach 100 years) and the mean population size after 100 years. To complement these, we visualised the extinction probability over time (i.e. the cumulative number of extinct repetitions at each timestep) and population size over time. To understand the development in space, we mapped the mean probability of patch occupancy after 100 years, the mean year of first occupancy, and the emergent space-use.

Population size was calculated as the number of independent individuals (age ≥ 1), since juvenile numbers fluctuate annually. Only simulation runs that reached 100 years were included in the calculation. Mean first occupation time and occupation probability were calculated at the patch level, with patches defined as areas of contiguous suitable habitat and calculated individually for each habitat map (global and local models of status quo and future). Occupation of a given patch was defined as at least 1 territorial resident female in that patch, since males do not become territorial without female presence.

For the subset of successful release locations (focal locations), we further examined the population genetic metrics of mean heterozygosity and mean allelic richness after 100 years and their development over time.

2.7. Metamodelling analysis

Metamodelling is a powerful tool long used in simulation modelling to improve understanding of highly dimensional parameter space[97]. We used metamodels to explore the overall reintroduction success and understand the most important drivers of success and failure. As response (dependent) variables, we used the simulation endpoints: extinction probability ≤ 5% (extinction probability, specified as binary success/failure) and population size (a continuous measure) for all simulations, and the genetic metrics heterozygosity and allelic richness (both continuous measures) for the subset of focal locations. The simulation input parameters were used as predictor (independent) variables (Table 1). We used RandomForest modelling[98,99] to rank simulation parameters by their importance in predicting reintroduction success. To visualise relationships and thresholds for the parameters, we used Classification and Regression Trees (CaRT)[100]. Based on the results of these metamodels we could narrow parameter-space when plotting the temporal development of reintroductions, as well as the maps of occupancy.

3. RESULTS

3.1. Drivers of reintroduction success

3.1.1. Overall simulation parameter importance (randomForest metamodeling)

For simulation set A, the set with the widest range of parameters (Table 1), the most important parameters for predicting the extinction probability and population size were the added and baseline mortality rates. In simulation set B, which focussed on the comparison between the status quo and the 'green future' habitat scenarios, the release location was of far greater importance for predicting extinction probability and population size than the habitat scenario. The number of lynx released was important for predicting extinction probability but of little importance for predicting population size. Simulation set C, was concerned with comparing single and combinations of focal release locations and consideration of population genetic endpoints. Here, release location was also important, especially for population size. Release timing was particularly important for extinction probability. Habitat model, number of lynx released, and sex-ratio were of low importance. Considering the genetic endpoints, the number of lynx released, release locations, and release-genetics were of high importance. For heterozygosity, the most important parameter was the released number, while for allelic richness it was released genetics. For both genetic metrics the habitat model was of moderate importance.

3.1.2. Parameter effects and thresholds (CaRT metamodeling)

3.1.2.1. Main simulations (set A)

The CaRT metamodels for extinction probability and population size based on simulation set A both attributed the first split to the parameter release location (Figure 4 and 5). The single release locations Cairngorms, Galloway, and Kielder Forest were found to be those with generally higher likelihood of success (extinction probability ≤ 5%), unless the baseline or added mortality rates were high. The release locations North Wales, North York Moors, Peak District, and Kintyre only had successful reintroductions under more specific parameters, namely with low or medium added and baseline mortality, and small or medium territory sizes. Further, the success for these release locations depended on the habitat model, with Kintyre only successful (extinction ≤ 5%) with the global habitat map. The release locations New Forest, Southeast England, and South Wales did not meet the criteria under any simulation conditions. The simulation parameters sex-ratio, vehicle mortality for residents and dispersers, and the number of lynx released were not relevant for extinction probability compared to the other parameters.
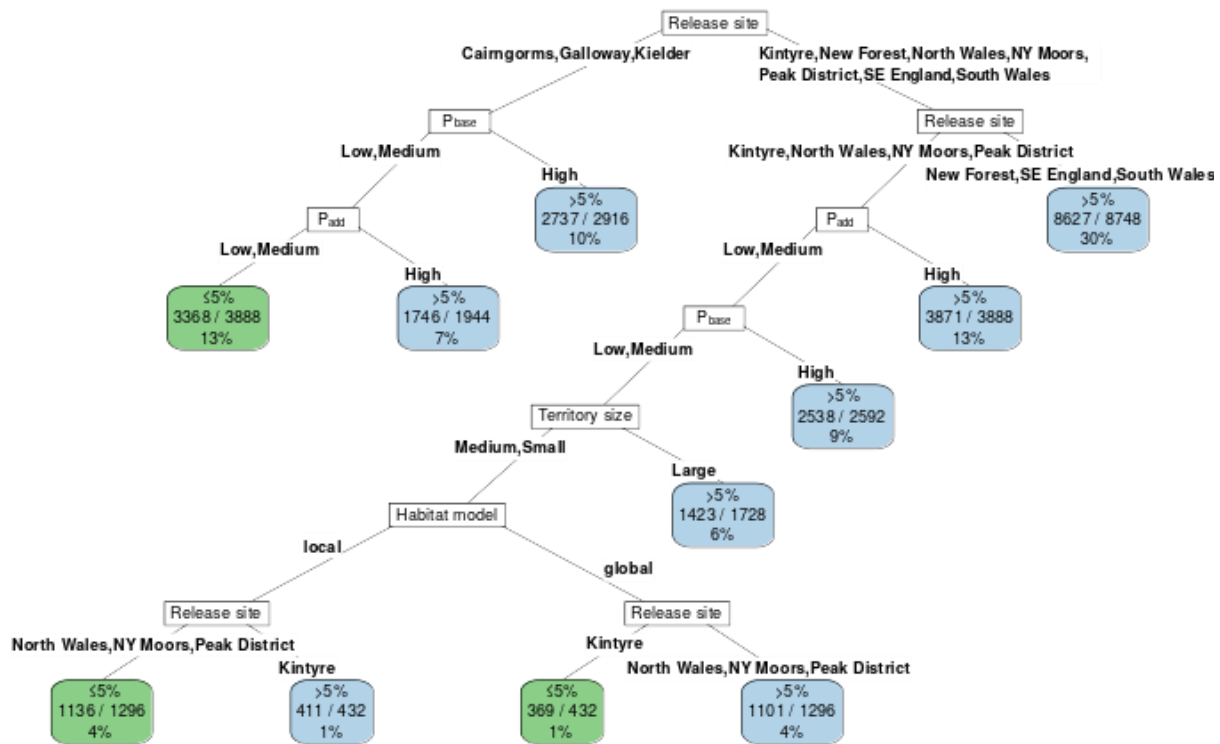
Figure 4. Classification tree metamodel for probability of extinction after 100 years since release based on set A. Binary response with extinction probability ≤ 5% and > 5% indicating success and failure, respectively. At each node the data are split based on the parameter in the node and its values on the branches. At the terminal nodes, the predicted classifications, success (green) and failure (blue), are indicated with the response, the fraction of the data subset in agreement and the percentage of the entire dataset within the subset.

Cairngorms and Kintyre were differentiated from the other release locations by their tendency to develop larger lynx populations after 100 years (Figure 5). Under medium simulation conditions a population size of 302 independent individuals was expected on average. For releases in Cairngorms and Kintyre, high baseline and added mortality caused the smallest population sizes (17 to 73). The largest population sizes were found with small territories and low disperser vehicle mortality, resulting in around 400 independent lynx. Of the other release locations, only Galloway and Kielder Forest resulted in population sizes exceeding 10 lynx, with all their terminal nodes resulting in a population of over 25 independent lynx. Territory size, added, baseline, and disperser vehicle mortalities had large effects on population size, with values ranging from 25 to 183 under more and less difficult simulation conditions, respectively. The remaining parameters, habitat model, number of lynx released, resident vehicle mortality, and sex-ratio, had smaller effects on population size.
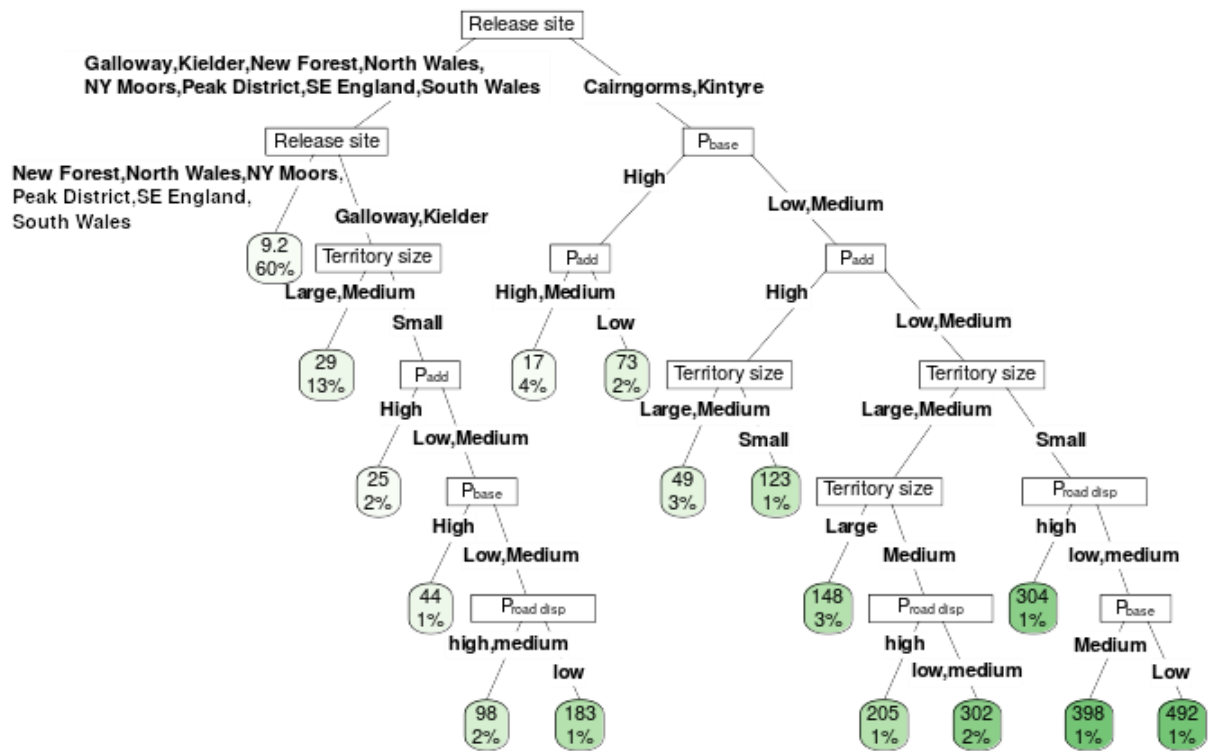
Figure 5. Regression tree metamodel for population size after 100 years since release based on set A. Continuous response indicates the number of independent individuals, considering only simulation repetitions that reached 100 years. At each node the data are split based on the parameter in the node and its values on the branches. At the terminal nodes the predicted population size for the subset is stated and the percentage of the entire dataset within the subset. Higher numbers indicated by darker green node colours.

3.1.2.2. Status quo vs "green future" (set B)

We found that the habitat scenarios status quo and green future, were of low importance in predicting the extinction probability of reintroductions (Figure 6). Further, this parameter was not responsible for improving the likelihood of reintroduction success below the 5% threshold. Under these medium simulation conditions, the CaRT metamodel showed at least 20 individuals should be released for reintroduction success under both habitat suitability models.

In contrast, the metamodel for population size did partition the data based on the habitat scenario parameter (Figure 7). The tree diagram indicates the release locations Cairngorms or Kintyre generally resulted in larger populations and that the population size could be increased by around 30 independent individuals under future habitat conditions. The New Forest and Southeast England release locations exhibited population sizes near zero, regardless of habitat conditions. Concerning the other release locations, the population sizes approximately doubled from the status quo to future habitat conditions. Releases at the locations Galloway or Kielder Forest more than doubled, from 54 to 124.
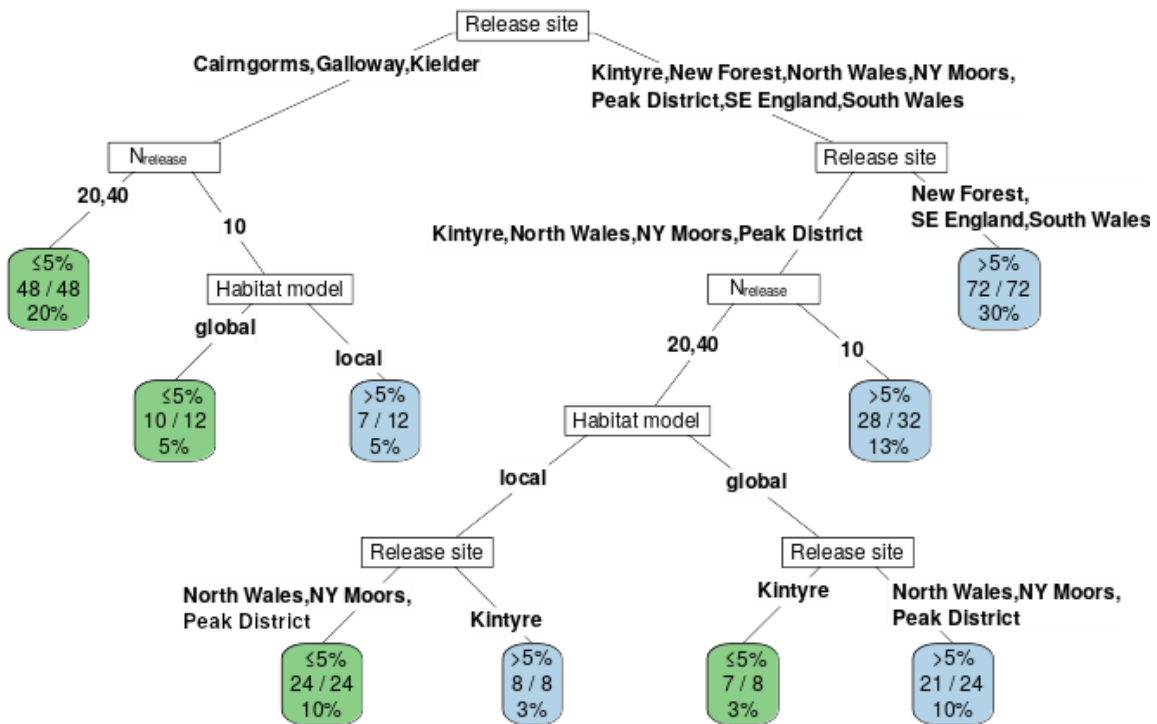
Figure 6. Classification tree metamodel for probability of extinction after 100 years since release based on set B - the habitat scenario. Binary response with extinction probability ≤ 5% and > 5% indicating success and failure, respectively. At each node the data are split based on the parameter in the node and its values on the branches. At the terminal nodes, the predicted classifications, success (green) and failure (blue), are indicated with the class, the fraction of the data subset in agreement and the percentage of the entire dataset within the subset.

3.1.2.3. Focal location combinations (set C)

Cairngorms, Galloway, and Kielder Forest consistently had extinction probabilities under 5% and were therefore identified as the focal release locations. Since these locations were all successful the extinction probability metamodel was fitted as a continuous response (Figure 8). The first split indicates that releasing many individuals provided a low extinction probability. The highest extinction probability for the focal locations were found with when 20 lynx were released with the local habitat model and specific release location combinations (CGK, CK, and K). Further, the intermediate release timing (over 3 years) reduced the extinction probability in this subset of the simulations.
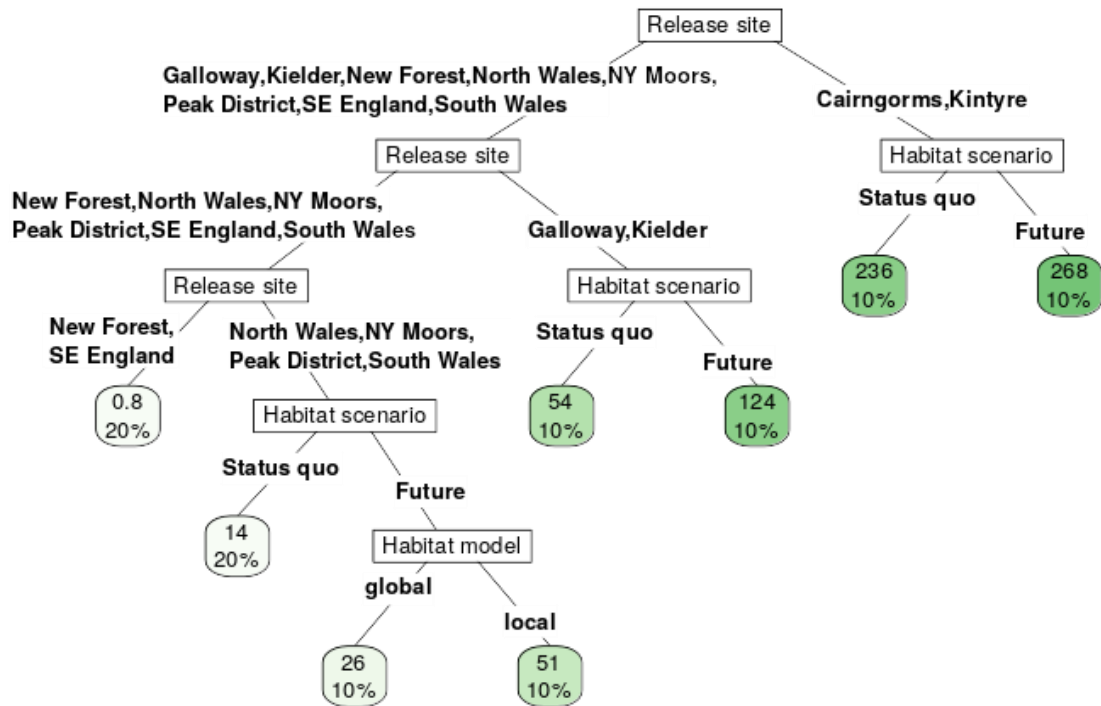
Figure 7. Regression tree metamodel for population size after 100 years since release based on set B - the habitat scenario. Continuous response indicates the number of independent individuals, considering only simulation repetitions that reached 100 years. At each node the data are split based on the parameter in the node and its values on the branches. At the terminal nodes the predicted population size for the subset is stated and the percentage of the entire dataset within the subset. Higher numbers indicated by darker green node colours.
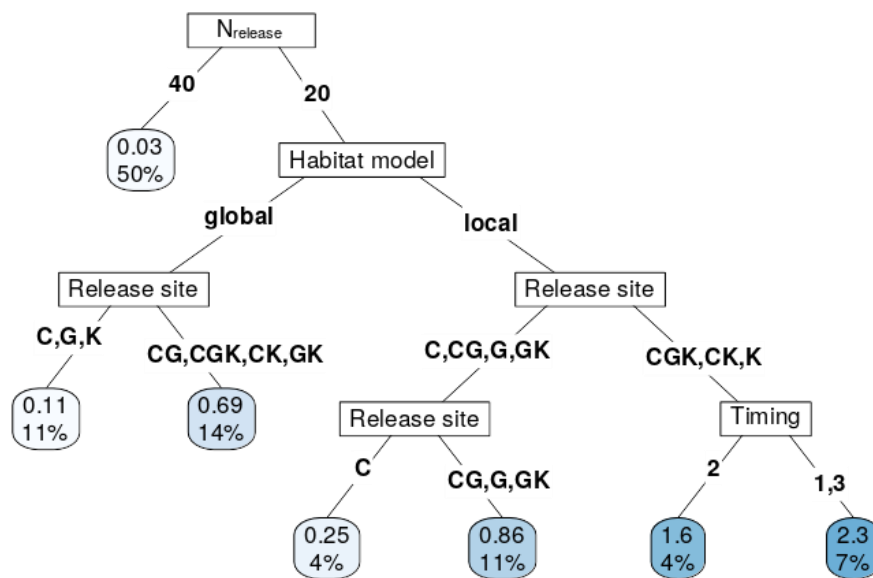
Figure 8. Regression tree metamodel for probability of extinction as a continuous response (categorical not possible since all less than 5% extinction probability) based on set C - considering releases in single and combinations of focal release locations: C - Cairngorms, G - Galloway, and K – Kielder Forest. Continuous response indicates the value of extinction probability (0-1). At each node 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 for the subset is stated and the percentage of the entire dataset within the subset. Higher numbers indicated by darker blue node colours.

The location combinations that only included Galloway and Kielder Forest (G, GK, K) were expected to reach a population size of around 60 independent individuals (Figure 9). Location combinations that also included Cairngorms, were expected to reach between 214 and 288 independent individuals, from 20 and 40 released lynx respectively. The largest populations were achieved by releasing in Cairngorms and at least one of Galloway or Kielder Forest.
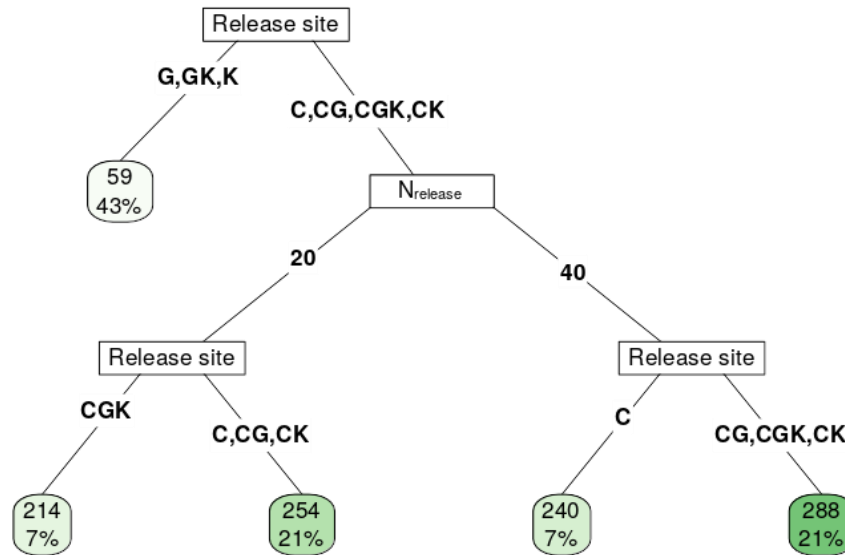
Figure 9. Regression tree metamodel for population size after 100 years since release based on set C - considering releases in single and combinations of focal release locations: C - Cairngorms, G - Galloway, and K – Kielder Forest. Continuous response indicates the number of independent individuals, considering only simulation repetitions that reached 100 years. At each node the data are split based on the parameter in the node and its values on the branches. At the terminal nodes the predicted population size for the subset is stated and the percentage of the entire dataset within the subset. Higher numbers indicated by darker green node colours.

We also explored the effect of combinations of release locations on population genetic endpoints. The highest heterozygosity values were found by releasing in Cairngorms (Figure 10). In general, releasing more individuals and from more diverse origins (genetics = higher) increased heterozygosity. Aside from releasing in just Cairngorms, high diversity was also found for location combinations that included Cairngorms. If releasing just in Kielder Forest or Galloway, the local habitat model tended to decrease heterozygosity. The lowest heterozygosity (less than 0.28) was found when releasing in just Galloway with the local habitat model, or when a combined release in Cairngorms, Galloway, and Kielder Forest was simulated with a release of 20 lynx. For comparison, a single location release in Kielder Forest resulted on average with heterozygosity greater than 0.3, according to the metamodel.

The development of allelic richness after single and combined releases in the three release sites were similar to those stated for heterozygosity. Again, releasing more lynx and with diverse origins increased the genetic diversity (Figure 11). Among the three release sites and their possible combinations, allelic richness was higher in the combinations that included Cairngorms (2.9 to 4.2) than the standalone releases in Kielder Forest or Galloway. Lower values of allelic richness were found for standalone releases in either Kielder Forest or Galloway compared to the Cairngorms (2.3 to 2.8).
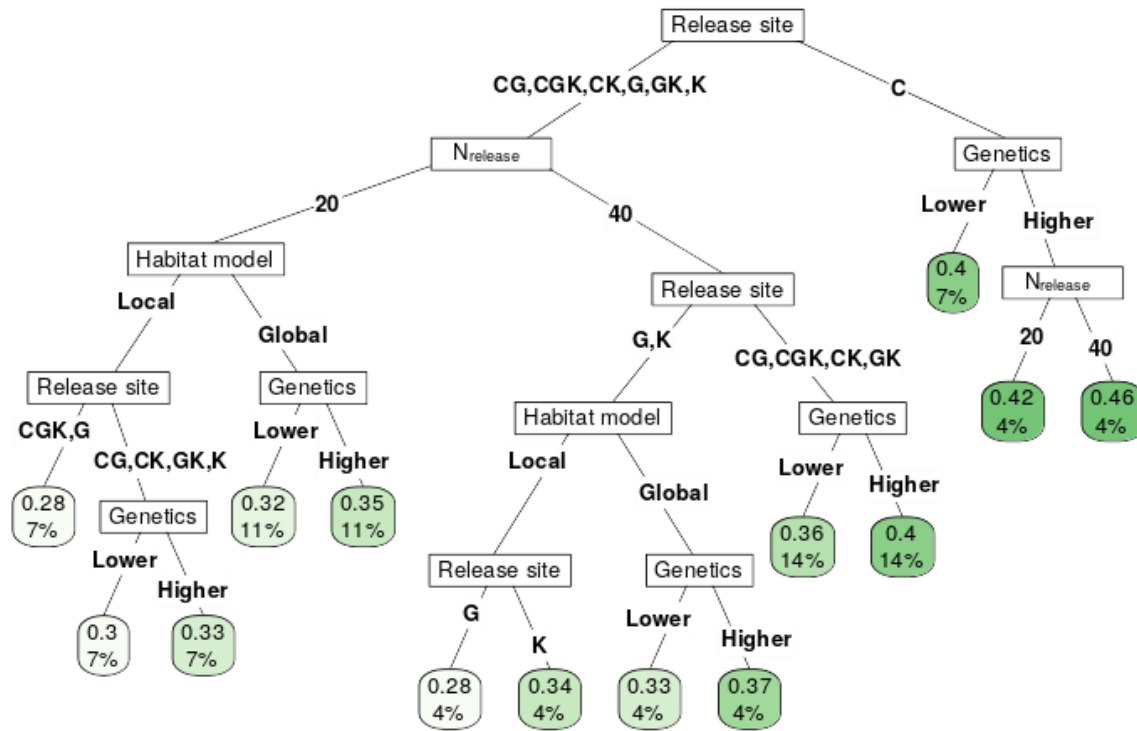
Figure 10. Regression tree metamodel for heterozygosity after 100 years since release based on set C - considering releases in single and combinations of focal release locations: C - Cairngorms, G - Galloway, and K – Kielder Forest. Continuous response indicates the predicted value of heterozygosity after 100 years. At each node the data are split based on the parameter in the node and its values on the branches. At the terminal nodes the predicted heterozygosity for the subset is stated and the percentage of the entire dataset within the subset. Higher numbers indicated by darker green node colours.
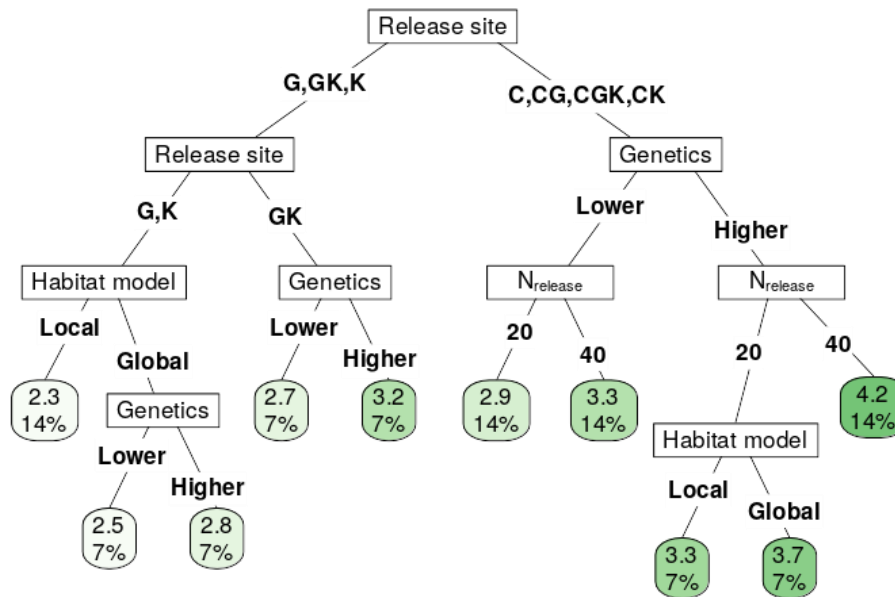
Figure 11. Regression tree metamodel for allelic richness after 100 years since release based on set C - considering releases in single and combinations of focal release locations: C - Cairngorms, G - Galloway, and K – Kielder Forest. Continuous response indicates the predicted value of allelic richness after 100 years. At each node the data are split based on the parameter in the node and its values on the branches. At the terminal nodes the predicted allelic richness for the subset is stated and the percentage of the entire dataset within the subset. Higher numbers indicated by darker green node colours.

3.2. Temporal population development

To gauge the likelihood of reintroduction success we visualised the temporal development of the population endpoints under medium parameter conditions (Table 1) and specifying the ideal release parameters from the metamodel results (40 released lynx with a ratio of 1 male to 3 females).

3.2.1. Probability of extinction

Examining the probability of extinction at each timestep shows that many release locations quickly exceed the 5% extinction probability threshold (Figure 12), including the New Forest and Southeast England. Even under the improved future habitat conditions these release locations exceeded 5% after 15 years. The success of several release locations depended on the habitat model. For example, the North York Moors, North Wales, Peak District, or Kintyre release locations were under 5% extinction for both current and future conditions when using the local habitat model, while when using the global habitat model extinction probability went above 5% before 70 years for all four release locations even in the green future scenario. The locations Cairngorms, Galloway, and Kielder Forest (i.e. the focal release locations) remained under the threshold for both habitat models and habitat scenarios.
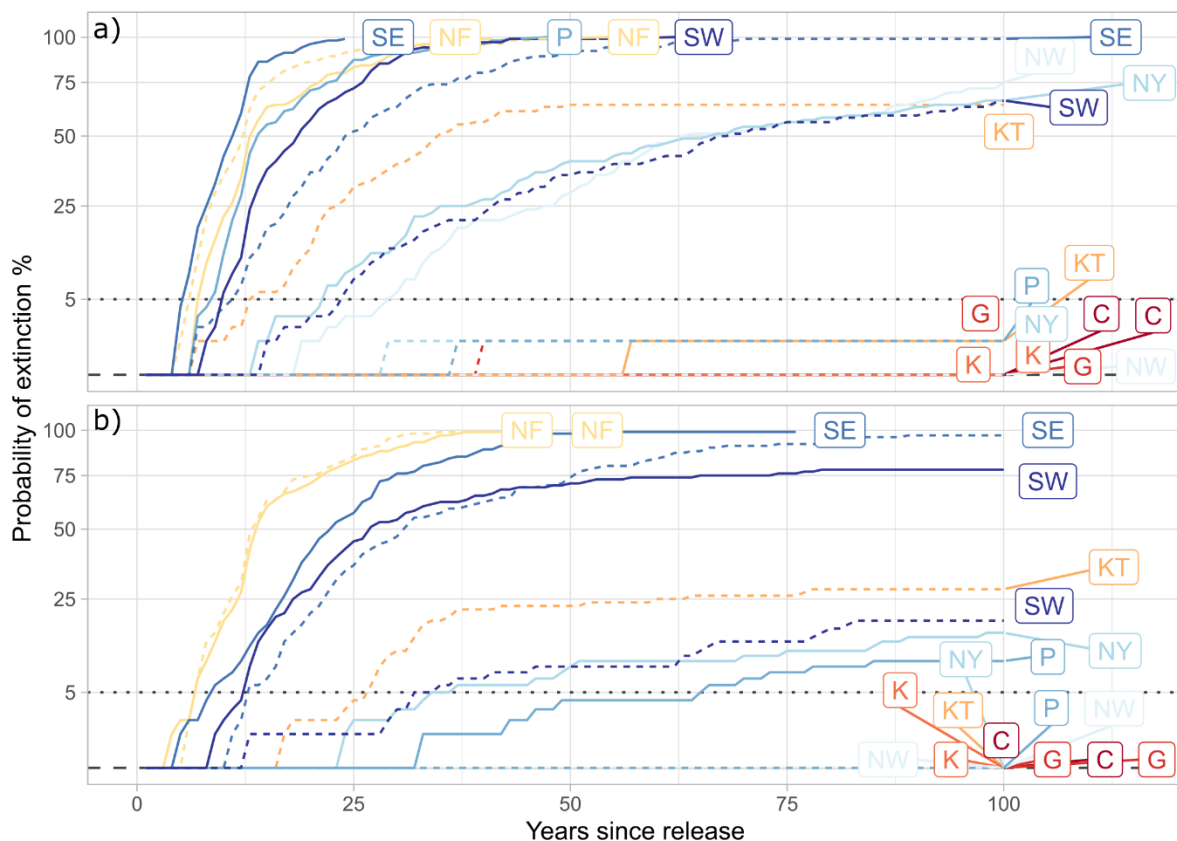
Figure 12. Extinction probability over time for different single release locations under: a) status quo and b) green future habitat scenarios and medium simulation parameters. Solid line – global and dashed line – local habitat models. Release locations are indicated with the names: C - Cairngorms, G - 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.

3.2.2. Population size

Releases in Cairngorms and Kintyre developed the largest populations, reaching between 200 and 250 independent individuals under any habitat model and habitat scenario (Figure 13). Populations released in Galloway or Kielder Forest increased at a slower rate and reached around 50 individuals under the status quo and 100-130 individuals under future habitat conditions. However, the population growth did not appear to have plateaued and can be assumed to continue. Releases in the Peak District, North York Moors, North Wales, and South Wales individually achieved around 30-50 individuals depending on the habitat model. The Southeast England location was always under 20 individuals, while the New Forest location could not be plotted since no repetitions reached 100 years.
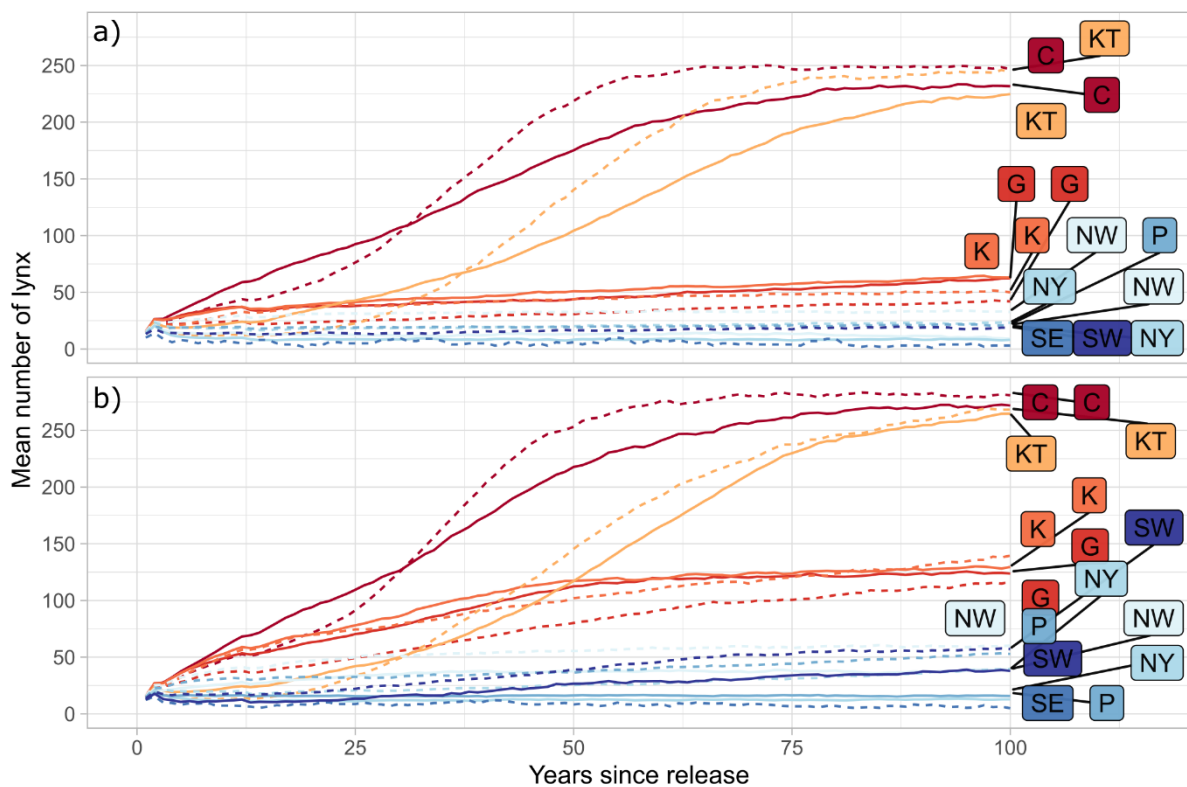
Figure 13. Population size for different single release locations under: a) status quo and b) green future habitat scenarios and medium simulation parameters. Solid line – global and dashed line – local habitat models. Release locations are indicated with the names: C - Cairngorms, G - Galloway, K – 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 runs that reached 100 years.

Releasing lynx at multiple locations increased the rate of population growth over single location releases (Figure 14). 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 largest population (approx. 280) was achieved with releases including Cairngorms and at least one of Galloway or Kielder Forest. Single location releases in Cairngorms grew at a similar rate but plateaued with 30-50 individuals less (230-250).
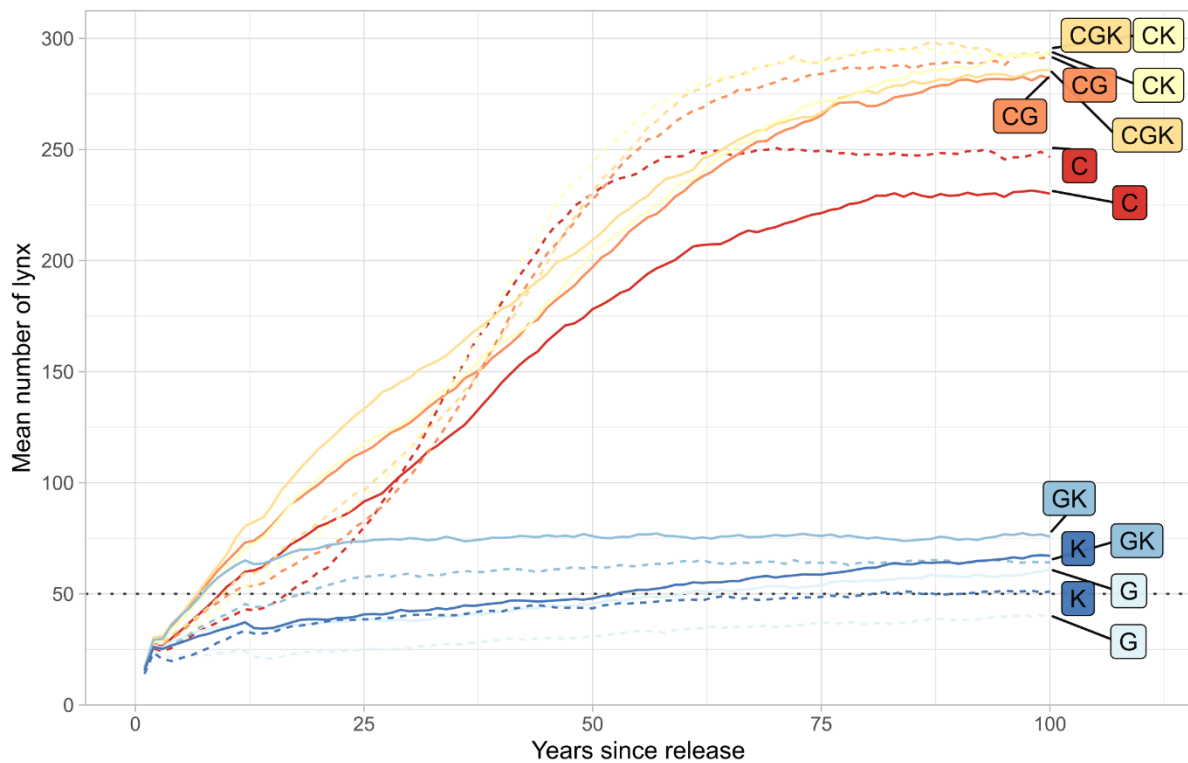
Figure 14. Overall population size over time from different combinations of focal release locations. Release locations are indicated with the names: C - Cairngorms, G - Galloway, K – Kielder Forest, and combinations thereof. Solid line – global and dashed line – local habitat models.

3.2.3. Genetics

For simulations with more diverse origins (higher diversity) heterozygosity increased to 0.6 between 5 and 10 years for all release locations (single or combinations of locations), while the less diverse releases immediately decreased from 0.6 (Figure 15). Subsequently, heterozygosity declined to values between 0.48 and 0.25. Higher values were associated with the global habitat model. Releasing all individuals in the Cairngorms maintained the highest heterozygosity and the lowest was found when all individuals were released in Galloway, especially under the local model. Simultaneous releases in these two locations resulted in higher heterozygosity than each individually, especially for the global habitat model.

The allelic richness in simulations with higher initial diversity increased rapidly to approx. 6, while the lower initial diversity simulations increased slightly to approx. 4 (Figure 16). Over time allelic richness decreased to between 2.3 - 4.5 and 2.0 - 3.5 for higher and lower diversity simulations, respectively. In contrast to heterozygosity, the highest allelic richness emerged in multi- location releases, with the highest found when the individuals were divided among all three focal release locations. Combinations of two locations, such as Cairngorms and Galloway, or Cairngorms and Kielder Forest exhibited similar maintenance of allelic richness. Again, higher diversity was associated with global habitat models. A single location release in Galloway has the lowest allelic richness after 100 years, especially for the local habitat model, with the effect most pronounced with founders of more diverse genetic origins.

Figure 15. Heterozygosity over time for a) higher and b) lower genetically diverse origins. From different combinations of focal release locations. Release locations are indicated with the names: C - Cairngorm, G - Galloway, K – Kielder Forest, and combinations thereof. Solid line – global and dashed line – local habitat models.

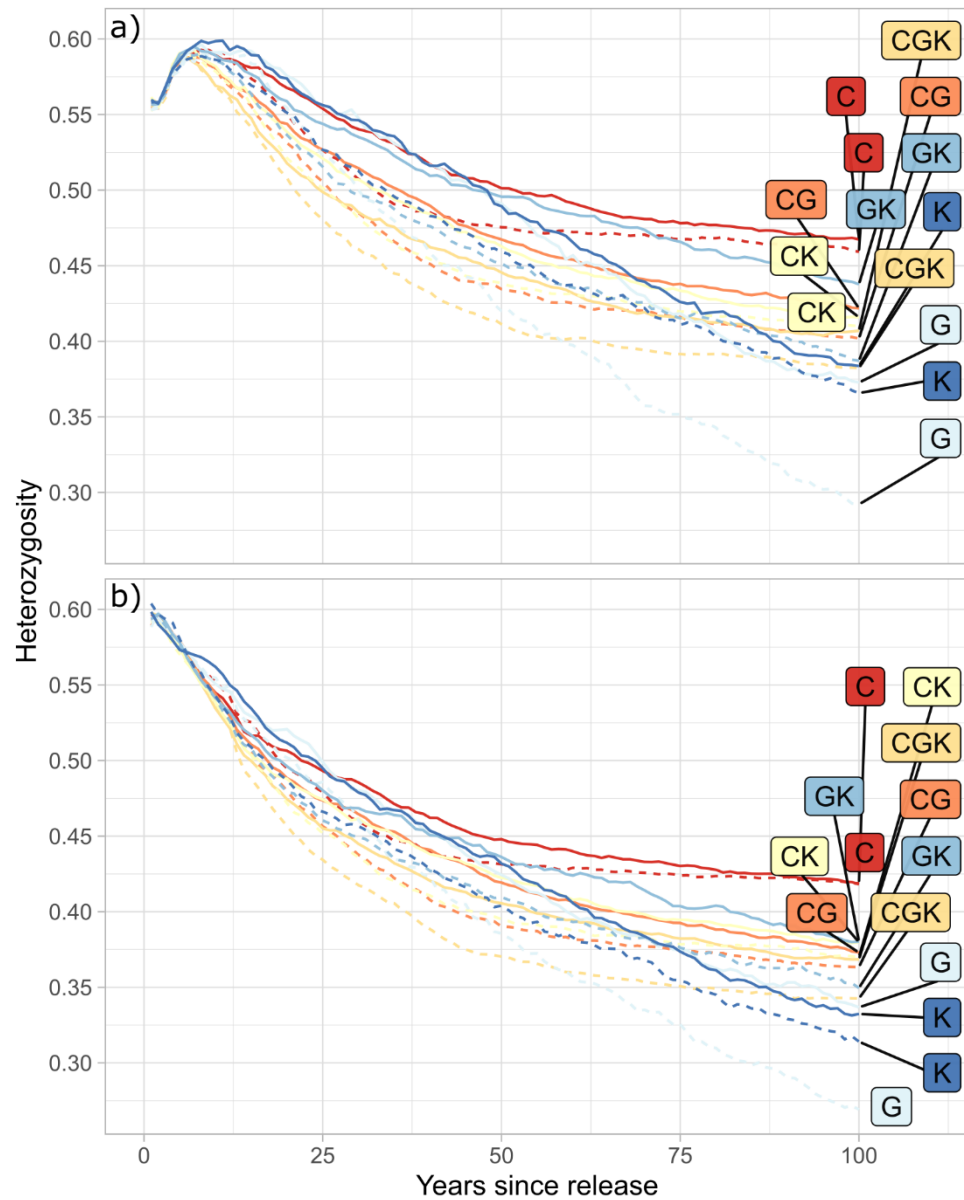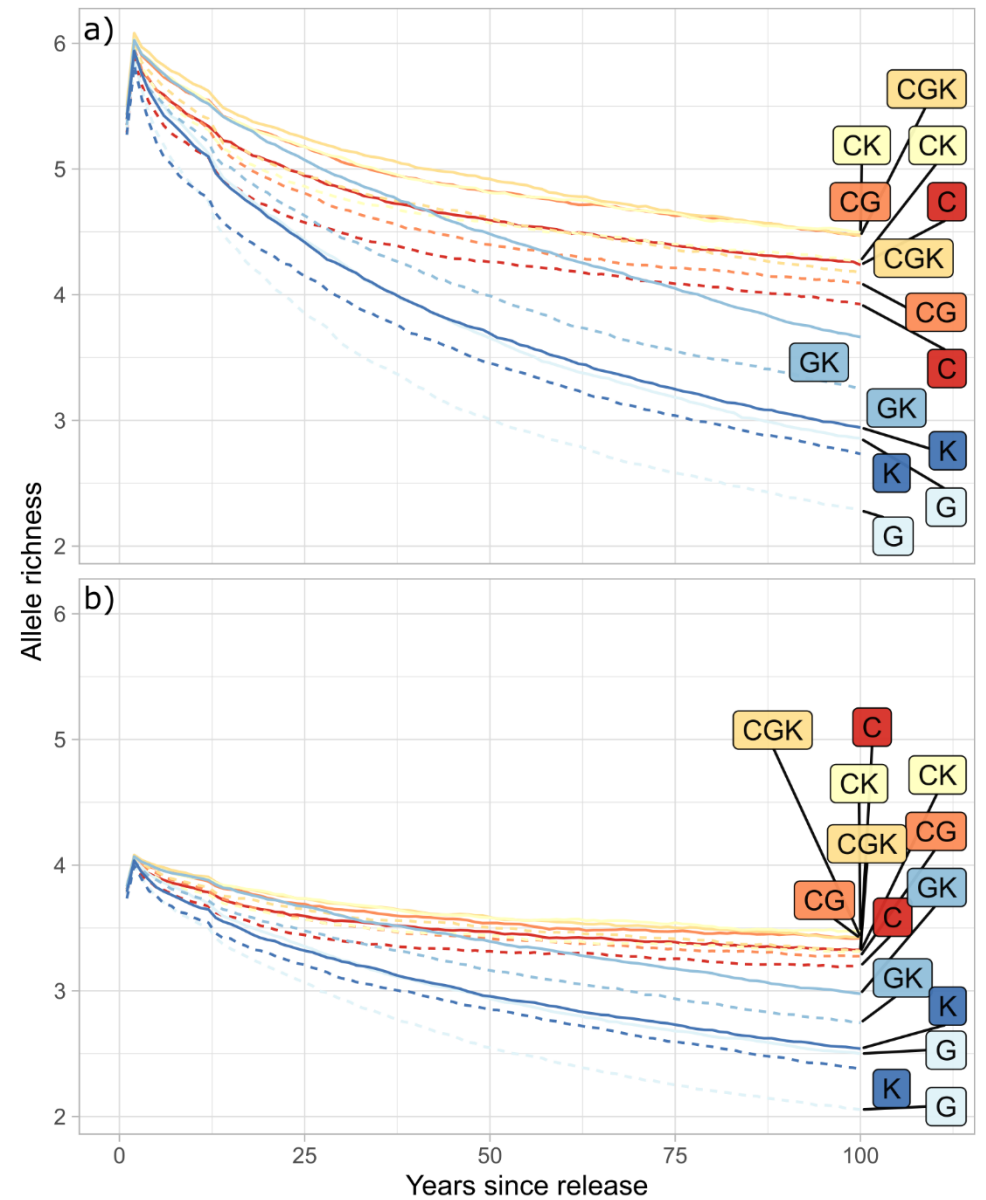**Figure 16. Allelic richness over time for a) higher and b) lower genetically diverse origins. From different combinations of focal release locations. Release locations are indicated with the names: C - Cairngorm, G - Galloway, K – Kielder Forest, and combinations thereof. Solid line – global and dashed line – local habitat models.**

3.3. Spatial distribution

3.3.1. Occupancy probability

3.3.1.1. Single location releases (status quo vs future green scenarios)

There was a high probability of lynx occurrence across Northern Scotland after releases from the Cairngorms for both habitat models (global – Figure 17, local – Figure 18). The occurrence of lynx was more extensive with the global habitat model than the local model under the status quo scenario, with high probabilities in areas of northernmost Scotland where no large suitable areas were predicted by the local model. Under the local model there was a low probability (< 5%) of reaching patches south of the Central Belt. Under future habitat scenario, using either habitat model, there was more extensive occupation of southern patches but still with low probabilities (< 5%).

The Kintyre release location resulted in similar spatial patterns of occurrence in Northern Scotland as the Cairngorms release locations, however with lower probabilities. For the status quo scenario, the local habitat model reached an occupancy probability of 40% in the bulk of Northern Scotland where the global model reached 100%. The global model also showed less than 5% occupancy probability in patches south of the Central Belt. Under future habitat conditions the local model simulations improved with around 70% occupancy probability in patches of Northern Scotland and connectivity to the south, while the global model remained similar in southward connectivity.

Releases in Galloway resulted in occurrences in Kielder Forest with over 60% probability for both global and local models for status quo habitat. There was a low probability (< 5%) of occupying patches further south and no occupancy north of the Central Belt. Under future conditions connectivity improved, with 100% probability of occupying the Kielder Forest patch and more non-zero occupancy probabilities of patches north and southward. Especially for the local habitat model, there was higher occupancy probabilities in England relative to the global habitat model.

Similar results were found with releases in Kielder Forest, specifically more than 60% occupancy probability in Galloway for status quo and higher probability under future conditions with greater spatial distribution. Differing from the Galloway release location, the Kielder Forest release location had a non-zero probability of occupying small patches north of the Central Belt under status quo conditions, for both habitat models. In other words, a small amount of connectivity was found between Northern Scotland and the Kielder Forest release location.

For the remaining six release locations, occupancy probabilities were below 50% under status quo conditions for at least one habitat model, or there was significant disparity in the predictions from the two models. Therefore, we do not describe these further.

3.3.1.2. Combinations of focal release locations

Releases that comprised two release locations increased the extent of occupied patches compared to single locations (Figure 19). The probabilities also increased, especially when the Cairngorms was included. 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 the patches in Cairngorms and Northern Scotland. The differences in occupancy based on the local and global habitat models were broadly negligible.
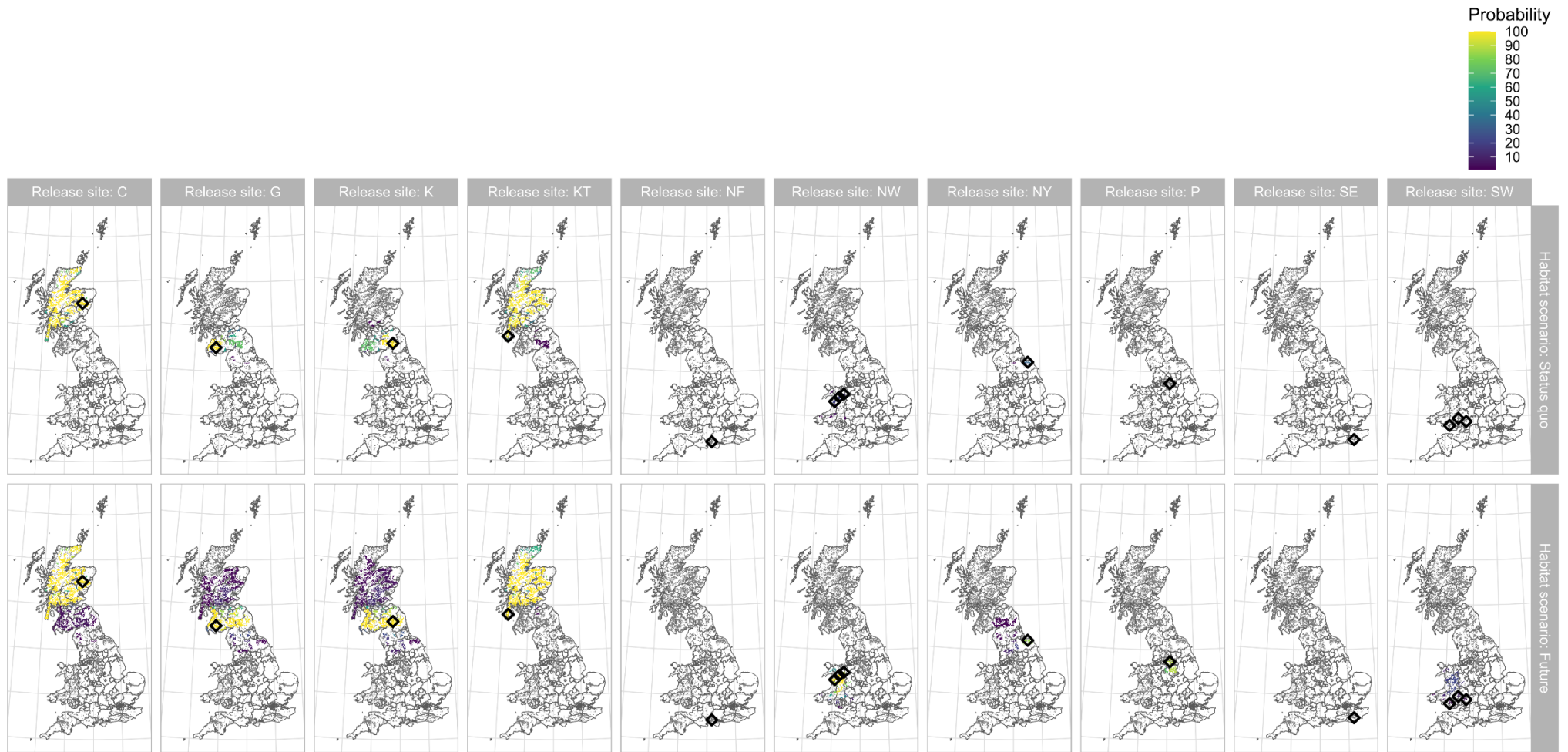
Figure 17. Probability of occupancy after 100 years based on the global habitat model, single release locations, and under status quo or future habitat scenarios. Release locations are indicated by diamonds, and with the names: C - Cairngorms, G - Galloway, K – Kielder Forest, KT - Kintyre, NF - New Forest, NW - North Wales, NY - North York Moors, P - Peak District, SE - Southeast England, SW - South Wales.

Figure 18. 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: C - Cairngorms, 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.
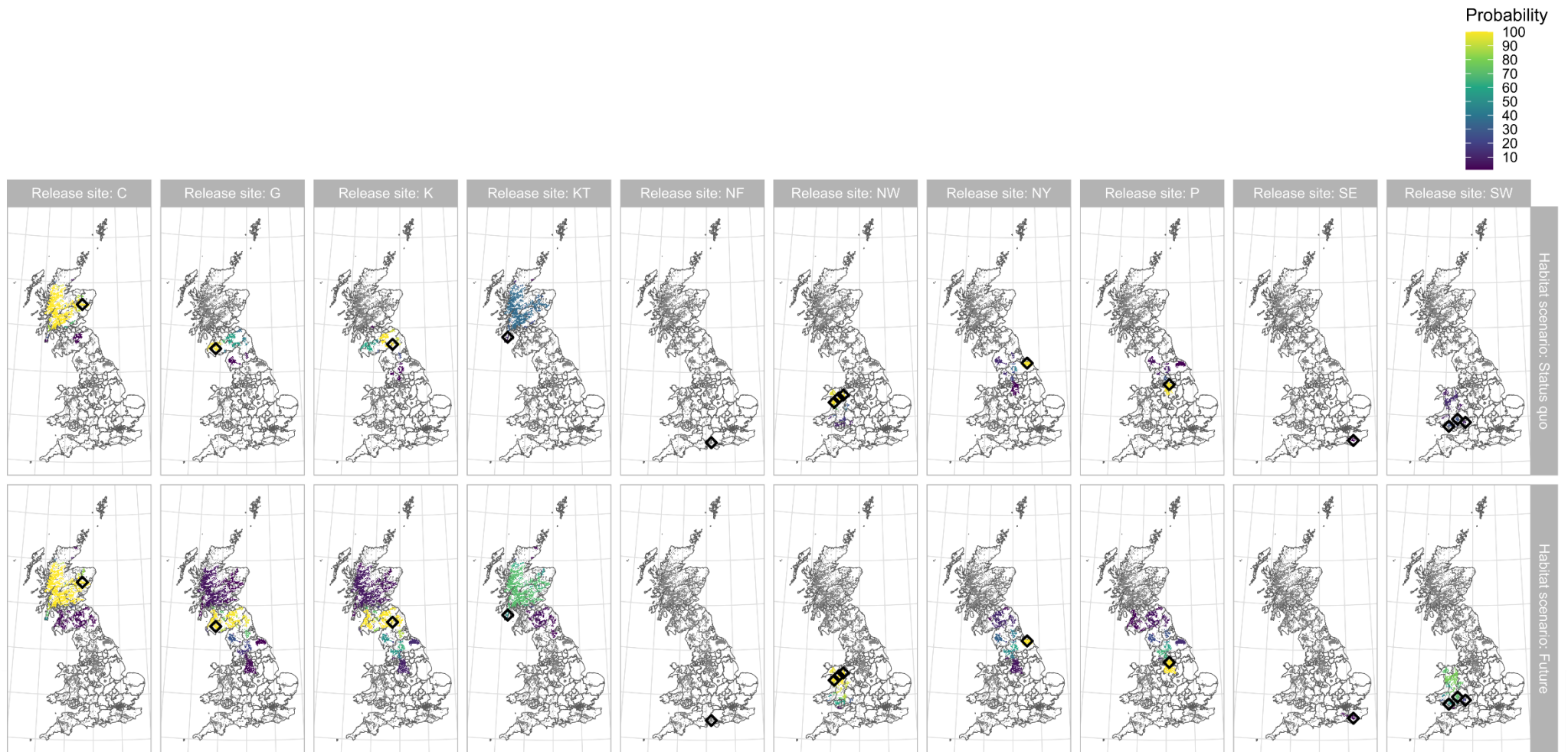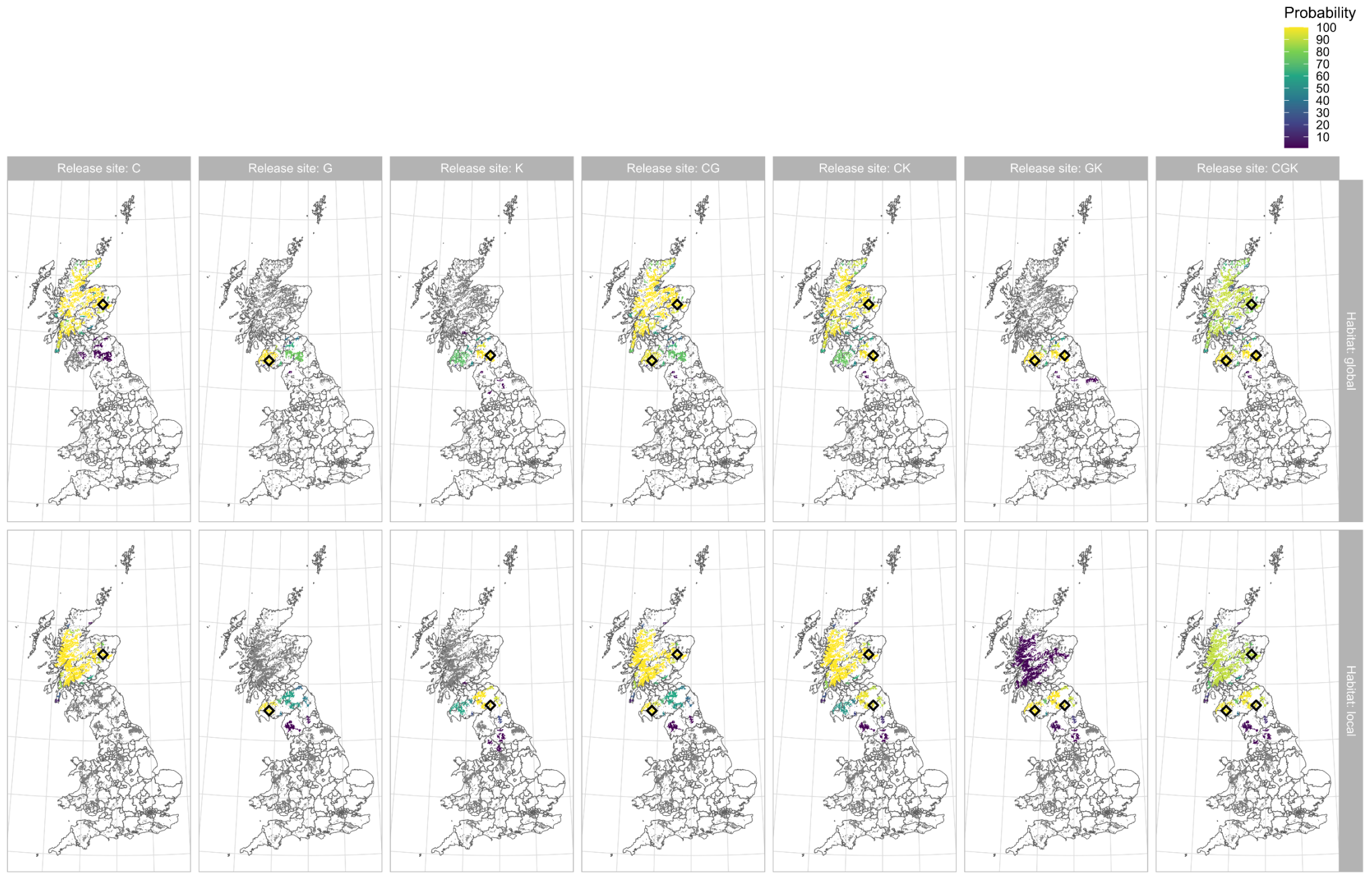
Figure 19. Probability of occupancy after 100 years based on combinations of focal release locations. Release locations are indicated by diamonds, and with the names: C - Cairngorms, G - Galloway, K – Kielder Forest, and combinations thereof.

3.3.2. Mean first occupation time

3.3.2.1. Single location releases (status quo vs green future scenarios)

After a release in Cairngorms the arrival and occupation of subsequent patches happened in less than a decade under status quo conditions for both habitat models (global – Figure 20, local – Figure 21). The local model showed a larger more contiguous patch in Northern Scotland, which appeared to be occupied faster than the same region when using the global model. The first occupation time of patches in Kintyre and patches in Northern Scotland took approx. 50 years on average and the maximum extent was reached after approx. 75 years, for both habitat models. Under future conditions the connectivity was greatly improved. Patches in Galloway and Kielder Forest were reached in around 75 years. For the global habitat model the population expansion in space appeared faster in the south-westerly direction than under status quo conditions and after 100 years patches as far south as Yorkshire in England were occupied.

A similar but directionally opposite development was seen after releases in Kintyre. If Kielder Forest was reached it took about 100 years under status quo conditions using the global model. With the future scenario the first patches south of the Central Belt were occupied on average after 75 years.

Releases in Galloway or Kielder Forest had similar but spatially opposite developments. Under status quo conditions and either habitat models the other patch was occupied within 50 years. Under future conditions this reduced to around 25 years, and expansions into Northern Scotland were already at an advanced stage after 75 years.

3.3.2.2. Combinations of focal release locations

Dividing the released individuals among various locations inevitably resulted in faster occupation of those patches (Figure 22). The arrival times for non-release patches occupied after 100 years were only slightly earlier for single location releases compared to when the individuals were divided for multi-location releases. For example, lynx occupied the southernmost patch of the Kintyre peninsula within 75 years whether 40 individuals were released in Cairngorms, or if 14 individuals we released in Cairngorms and 13 each in Galloway and Kielder Forest simultaneously.
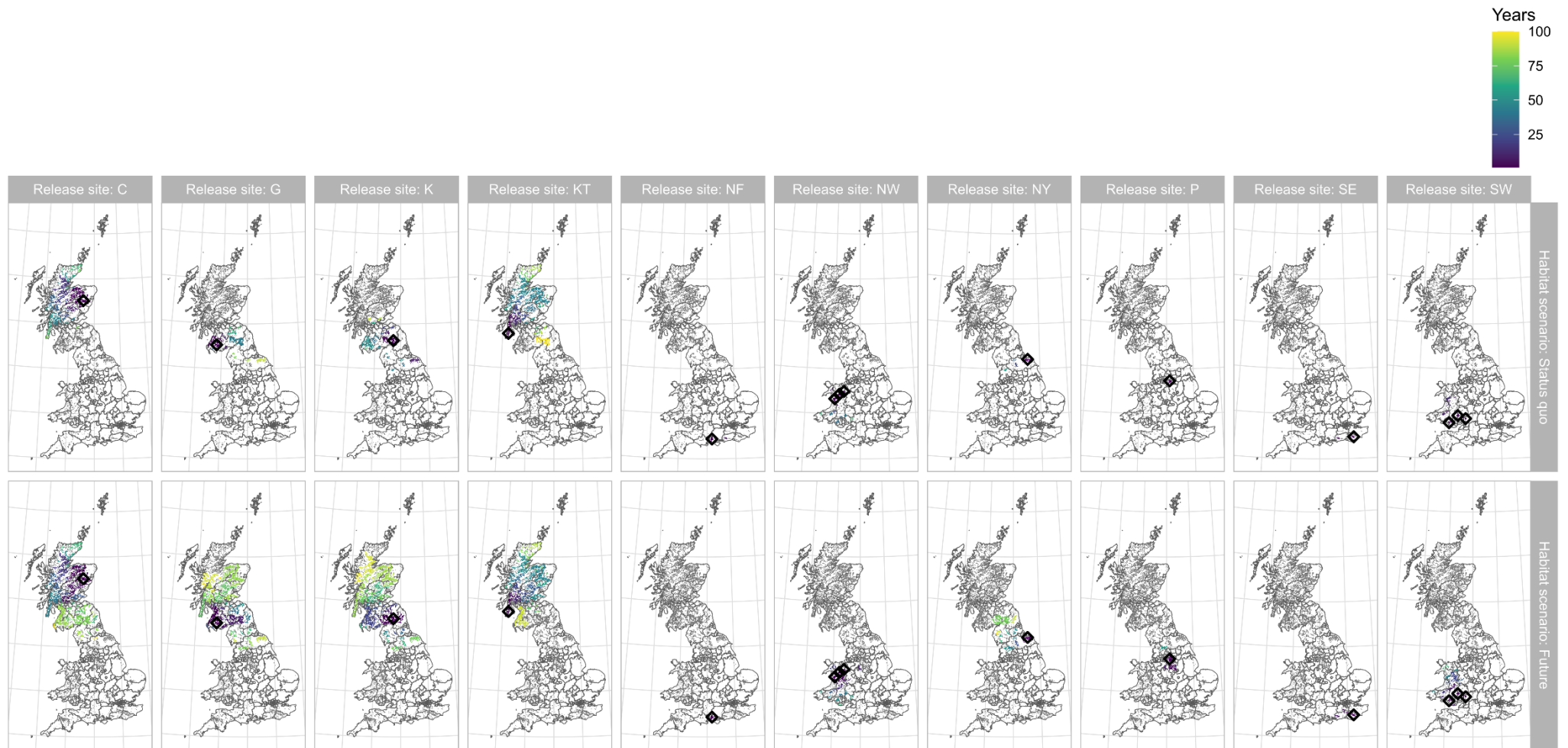
Figure 20. Mean first occupancy year based on the global habitat model, single release locations, and under status quo or future habitat scenarios. Release locations are indicated by diamonds, and with the names: C - Cairngorms, G - Galloway, K – Kielder Forest, KT - Kintyre, NF - New Forest, NW - North 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.
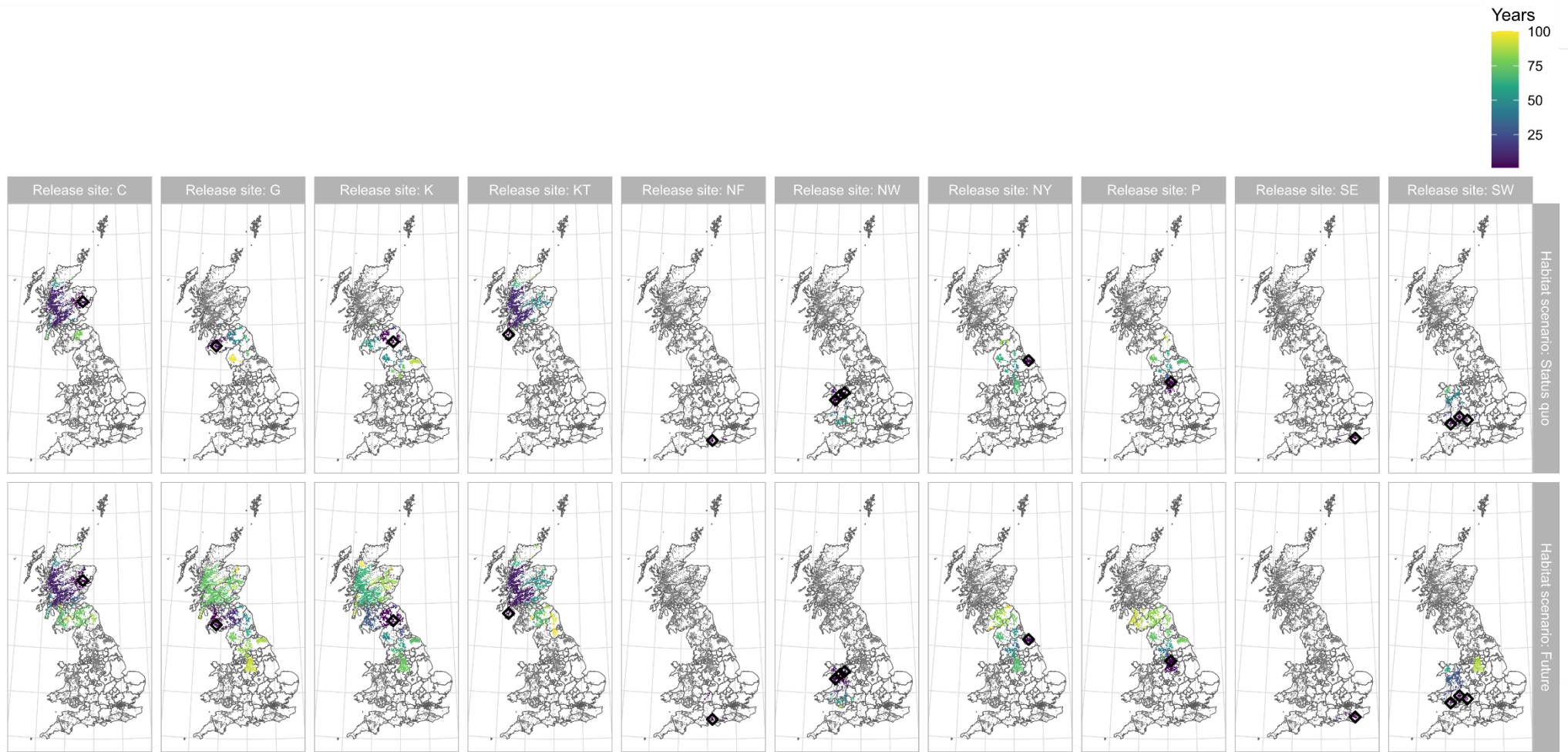
Figure 21. Mean first occupancy year based on the local habitat model, single release locations s, and under status quo or future habitat scenarios. Release locations are indicated by diamonds, and with the names: C - Cairngorms, G - Galloway, K – Kielder Forest, KT - Kintyre, NF - New Forest, NW - North 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.

Figure 22. Mean first occupancy year based on combinations of focal release locations. Release locations are indicated by diamonds, and with the names: C - Cairngorms, 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.
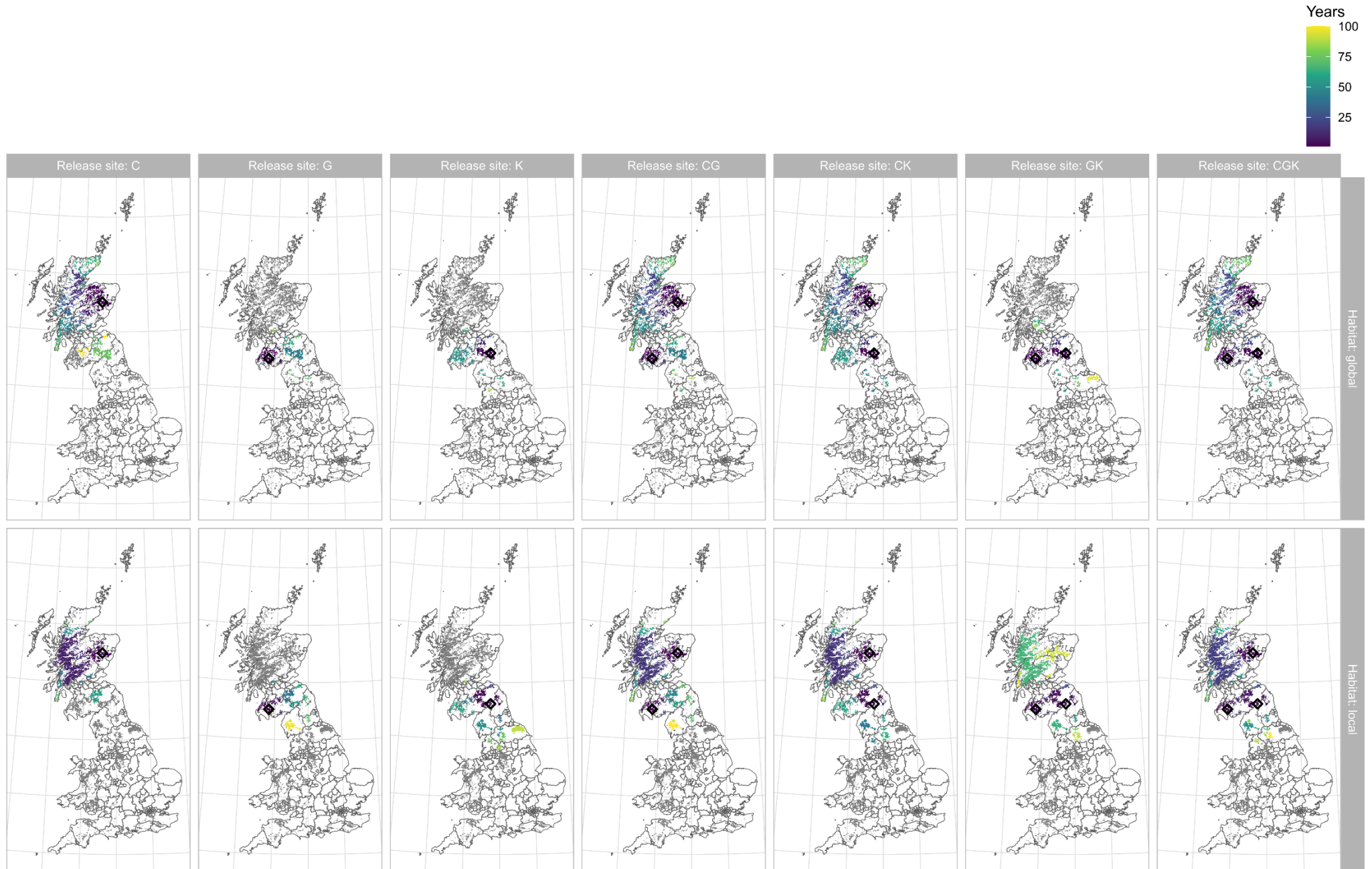
3.3.3. Landscape usage

3.3.3.1. Single location releases (status quo vs green future scenarios)

Under the status quo scenario, the Cairngorms release location showed higher usage in the east of Scotland (close to the release location) with the global habitat model, while the local model had higher usage in Northern Scotland (global - Figure 23, local – Figure 24). Despite some barriers (usage = 0) north of the Central Belt, dispersal was possible across this region. For both habitat models the highest connectivity through the Central Belt was in the east toward Kielder Forest. Also, under future habitat conditions the landscape usage was higher in the southeast part of Northern Scotland compared to Galloway in the west, for both habitat models.

The landscape usage that emerged from releases in Kintyre was disparate among habitat models. The global habitat model showed higher usage near the release location and northwards towards Northern Scotland than the local model, which showed weaker connectivity. The eastern route through the Central Belt again provided connectivity to Northern Scotland. Despite the lower usage of Kintyre with the local habitat model, under future conditions there was still higher usage of Southern Scotland and Northern England compared to the global model.

Releases in Galloway or Kielder Forest showed similar emergent connectivity. Specifically, the landscape usage was bisected by a motorway, with lynx only able to connect these patches through a small number of corridors. The same motorway caused low connectivity with Cumbria in Northwest England. Landscape usage to the north of Galloway and Kielder Forest, i.e. the Central Belt that comprises the highest infrastructure density in Scotland, was low for the status quo scenario for both habitat models. The most used dispersal corridor lay between Glasgow and Edinburgh and to the east of the M74 motorway. This was more easily reached from the Kielder Forest patch and the eastern part of the Southern Uplands. Under future conditions connectivity was improved northward, via the same corridor, with another narrow corridor west of Glasgow as well as southward into England for both habitat models.

3.3.3.2. Combinations of focal release locations

The landscape usage when lynx were released at multiple locations simultaneously was found to be an aggregation of usage patterns of the single location releases (Figure 25). Consistent with the preceding spatial results, simultaneous releases in Cairngorms, Galloway, and Kielder Forest resulted in the largest spatial distribution of lynx, though only slightly greater (in a southerly direction) than paired combinations of Cairngorms and Galloway, or Cairngorms and Kielder Forest. It appeared that releases combining Galloway and Kielder Forest patches might slightly promote dispersal into the North of Scotland.
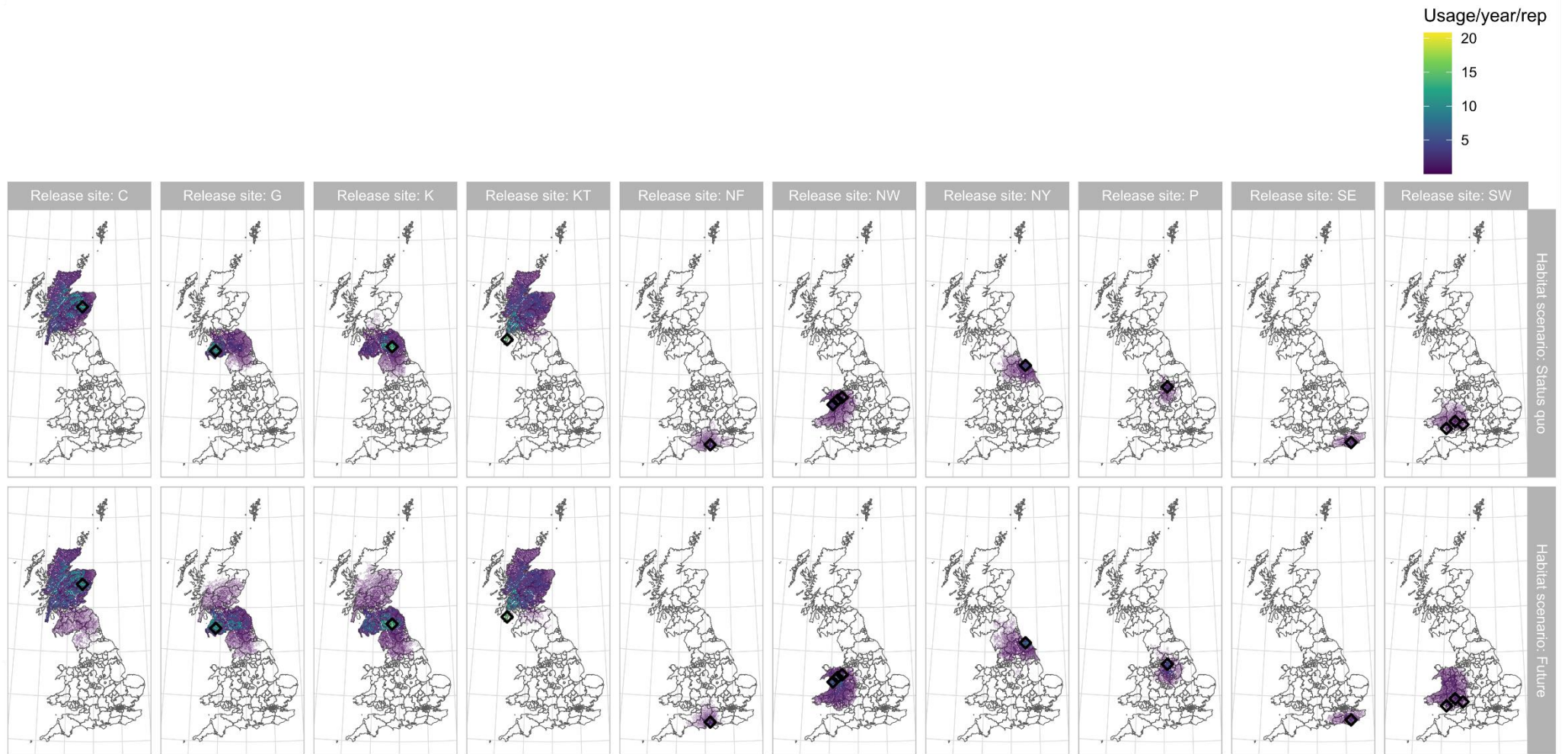
Figure 21. Landscape usage based on the global habitat model, single release locations, and under status quo or future habitat scenarios. Release locations are indicated by diamonds, and with the names: C - Cairngorms, G - Galloway, K – Kielder Forest, KT - Kintyre, NF - New Forest, NW - North Wales, NY - North York Moors, P - Peak District, SE - Southeast England, SW - South Wales.
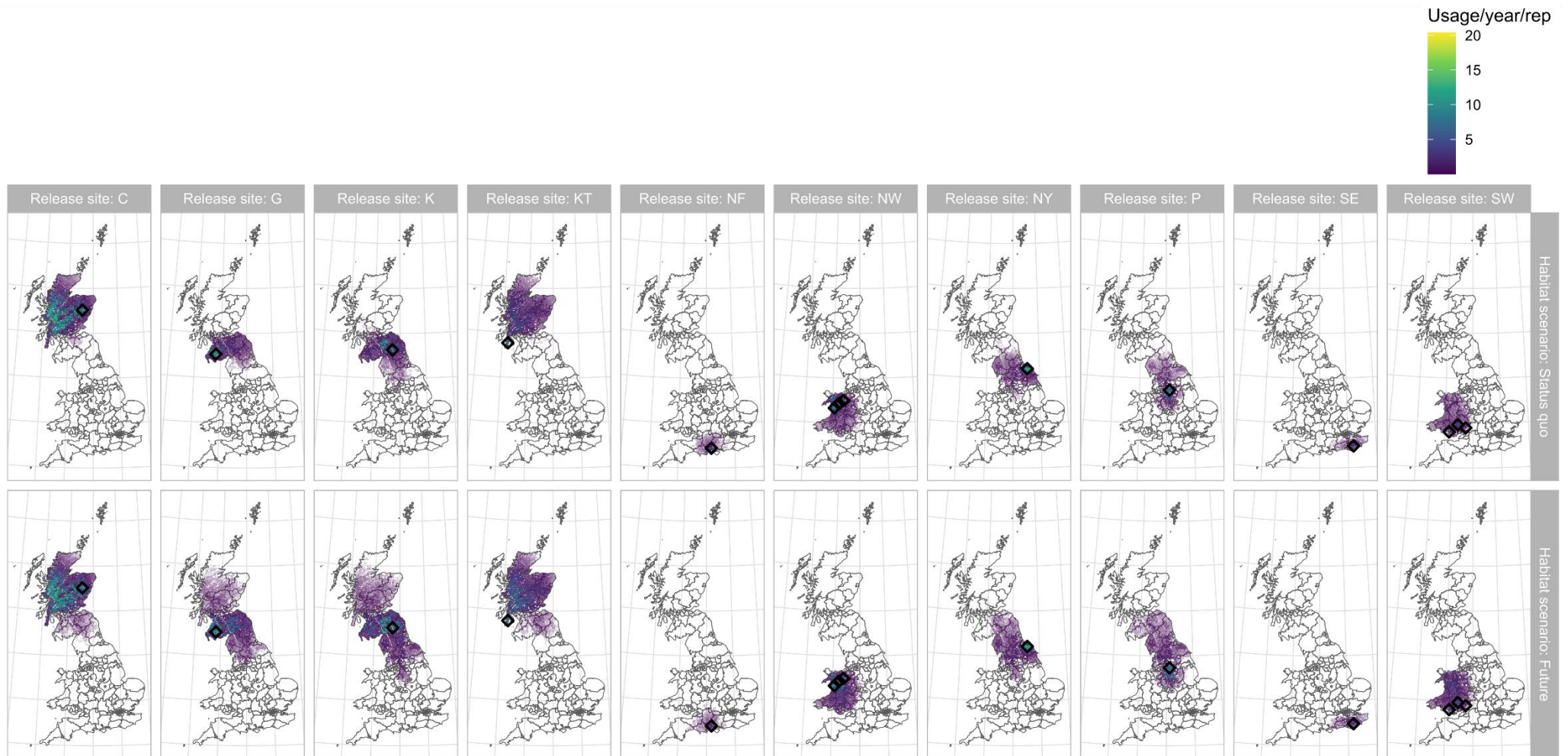
Figure 22. Landscape usage based on the local habitat model, single release locations, and under status quo or future habitat scenarios. Release locations are indicated by diamonds, and with the names: C - Cairngorms, G - Galloway, K – Kielder Forest, KT - Kintyre, NF - New Forest, NW - North Wales, NY - North York Moors, P - Peak District, SE - Southeast England, SW - South Wales.
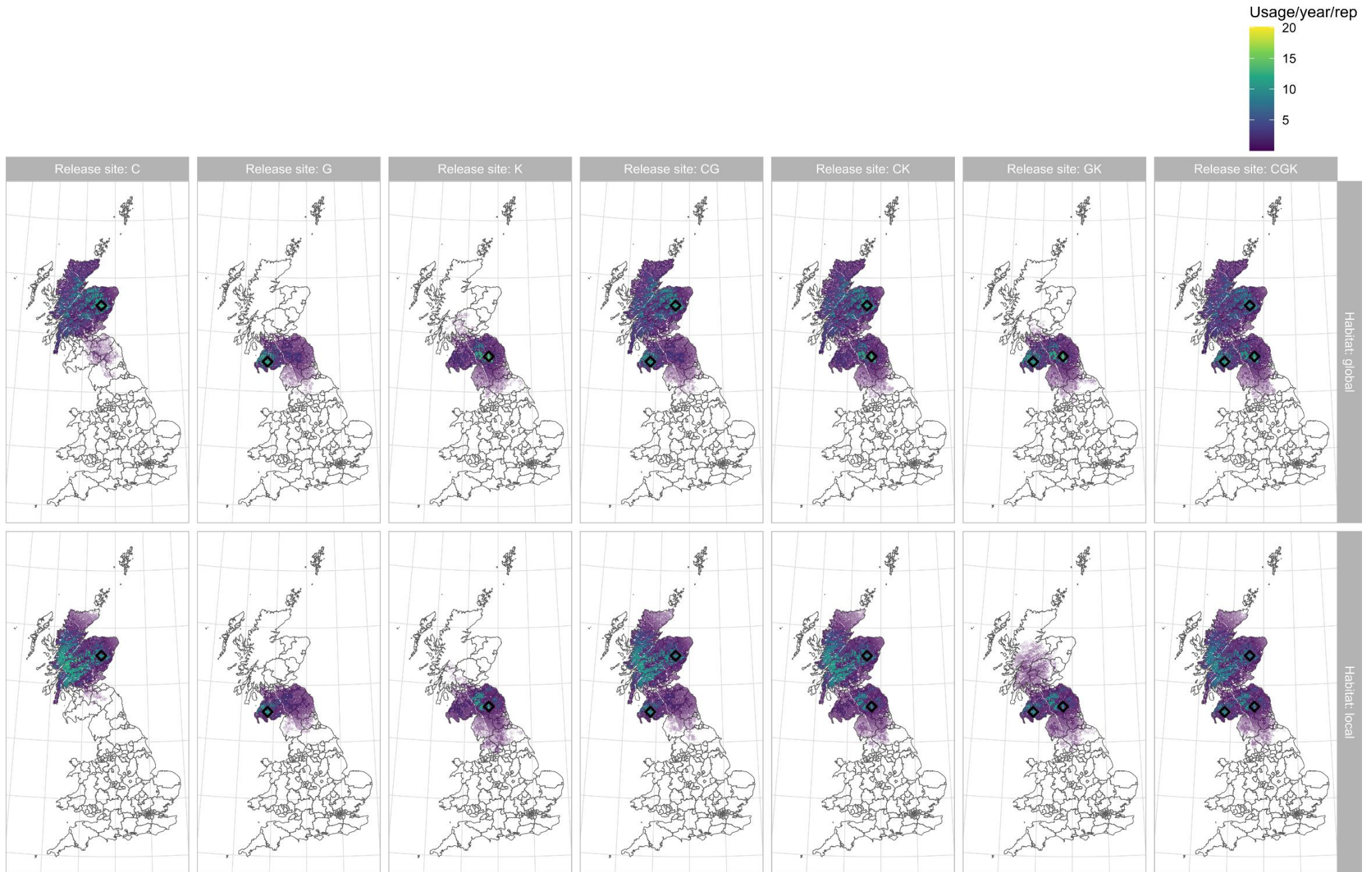
Figure 25. Landscape usage based on combinations of focal release locations. Release locations are indicated by diamonds, and with the names: C - Cairngorms, G - Galloway, K – Kielder Forest, and combinations thereof.

4. DISCUSSION

We conducted a wide-ranging exploration of the potential scenarios that could be faced by a reintroduction of lynx into Britain, including different values of the main practical parameters that would be controlled by conservation practitioners, as well as ecological and human aspects that cannot be controlled, and are unknown in Britain due to the species' absence of around five centuries[1,2], based on empirical knowledge.

Our results showed the importance of choosing the right release location to minimise the probability of extinction and maximise population size and genetic diversity. Specifically, release locations in Cairngorms, Galloway, and Kielder Forest (the focal release locations) had the highest probabilities of success across diverse conditions. We also showed that provided enough lynx are available, releasing them in more than one of these focal locations was the most effective way of founding a large British lynx population.

The potential habitat improvements across Britain we tested increased population size and improved connectivity among habitat patches, though these habitat improvements were not necessary for reintroduction to be successful in the focal patches identified. Without habitat improvements, connectivity between Kielder Forest and Galloway was possible but slowed by the M74 motorway. Connectivity between the Southern Uplands and Kielder Forest region and Northern Scotland was most likely via a corridor in the east of the Central Belt and M74. This suggests a release in Kielder Forest has a higher potential for expansion to the north than a release in Galloway.

Our results restated the importance of releasing many lynx and with diverse origins to provide the best population genetic starting point and we showed that certain combinations of the focal release locations might maintain this long term viability better, namely, Cairngorms alongside either Galloway or Kielder Forest, with a preference for Kielder Forest. The expected development of genetic diversity over 100 years under medium simulation parameters showed that a lynx reintroduction in one or more of the focal release locations could fare better than reintroduction projects conducted in Central Europe, provided it has sufficiently diverse origins[21,22,96,101].

Overall, we found that higher resident or disperser road mortality did not present a problem for population persistence, with the latter only affecting population size. In contrast, simultaneously high baseline and added mortality rates made reintroduction success less likely, even in the focal release locations. However, a scenario of such high mortality might be considered unlikely.

Based on our findings, a reintroduction in England and Wales would be most viable with a release in Kielder Forest. Scotland's Central Belt provided a difficult barrier that makes successful population expansions through this area improbable. Therefore, an ideal lynx reintroduction project for Britain would release lynx both north and south of the Central Belt (e.g. Cairngorms and Kielder Forest). For all release locations, we have provided the landscape usage that shows the potential dispersal corridors and where green initiatives could engage to improve connectivity.

4.1. Management considerations

The importance of releasing sufficient individuals for species reintroductions is now well-known in conservation science[102]. This factor has also been expressed in lynx literature [21,22,49]. In the past lynx reintroductions were based on very few individuals[103], but since the 21st century, reintroductions have been releasing at least 20 individuals and from various sources. For example, the Harz

Mountains population was founded on 20 individuals from captive breeding[101], the Palatinate Forest reintroduction was 20 individuals from Switzerland and Slovakia[6], and the most recent West Pomeranian reintroduction with 61 captive bred animals[7].

Our results also showed the importance of releasing more lynx to maximise genetic diversity in the long run. We showed that starting with more diverse origins is better than using a single source. Even with this, genetic drift is inevitable in isolated populations, as shown with the diverse origin Harz Mountains population whose genetic diversity is still in decline[101].

That said, the expected development of genetic diversity over 100 years under our medium simulation parameters showed that a lynx population in Britain has the potential to retain more diversity than many of the reintroduction projects conducted in Central Europe, provided it uses a good starting point. Specifically, after 100 years simulations with high starting diversity maintained a higher heterozygosity and allelic richness than most reintroductions did over 20 to 50 years, and allele richness was even comparable to large autochthone populations (allelic richness approx. 4.5).

Our approach focused on reintroduction conditions and their success over 100 years as a standalone British population, without subsequent management actions. In continental Europe however, fragmentation of habitats means lynx populations are isolated[10]. Ideally, natural dispersal events would provide sufficient connectivity and genetic exchange between these subpopulations[24], but the success of a potential European metapopulation of lynx might depend on the implementation of artificial methods of genetic exchange[23]. It is therefore no great leap to imagine that a potential British population of lynx could form an additional subpopulation of an already artificially connected European metapopulation.

A recent reinforcement project took place in the Dinaric Mountains[104], as well as numerous reintroductions focused on strengthening different metapopulation structures, e.g. Alpine stepping-stones[105], or the "Upper Rhine Metapopulation"[106]. These show that the conservation management of reintroduced lynx populations is not a single intervention. In this respect the expectations we set for 100 years are ideal but not realistic and a real reintroduction might later be followed by local translocations within Britain or subsequent reinforcements from other European populations.

Finally, the phylogenetic origins of reintroduced populations may be important for reintroduction success[107]. Evolutionary processes drive adaptation of species traits to fit local conditions[108]. As such, the ability of released animals to interact successfully with the novel ecological conditions at the release site will depend on their genetic origins. This was identified by the International Union for Conservation of Nature[109], and is assumed to be the case also for lynx in expert discussions[110]. Although this aspect of the ecology was not covered explicitly in our approach, the combinations of territory size and habitat selection behaviour we tested have indirectly showed that different traits for space use can be suited for release in Britain for different models of habitat suitability.

4.2. Mortality factors

We found that high added mortality and baseline (natural + unknown) mortality made it difficult for otherwise viable release locations to persist until 100 years. To understand the potential effects of these mortality causes, we chose the maximum range of cause-specific mortality rates from across Europe[76].

The highest values of these were respectively from the Harz Mountains for natural mortality and Białowieża Forest for illegal killing. Such high values might be a peculiarity of the tracking periods and

datasets in question, where particularly high levels of these rates took place. For instance, the Harz Mountains is considered to be a lynx population with high survival rates within its core, due to the low rates of illegal killing[101]. Combining this knowledge with the relatively small sample of tracked individuals (n = 9) as the basis for the mortality statistic, suggests that the natural mortality rate is not representative of the whole population. As for Białowieża Forest, the high rate of illegal killing is likely real but was probably the result of a particular period of high persecution[111]. This mortality pressure has since reduced.

Therefore, we can say that such combined high rates of natural and illegal killing mortality would be an extreme circumstance and would perhaps unsurprisingly exacerbate Allee effects[112,113]. This is not conducive to establishment of a population that would already be sensitive to Allee effects due to their inherent low density and slow reproduction rate. The medium mortality rates we simulated offer a more reasonable expectation of population development, since these represent the mean rates for all the available European data[76]. In addition, if the social aspects of a reintroduction are well managed, persecution may well be reduced to below the European average.

Natural mortality should not be a problem if any reintroduction is well-managed since animals are carefully selected and treated prior to release to ensure their health[114] and other natural mortality factors (e.g. falls, intraspecific killing) are relatively rare Europe-wide[76]. Concerning illegal killing, it has been the leading mortality cause of lynx for the past decades[14,115]. This could be driven by stakeholder attitudes and misinformation[12,116]. However, the magnitude of this problem varies both spatially and temporally and depends on activities of a minority of parties[111]. As such, high risk areas could be discrete in space[117]. We simulated added mortality, which includes illegal killing, non-spatially, perhaps leading to an overestimation of risk in some areas. Whether or not this is the case, prior experiences, and our results, advocate for a strong public-engagement in diverse stakeholder groups before a reintroduction is planned[118,119].

Road mortality can be a significant source of mortality for lynx, especially for dispersing individuals[44]. Overall, our results showed that resident and disperser 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 exacerbated by the mortality rates for dispersing individuals who must cross countless roads to reach other patches. Our results showed that improving habitat or reducing road mortality would both improve connectivity and increase population sizes (based on a Galloway or Kielder Forest release location).

4.3. Prey availability and habitat selection

Prey availability in Britain for lynx is poorly understood. To date, there have been only a few studies concerning the density of deer species in certain study areas (e.g.[120]). These can be supplemented with mapping of occupancy probabilities[61], and monitoring of distributions[66]. However, this still leaves gaps in our knowledge of prey availability. Lynx can occur in low resource areas, with low prey availability, due to their hunting efficiency[121]. Therefore, prey availability is unlikely to be a limiting factor for lynx persistence in Britain, but it could affect lynx's eventual population density.

In our analysis, we tried to account for these unknowns by exploring reintroductions with different habitat selection models that comprise differences in behaviour due to habitat availability[36], and by simulating a conservative range of mean territory sizes to allow the emergence of lynx population densities more typical of European populations (i.e. 0.83 to 1.8 lynx per 100 km^2). This is in contrast

to previous analyses[28,30], which defined densities using the relationship between prey density, converted to biomass, and lynx density[29].

In comparison to most European populations, the densities predicted by the model in [28] and [30] seem to be rather high, for example, per 100 km^2: 2.63 in Northern Scotland[29], 3.75 in Southeast England, and 5.57 in Thetford[30]. Conversely, in Wales where deer densities are lower, 0.21 lynx per 100 km^2 was predicted[30]. This is despite, as the authors discussed, the estimates ignoring lagomorphs and interactions with human disturbances. Our approach represents a more conservative approach since we instead altered the possible distribution of territory sizes (3 distributions simulated), whereby density emerges as a function of the habitat and territory selection, as well as demographic processes, of the individuals. We could then determine which release locations offer high probabilities of reintroduction success under a range of emergent population properties. Specifically, the focal release locations of Cairngorms, Galloway, and Kielder Forest, have good potential for reintroduction success despite the potentially diverse spatial distributions of lynx.

The conservative assumptions we made could be investigated empirically before a reintroduction to reassure practitioners that sufficient resources are available. For example, the deer kill rates of lynx from European populations could be used to estimate the amount of ungulate prey typically predated by lynx per unit area per year and compared against deer density or hunting bag numbers in the area of a potential release.

4.4. Reintroduction potential in England and Wales

We tested several release locations in England and Wales, namely: Kielder Forest, Peak District, New Forest, North York Moors, Southeast England, North Wales, and South Wales. Of these, our results indicated that Kielder Forest is the only viable release location for reintroduction in England and Wales. Releases in Kielder Forest had low extinction probabilities (i.e. high population success) 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 as discussed above.

Reintroduction in Kielder Forest resulted in 50 to 60 independent individuals for status quo and 130 to 140 for green future habitat conditions, respectively, depending on the habitat model and with medium parameters. Also, the population development over time had not reached a plateau. Kielder Forest and the connected Southern Uplands was previously identified as a suitable patch [28,30,42], who respectively estimated 50.0, 55.0, and 52.2 lynx in the Southern Uplands and Kielder Forest region, despite assuming densities of 0.83, 2.63, and 1.33 lynx per 100 km^2, respectively. Despite the different densities, these estimates are similar to our own predictions.

In this study we aimed to find out which areas are most suitable for reintroduction of lynx and did not compare different potential local release sites within each ecologically connected area. For example, the Kielder Forest releases we simulated were from one site in the centre of a large, connected habitat patch that contained its namesake, Kielder Forest, but also extended into Scotland. Within this patch the selection of a slightly different release location could reveal fine scale differences in population expansion. An investigation of alternative sites in the Kielder Forest patch would be a useful next step to find out whether the position of the release site makes a significant difference and, if so, where the optimum location for the release site would be.

4.5. Reintroduction potential in Scotland

Compared to England and Wales, more research attention has hitherto been focused on a potential Scottish lynx population[28,29,42,43], including estimated population sizes of 450 and 235 lynx[28,42]. Our estimates are more consistent with the lower estimate, at around 290 individuals (based on a combined Cairngorms and Galloway release), however in all these studies different habitat maps, densities, and estimation frameworks were used. Furthermore, the ecologically connected patches across the English border were not considered[42].

In one study, a Kintyre release had the lowest extinction probability of the tested sites[42]. In our analysis Kintyre was worse than both Cairngorms and Galloway, depending on the habitat model used. The connectivity of this peninsula to the bulk of Northern Scotland appears to depend strongly on how lynx will truly utilise the landscape. For this reason, our results suggest Cairngorms is a better release site, due to the low extinction risk and good connectivity to the rest of Northern Scotland.

The Southern Uplands and Kielder Forest have been considered as an ecological patch for lynx previously[28,30,42]. We found fair connectivity between Galloway and Kielder Forest, with a mean first occupation time of around 50 years, similar to [42]. Our finding that the Central Belt poses a difficult barrier for lynx movements was consistent with the earlier studies. Even under the green future habitat scenario, the probability of colonising opposite patches in either direction was lower than 10%.

For this study we selected release sites in Scotland based on precedent[42] to find out which areas are most suitable for reintroduction of lynx. As for England, we did not test various release sites within each ecologically connected area. For example, the Cairngorms releases we simulated were from one site. However, there are a number of potential release sites in the large patch of the Cairngorms region, as well other potential sites in the rest of the Highlands (e.g., Northwest) that exhibit plentiful habitat and were found to be well connected to the rest of the Highlands. These different release sites could result in fine scale differences in population expansion. Therefore, an investigation of alternative sites in Scotland would be an important next step to find out whether the exact release site makes a significant difference and, if so, which is the ideal potential release site.

4.6. Single or multi-site reintroductions

Multi-site reintroductions have been suggested as an important method in species restoration to reduce extinction risk due to stochastic events[122], and might therefore be beneficial for lynx in highly fragmented landscapes[123]. Further, creating a larger population preserves more genetic diversity after a founding event[124].

A prior study found a multi-site release of lynx in Scotland improved the chance of success compared to single-site releases[42]. We only tested multi-site releases in patches that alone had low extinction probabilities, therefore extinction risk was not greatly reduced. 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, due partly to the low connectivity between the main ecological patches (i.e., Southern Uplands and Kielder Forest, and Northern Scotland).

Releasing 40 individuals across two or three sites conserved the founders' allelic diversity best, while heterozygosity did not differ greatly between a Cairngorms release and a multi-site release. Allelic richness is important for understanding the adaptability and evolutionary potential species[125,126], and

therefore of utmost importance for reintroduced populations. For multi-site releases it is still important to release sufficient individuals to avoid founder effects on genetic diversity or local extinction.

Comparing the multi-site releases Cairngorms-Galloway and Cairngorms-Kielder Forest, although these were broadly comparable the latter combination gave a higher allelic richness than the former, especially when using the local habitat model. This was also reflected in the single site release of Galloway and Kielder Forest, where Kielder Forest returned higher allelic richness than Galloway with either habitat model. Further, the landscape usage showed that the most promising corridor connecting northern and southern Scotland lies between Glasgow and Edinburgh to the east of the M74. This seemed more accessible from the east, i.e. from Kielder Forest, than from the west, i.e. Galloway.

The low connectivity between the release sites divided by the Central Belt in Scotland means colonisation from a single site release of all suitable habitat in these areas is improbable. The sex-biased dispersal of lynx, whereby males tend to travel further from the natal range than females[85], could mean that these patches could be connected by males, but without any females colonisation cannot take place. One region of Central Europe that has faced this problem for decades is the Black Forest in Germany, where male lynx have made it from the nearby Swiss populations but until now no female has done so[127]. An analysis of this case, conducted with the same simulation model[48], showed that without translocation of female lynx population establishment in the Black Forest is unlikely.

To avoid this happening in Britain, and supported by our other results, a reintroduction into at least two separate locations would provide maximum success. The best combination of two sites to achieve this would be releases in the Cairngorms and in Kielder Forest. Given occupation of patches north and south of the Central Belt (e.g. Kielder Forest and Cairngorms), it is possible that genetic exchange between them will be sufficient solely from male dispersal. However, these aspects were outside the scope of this current work and necessitate dedicated study.

4.7. Study limitations

In this study we used parameters informed by previous work from European lynx populations. Extrapolating empirical observations to a novel region is not without uncertainty. Despite this, we believe we have explored the ranges of the major parameters and therefore provided the most thorough viability assessment for a potential lynx reintroduction in Britain to date.

We considered all major sources of mortality to see their effects on reintroduction success. However, we did not consider added mortality in a spatially explicit manner. Considering a non-uniform risk of added mortality in space could help to understand population development based on different scenarios or assumptions[13]. That said, persecution is often spatially inconsistent, depending as it does on the occasional and opportunistic actions of few individuals. Therefore, the aspatial (i.e. spatially random) rate we applied might even better depict the true nature of persecution.

Another major source of mortality for lynx in Europe is road collisions. We modelled road risk based on road densities and the relative mortality risk posed by different road classes for deer[92]. In the absence of empirical data from lynx in Britain, we believe the relative risk of road classes based on deer data is adequate. Road risk for deer has been used for lynx population simulations previously[13]. Collision rates for deer reflect the risk of different road classes well since these are correlated to

traffic density and speed, which should also be the main factors for lynx. Furthermore, deer are lynx's main prey so we can expect their road mortality risk to be well correlated.

We only considered three focal release sites, and indeed only four release sites in the largest conglomerations of suitable habitat in England and Scotland. These were selected in part based on the size of the contiguous suitable habitat patches and in part based on previous studies [42]. Our study showed that success based on these sites for a lynx reintroduction was likely. However, the population development might be improved if different combinations of sites, single or multi, were used. Further, we simulated all releases at one pixel, or release location, for a given release site. In practise some reintroductions have indeed done this, to ensure lynx can detect the presence of conspecifics in the area[6], while others have distributed releases across suitable habitats of a given region[7]. These differences may affect the population founding and influence reintroduction success. This could be the subject of further viability analysis for a subset of release patches, especially focused on the first years after release.

Finally, in this study we tended to focus on the best possible conditions for reintroduction. These may not be achievable in practice because reintroduction planning is constrained by governance, logistical, and stakeholder concerns that do not always allow them to take an optimal strategy. Therefore, it would also be important for reintroduction practitioners to test the viability of a specific release strategy before a project begins.

Lynx is an elusive and shy medium-sized carnivore that poses no threat to humans. Despite this, the species does not escape controversy [11,12,128]. As such, reintroduction of lynx is a contentious issue with many stakeholders that means reintroduction planning is not a straightforward undertaking. We found that very high levels of added mortality would make population establishment difficult in most circumstances, which highlights the importance of garnering public support before a release.

Despite the limitations, our results provide information that can contribute to communication and discussions with stakeholder groups, thereby promoting an open and informed decision-process that is expected of contemporary social consultations and reintroduction projects[129].

5. CONCLUSIONS

In this study we explored the main parameters that determine population development of lynx under different reintroduction scenarios in Britain, with a focus on empirically derived data. Several release sites were found to support lynx populations under certain conditions. Of the ten potential habitat patches tested, releases in Kielder Forest, Galloway, and the Cairngorms were the most likely to succeed under diverse scenarios, including different habitat selection behaviours.

These focal release sites were predicted to produce the largest populations and genetic diversity, though combinations of these focal release sites performed even better, provided enough individuals were released. If only two sites were selected as focal areas for lynx reintroductions, the best combination would be a release in the Highlands (Cairngorms) and Northern England (Kielder Forest). Each of these was also predicted to be successful independently. Releases elsewhere in Britain did not offer the same likelihood of success, although some could be viable given the right habitat selection behaviour (North Wales, North York Moors, Peak District, or Kintyre). The results suggested a successful approach to restoring lynx to Britain would be a release project in the Highlands or Northern England, or ideally both.

Our findings reiterate the importance of releasing many lynx and with diverse origins to provide the most advantageous population genetic maintenance scenario. Despite the generally fragmented habitat across Britain, populations could persist in some patches, though connectivity between existing suitable areas was poor. Our simulation output included predictions of landscape usage by lynx that highlights the potential dispersal corridors and therefore where future improvements in connectivity should be focused.

6. ACKNOWLEDGEMENTS

7. REFERENCE LIST

[1] Hetherington, D. A., Lord, T. C., & Jacobi, R. M. (2006). New evidence for the occurrence of Eurasian lynx (Lynx lynx) in medieval Britain. *Journal of Quaternary Science: Published for the Quaternary Research Association*, 21(1), 3-8.

[2] Hetherington, D. A. (2005). *The feasibility of reintroducing the Eurasian lynx, Lynx lynx to Scotland* (Doctoral dissertation, University of Aberdeen).

[3] Raye, L. (2021). An 18th century reference to a Eurasian lynx (Lynx lynx) in Scotland. *Mamm. Commun*, 7, 47-52.

[4] Chapron, G., Kaczensky, P., Linnell, J. D., von Arx, M., Huber, D., Andrén, H., ... & Boitani, L. (2014). Recovery of large carnivores in Europe's modern human-dominated landscapes. *science*, 346(6216), 1517-1519.

[5] Linnell, J. D., Breitenmoser, U., Breitenmoser-Würsten, C., Odden, J., & von Arx, M. (2009). Recovery of Eurasian lynx in Europe: what part has reintroduction played. Reintroduction of top-order predators, 72-91.

[6] Idelberger, S., Back, M., Ohm, J., Prüssing, A., Sandrini, J., & Huckschlag, D. (2021). Reintroduction of Eurasian lynx in the palatinate forest, Germany. *Cat News*, *14*, 38-42.

[7] Tracz, M., Tracz, M., Grzegorzek, M., Ratkiewicz, M., Matosiuk, M., Górny, M., & Schmidt, K. (2021). The return of lynx to northwestern Poland. *Cat News Special*, (14), 43-44.

[8] Luchs Thüringen, Germany: https://luchs-thueringen.de/en/projekt (Accessed 08/12/2023)

[9] European Environment Agency (2012). Lynx lynx - Report under the Article 17 of the Habitats Directive Period 2007-2012. European Environment Agency, European Topic Centre on Biological Diversity. https://forum.eionet.europa.eu/habitat-art17report/library/2007-2012-reporting/factsheets/species/mammals/lynx-lynx/download/en/1/lynx-lynx.pdf (Accessed 07/04/2021).

[10] Kramer-Schadt, S., Revilla, E., & Wiegand, T. (2005). Lynx reintroductions in fragmented landscapes of Germany: Projects with a future or misunderstood wildlife conservation?. *Biological Conservation*, *125*(2), 169-182.

[11] Lüchtrath, A., & Schraml, U. (2015). The missing lynx—understanding hunters' opposition to large carnivores. *Wildlife Biology*, 21(2), 110-119.

[12] Červený, J., Krojerová-Prokešová, J., Kušta, T., & Koubek, P. (2019). The change in the attitudes of Czech hunters towards Eurasian lynx: Is poaching restricting lynx population growth?. *Journal for nature conservation*, *47*, 28-37.

[13] Heurich, M., Schultze-Naumburg, J., Piacenza, N., Magg, N., Červený, J., Engleder, T., ... & Kramer-Schadt, S. (2018). Illegal hunting as a major driver of the source-sink dynamics of a reintroduced lynx population in Central Europe. *Biological conservation*, 224, 355-365.

[14] Sindičić, M., Gomerčić, T., Kusak, J., Slijepčević, V., Huber, Đ., & Frković, A. (2016). Mortality in the Eurasian lynx population in Croatia over the course of 40 years. *Mammalian Biology*, *81*(3), 290-294.

[15] Schmidt-Posthaus, H., Breitenmoser-Würsten, C., Posthaus, H., Bacciarini, L., & Breitenmoser, U. (2002). Causes of mortality in reintroduced Eurasian lynx in Switzerland. *Journal of Wildlife Diseases*, 38(1), 84-92.

[16] Sanderson, C. E., Jobbins, S. E., & Alexander, K. A. (2014). With Allee effects, life for the social carnivore is complicated. *Population ecology*, 56(2), 417-425.

[17] Keller, L. F., Biebach, I., Ewing, S. R., & Hoeck, P. E. (2012). The genetics of reintroductions: inbreeding and genetic drift. Reintroduction biology: integrating science and management, 9, 360.

[18] Ryser-Degiorgis, M. P., & Robert, N. (2006). Causes of mortality and diseases in free-ranging Eurasian lynx from Switzerland—an update. In *Proceedings of the Iberian Lynx ex-situ Conservation Seminar Series. Sevilla & Doñana: Fundación Biodiversidad* (pp. 36-41).

[19] Keller, L. F., & Waller, D. M. (2002). Inbreeding effects in wild populations. *Trends in ecology & evolution*, *17*(5), 230-241.

[20] Wilson, S. M. (2018). Lessons learned from past reintroduction and translocation efforts with an emphasis on carnivores. Life lynx https://www. lifelynx. eu/wpcontent/uploads/2018/10/Lessons-Carnivore-Reintroduction-Efforts-Final-Version-4.0-2018. pdf.

[21] Sindičić, M., Polanc, P., Gomerčić, T., Jelenčič, M., Huber, Đ., Trontelj, P., & Skrbinšek, T. (2013). Genetic data confirm critical status of the reintroduced Dinaric population of Eurasian lynx. *Conservation genetics*, *14*(5), 1009-1018.

[22] Bull, J. K., Heurich, M., Saveljev, A. P., Schmidt, K., Fickel, J., & Förster, D. W. (2016). The effect of reintroductions on the genetic variability in Eurasian lynx populations: the cases of Bohemian–Bavarian and Vosges–Palatinian populations. *Conservation Genetics*, *17*(5), 1229-1234.

[23] Premier, J., Kramer-Schadt, S., Fickel, J., Heurich, M. (2021). Effects of fragmentation and connectivity of lynx habitats on population genetics in continental Europe. *The Eurasian lynx in Continental Europe*.

[24] Gajdárová, B., Belotti, E., Bufka, L., Duľa, M., Kleven, O., Kutal, M., ... & Krojerová-Prokešová, J. (2021). Long-distance Eurasian lynx dispersal—a prospect for connecting native and reintroduced populations in Central Europe. *Conservation Genetics*, *22*(5), 799-809.

[25] Linking lynx meeting 2023. https://www.nationalpark-harz.de/luchsprojekt/de/QuoVadisLynx2023

[26] Kitchener, A. C. (2001). Two tales of two kitties: Restoring the wildcat, *Felis silvestris*, and the lynx, *Lynx lynx*, to Britain. *In:* Bowen, C.P. (ed.). *The return of the native – the reintroduction of native species back into their natural habitat,* pp. 24–27. People's Trust for Endangered Species /Mammal Trust UK: London.

[27] Breitenmoser, U., Breitenmoser-Wursten, C., & Carbyn, L. N. (2001). Assessment of carnivore reintroductions. In *Carnivore Conservation*. Eds Gittleman, J.L., Funk, S.M., Macdonald, D.W., and Wayne, R.K. pp. 241–280.

[28] Hetherington, D. A., Miller, D. R., Macleod, C. D., & Gorman, M. L. (2008). A potential habitat network for the Eurasian lynx Lynx lynx in Scotland. *Mammal review*, *38*(4), 285-303.

[29] Hetherington, D. A., & Gorman, M. L. (2007). Using prey densities to estimate the potential size of reintroduced populations of Eurasian lynx. *Biological Conservation*, *137*(1), 37-44.

[30] Johnson, R., & Greenwood, S. (2020). Assessing the ecological feasibility of reintroducing the Eurasian lynx (Lynx lynx) to southern Scotland, England and Wales. *Biodiversity and Conservation*, *29*(3), 771-797.

31 Carroll, C., Noss, R. F., & Paquet, P. C. (2001). Carnivores as focal species for conservation planning in the Rocky Mountain region. *Ecological applications*, *11*(4), 961-980.

32 Raxworthy, C. J., Martinez-Meyer, E., Horning, N., Nussbaum, R. A., Schneider, G. E., Ortega-Huerta, M. A., & Townsend Peterson, A. (2003). Predicting distributions of known and unknown reptile species in Madagascar. *Nature*, *426*(6968), 837-841.

33 Schadt, S., Knauer, F., Kaczensky, P., Revilla, E., Wiegand, T., & Trepl, L. (2002). Rule-based assessment of suitable habitat and patch connectivity for the Eurasian lynx. *Ecological applications*, 12(5), 1469-1483.

34 Guisan, A., Thuiller, W., & Zimmermann, N. E. (2017). *Habitat suitability and distribution models: with applications in R*. Cambridge University Press.

35 Heurich, M., Premier, J., Oeser, J., Streif, S., Bastianelli, M., Morelle, K., ... & Cagnacci, F. (2021). EUROLYNX: Collaborative science for studying Eurasian lynx movement ecology at the range of its distribution. *Cat News Special*, (14), 60-63.

36 Oeser, J., Heurich, M., Kramer-Schadt, S., Mattisson, J., Krofel, M., Krojerová-Prokešová, J., ... & Kuemmerle, T. (2023). Integrating animal tracking datasets at a continental scale for mapping Eurasian lynx habitat. *Diversity and Distributions.*

37 Beissinger, S. R., & McCullough, D. R. (Eds.). (2002). *Population viability analysis*. University of Chicago Press.

38 IUCN Standards and Petitions Subcommittee (2019). *Guidelines for using the IUCN Red List Categories and Criteria*. Version 14. Prepared by the Standards and Petitions Subcommittee. http://www.iucnredlist.org/documents/RedListGuidelines.pdf

39 Grimm, V., & Railsback, S. F. (2013). Individual-based modeling and ecology. In *Individual-Based Modeling and Ecology*. Princeton University press.

40 DeAngelis, D. L., & Grimm, V. (2014). Individual-based models in ecology after four decades. *F1000prime reports*, *6*.

41 Vanlandeghem, V., Drapeau, P., Prima, M. C., St-Laurent, M. H., & Fortin, D. (2021). Management-mediated predation rate in the caribou–moose–wolf system: spatial configuration of logging activities matters. *Ecosphere*, *12*(6), e03550.

42 Ovenden, T. S., Palmer, S. C., Travis, J. M., & Healey, J. R. (2019). Improving reintroduction success in large carnivores through individual-based modelling: How to reintroduce Eurasian lynx (Lynx lynx) to Scotland. *Biological Conservation*, *234*, 140-153.

43 Philips, I. (2020). An agent based model to estimate lynx dispersal if re-introduced to Scotland. *Applied Spatial Analysis and Policy*, *13*(1), 161-185.

44 Kramer-Schadt, S., Revilla, E., Wiegand, T., & Breitenmoser, U. (2004). Fragmented Landscapes, Road Mortality and Patch Connectivity: Modelling Influences on the Dispersal of Eurasian Lynx. *Journal of Applied Ecology*, 711-723.

45 Schadt, S., Revilla, E., Wiegand, T., Knauer, F., Kaczensky, P., Breitenmoser, U., ... & Trepl, L. (2002). Assessing the suitability of central European landscapes for the reintroduction of Eurasian lynx. *Journal of Applied Ecology*, 39(2), 189-203.

46 Pe'er, G., & Kramer-Schadt, S. (2008). Incorporating the perceptual range of animals into connectivity models. *Ecological modelling*, *213*(1), 73-85.

47 Kramer-Schadt, S., S Kaiser, T., Frank, K., & Wiegand, T. (2011). Analyzing the effect of stepping stones on target patch colonisation in structured landscapes for Eurasian lynx. *Landscape ecology*, *26*(4), 501-513.

48 Herdtfelder, M. (2014). Natur-und sozialwissenschaftliche Analysen anthropogen bedingter Mortalitätsfaktoren und deren Einfluss auf die Überlebenswahrscheinlichkeit des Luchses (Lynx lynx). *Jahreshefte der Gesellschaft für Naturkunde in Württemberg*, *170*(1), 335-367.

49 Premier, J., Fickel, J., Heurich, M., & Kramer-Schadt, S. (2020). The boon and bane of boldness: movement syndrome as saviour and sink for population genetic diversity. *Movement ecology*, *8*(1), 1-17.

50 Kirk H, Freeland JR (2011). Applications and Implications of Neutral versus Non-neutral Markers. *Molecular Ecology*. Vol. 12. doi.org/10.3390/ijms12063966

51 Dunlop, E.S., Heino, M., Dieckmann, U. (2009). Eco-genetic modeling of contemporary life-history evolution. *Ecological Applications*. Oct;19(7):1815-34.

52 Defra. (2018). A green future: Our 25 year plan to improve the environment. London, UK: Department for Environment, Food and Rural Affairs.

53 Scottish Government (2022). Scottish Biodiversity Strategy (draft). https://www.gov.scot/binaries/content/documents/govscot/publications/strategy-plan/2022/12/scottish-biodiversity-strategy-2045-tackling-nature-emergency-scotland/documents/scottish-biodiversity-strategy-2045-tackling-nature-emergency-scotland/scottish-bi

54 Belotti, E., Weder, N., Bufka, L., Kaldhusdal, A., Küchenhoff, H., Seibold, H., ... & Heurich, M. (2015). Patterns of lynx predation at the interface between protected areas and multi-use landscapes in Central Europe. *PloS one*, *10*(9), e0138139.

55 Khorozyan, I., & Heurich, M. (2023). Patterns of predation by the Eurasian lynx Lynx lynx throughout its range: ecological and conservation implications. *Mammal Review*.

56 Khorozyan, I., & Heurich, M. (2023). Where, why and how carnivores kill domestic animals in different parts of their ranges: An example of the Eurasian lynx. *Global Ecology and Conservation*, e02585.

57 Jędrzejewski, W., Schmidt, K., Miłkowski, L., Jędrzejewska, B., & Okarma, H. (1993). Foraging by lynx and its role in ungulate mortality: the local (Białowieża Forest) and the Palaearctic viewpoints. *Acta theriologica*, *38*(4), 385-403.

58 Molinari-Jobin, A., Zimmermann, F., Ryser, A., Breitenmoser-Würsten, C., Capt, S., Breitenmoser, U., ... & Eyholzer, R. (2007). Variation in diet, prey selectivity and home-range size of Eurasian lynx Lynx lynx in Switzerland. *Wildlife Biology*, *13*(4), 393-405.

59 Krofel, M., Huber, D., & Kos, I. (2011). Diet of Eurasian lynx Lynx lynx in the northern Dinaric Mountains (Slovenia and Croatia). *Acta Theriologica*, *56*(4), 315-322.

[60] Herfindal, I., Linnell, J. D., Odden, J., Nilsen, E. B., & Andersen, R. (2005). Prey density, environmental productivity and home-range size in the Eurasian lynx (Lynx lynx). *Journal of Zoology*, 265(1), 63-71.

[61] Croft, S., Ward, A. I., Aegerter, J. N., & Smith, G. C. (2019). Modeling current and potential distributions of mammal species using presence-only data: A case study on British deer. *Ecology and evolution*, *9*(15), 8724-8735.

[62] Stahl, P., Vandel, J. M., Ruette, S., Coat, L., Coat, Y., & Balestra, L. (2002). Factors affecting lynx predation on sheep in the French Jura. *Journal of Applied Ecology*, *39*(2), 204-216.

[63] Odden, J., Herfindal, I., Linnell, J. D., & Andersen, R. (2008). Vulnerability of domestic sheep to lynx depredation in relation to roe deer density. *The journal of wildlife management*, *72*(1), 276-282.

[64] Odden, J., Linnell, J. D., & Andersen, R. (2006). Diet of Eurasian lynx, Lynx lynx, in the boreal forest of southeastern Norway: the relative importance of livestock and hares at low roe deer density. *European Journal of Wildlife Research*, *52*(4), 237-244.

[65] Milner, J. M., & Irvine, R. J. (2015). The potential for reintroduction of Eurasian lynx to Great Britain: a summary of the evidence. *British Deer Society Commissioned Report*, 1-33.

[66] Mathews, F., Kubasiewicz, L. M., Gurnell, J., Harrower, C. A., McDonald, R. A., Shore, R. F. (2018). A Review of the Population and Conservation Status of British Mammals. A report by the Mammal Society under contract to Natural England, Natural Resources Wales and Scottish Natural Heritage. Natural England, Peterborough. ISBN 978-1-78354-494-3.

[67] Crawley, D., et al. (2020). Atlas of the mammals of Great Britain and Northern Ireland. Exeter, Pelagic Publishing.

[68] Palmero, S., Belotti, E., Bufka, L., Gahbauer, M., Heibl, C., Premier, J., ... & Heurich, M. (2021). Demography of a Eurasian lynx (Lynx lynx) population within a strictly protected area in Central Europe. *Scientific Reports*, 11(1), 19868.

[69] Gimenez, O., Gatti, S., Duchamp, C., Germain, E., Laurent, A., Zimmermann, F., & Marboutin, E. (2019). Spatial density estimates of Eurasian lynx (Lynx lynx) in the French Jura and Vosges Mountains. *Ecology and Evolution*, 9(20), 11707-11715.

[70] Pesenti, E., & Zimmermann, F. (2013). Density estimations of the Eurasian lynx (Lynx lynx) in the Swiss Alps. *Journal of Mammalogy*, 94(1), 73-81.

[71] Duľa, M., Bojda, M., Chabanne, D. B., Drengubiak, P., Hrdý, Ľ., Krojerová-Prokešová, J., ... & Kutal, M. (2021). Multi-seasonal systematic camera-trapping reveals fluctuating densities and high turnover rates of Carpathian lynx on the western edge of its native range. *Scientific Reports*, 11(1), 9236.

[72] Avgan, B., Zimmermann, F., Güntert, M., Arıkan, F., & Breitenmoser, U. (2014). The first density estimation of an isolated Eurasian lynx population in southwest Asia. *Wildlife Biology*, 20(4), 217-221.

[73] Gavish, Y., O'Connell, J., & Benton, T. G. (2018). Quantifying and modelling decay in forecast proficiency indicates the limits of transferability in land-cover classification. *Methods in Ecology and Evolution*, *9*(2), 235-244.

[74] Breitenmoser, U., Kavczensky, P., Dötterer, M., Breitenmoser-Würsten, C., Capt, S., Bernhart, F., & Liberek, M. (1993). Spatial organization and recruitment of lynx (Lynx lynx) in a re-introduced population in the Swiss Jura Mountains. *Journal of Zoology*, 231(3), 449-464.

[75] Breitenmoser-Würsten, C., Zimmermann, F., Molinari-Jobin, A., Molinari, P., Capt, S., Vandel, J. M., ... & Breitenmoser, U. (2007). Spatial and social stability of a Eurasian lynx Lynx lynx population: an assessment of 10 years of observation in the Jura Mountains. *Wildlife Biology*, 13(4), 365-380.

[76] Premier, J., et al. (submitted). Human-caused mortality drives the survival of Eurasian lynx across a continent.

[77] Jedrzejewski, W., Jedrzejewska, B., Okarma, H., Schmidt, K., Bunevich, A. N., & Milkowski, L. (1996). Population dynamics (1869–1994), demography, and home ranges of the lynx in Bialowieza Primeval Forest (Poland and Belarus). *Ecography*, 19(2), 122-138.

[78] López-Bao, J. V., Aronsson, M., Linnell, J. D., Odden, J., Persson, J., & Andrén, H. (2019). Eurasian lynx fitness shows little variation across Scandinavian human-dominated landscapes. *Scientific reports*, 9(1), 8903.

[79] Boutros, D., Breitenmoser-Würsten, C., Zimmermann, F., Ryser, A., Molinari-Jobin, A., Capt, S., ... & Breitenmoser, U. (2007). Characterisation of Eurasian lynx Lynx lynx den sites and kitten survival. *Wildlife Biology*, 13(4), 417-429.

[80] Kaczensky, P. 1991: Untersuchungen zur Raumnutzungweiblicher Luchse (Lynx lynx), sowie zur Abwanderung und Mortalität ihrer Jungen im Schweizer Jura. Diploma thesis, Lehrstuhl für Wildbiologie und Jagdkunde, Forstwissenschaftlichen Fakultät an der Universität München, Germany, pp. 14-63.

[81] Gaillard, J. M., Nilsen, E. B., Odden, J., Andren, H., & Linnell, J. D. (2014). One size fits all: Eurasian lynx females share a common optimal litter size. *Journal of Animal Ecology*, 83(1), 107-115.

[82] Liu, C., Berry, P. M., Dawson, T. P., & Pearson, R. G. (2005). Selecting thresholds of occurrence in the prediction of species distributions. *Ecography*, *28*(3), 385-393.

[83] Magg, N., Müller, J., Heibl, C., Hackländer, K., Wölfl, S., Wölfl, M., ... & Heurich, M. (2016). Habitat availability is not limiting the distribution of the Bohemian–Bavarian lynx Lynx lynx population. *Oryx*, *50*(4), 742-752.

[84] Sánchez Arribas, E. et al. (in prep). Need for joint action: relocations support local but not regional connectivity in a large carnivore.

[85] Zimmermann, F., Breitenmoser-Würsten, C., & Breitenmoser, U. (2005). Natal dispersal of Eurasian lynx (Lynx lynx) in Switzerland. *Journal of Zoology*, *267*(4), 381-395.

[86] European Environment Agency (2020). Copernicus Land Monitoring Service, Corine Land Cover 2018 [dataset]. https://doi.org/10.2909/960998c1-1870-4e82-8051-6485205ebbac

[87] Allen, G. H., & Pavelsky, T. M. (2018). Global extent of rivers and streams. *Science*, 361(6402), 585-588.

[88] Bradfer-Lawrence, T., Finch, T., Bradbury, R. B., Buchanan, G. M., Midgley, A., & Field, R. H. (2021). The potential contribution of terrestrial nature-based solutions to a national 'net zero'climate target. *Journal of Applied Ecology*, *58*(11), 2349-2360.

[89] European Environment Agency (2020). Copernicus Land Monitoring Service, Tree Cover Density 2018 [dataset]. https://land.copernicus.eu/pan-european/high-resolution-layers/forests/tree-cover-density/status-maps/tree-cover-density-2018

[90] Niedziałkowska, M., Jędrzejewski, W., Mysłajek, R. W., Nowak, S., Jędrzejewska, B., & Schmidt, K. (2006). Environmental correlates of Eurasian lynx occurrence in Poland–Large scale census and GIS mapping. *Biological conservation*, *133*(1), 63-69.

[91] Seiler, A., & Helldin, J. O. (2006). Mortality in wildlife due to transportation. In *The ecology of transportation: Managing mobility for the environment* (pp. 165-189). Springer, Dordrecht.

[92] Langbein, J. (2007). National deer-vehicle collisions project: England 2003–2005. *Final report to the Highways Agency. The Deer Initiative, Wrexham, UK*.

[93] Schmidt, K., Jedrzejewski, W., & Okarma, H. (1997). Spatial organization and social relations in the Eurasian lynx population in Bialowieza Primeval Forest, Poland. *Acta theriologica*, *42*(3), 289-312.

[94] Breitenmoser-Würsten, C., Zimmermann, F., Molinari-Jobin, A., Molinari, P., Capt, S., Vandel, J. M., ... & Breitenmoser, U. (2007). Spatial and social stability of a Eurasian lynx Lynx lynx population: an assessment of 10 years of observation in the Jura Mountains. *Wildlife Biology*, *13*(4), 365-380.

[95] Kleinman-Ruiz, D., Soriano, L., Casas-Marce, M., Szychta, C., Sánchez, I., Fernández, J., & Godoy, J. A. (2019). Genetic evaluation of the Iberian lynx ex situ conservation programme. *Heredity*, *123*(5), 647-661.

[96] Mueller, S. A., Prost, S., Anders, O., Breitenmoser-Würsten, C., Kleven, O., Klinga, P., ... & Nowak, C. (2022). Genome-wide diversity loss in reintroduced Eurasian lynx populations urges immediate conservation management. *Biological Conservation*, *266*, 109442.

[97] Kleunen, J. P. (1979). Regression metamodels for generalizing simulation results. *IEEE transactions on systems, man, and cybernetics*, *9*, 93-96.

[98] Breiman, L. (2001). Random forests. *Machine learning*, *45*(1), 5-32.

[99] Pietzsch, B., Fiedler, S., Mertens, K. G., Richter, M., Scherer, C., Widyastuti, K., ... & Berger, U. (2020). Metamodels for evaluating, calibrating and applying agent-based models: A review. *The Journal of academic social science studies*, *23*(2).

[100] Breiman, L., Friedman, J. H., Olshen, R. A., & Stone, C. J. (2017). *Classification and regression trees*. Routledge.

[101] Mueller, S. A., Reiners, T. E., Middelhoff, T. L., Anders, O., Kasperkiewicz, A., & Nowak, C. (2020). The rise of a large carnivore population in Central Europe: genetic evaluation of lynx reintroduction in the Harz Mountains. *Conservation Genetics*, *21*(3), 577-587.

[102] Tracy, L. N., Wallis, G. P., Efford, M. G., & Jamieson, I. G. (2011). Preserving genetic diversity in threatened species reintroductions: how many individuals should be released?. *Animal Conservation*, *14*(4), 439-446.

[103] Breitenmoser-Würsten, C., & Obexer-Ruff, G. (2003). Population and conservation genetics of two re-introduced lynx (Lynx lynx) populations in Switzerland–a molecular evaluation 30 years after translocation. In *Proceedings of the 2nd Conference on the Status and Conservation of the Alpine Lynx Population (SCALP)* (pp. 7-9).

[104] Fležar, U., Pičulin, A., Bartol, M., Stergar, M., Sindičić, M., Gomerčič, M., ... & Černe, R. (2021). Eurasian lynx in the Dinaric Mountains and the south-eastern Alps, and the need for population reinforcement. *Cat News Special Issue*, *14*, 21-24.

[105] Molinari, P., Breitenmoser, U., Cerne, R., Fuxjäger, C., Weingarth, K., Ryser, A., & Molinari-Jobin, A. (2021). The contribution of stepping stone releases for enhancing lynx distribution. *Cat News*, *14*, 46-9.

[106] Krebühl, J., Idelberger, S., Zimmermann, F., Breitenmoser-Wursten, C., Breitenmoser, U., Herdtfelder, M., ... & Drouet-Hoguet, N. (2021). Transboundary cooperation in lynx conservation under the auspice of the Upper Rhine Conference. *Cat News Special*, (14), 55-56.

[107] Houde, A. L. S., Garner, S. R., & Neff, B. D. (2015). Restoring species through reintroductions: strategies for source population selection. *Restoration Ecology*, *23*(6), 746-753.

[108] Crandall, K. A., Bininda-Emonds, O. R., Mace, G. M., & Wayne, R. K. (2000). Considering evolutionary processes in conservation biology. *Trends in ecology & evolution*, *15*(7), 290-295.

[109] IUCN/SSC (2013). *Guidelines for reintroductions and other conservation translocations*. Version 1.0. IUCN Species Survival Commission, Gland, Switzerland, viiii+57pp. https://portals.iucn.org/library/efiles/documents/2013-009.pdf.

[110] Bonn Expert Group (2021). Recommendations for the conservation of the Eurasian lynx in Western and Central Europe: Conclusions from the workshop of the "Bonn Lynx Expert Group" in Bonn, Germany, 16–19 June 2019. *Cat News Special Issue*, *14*, *78-86.*

[111] Kowalczyk, R., Górny, M., & Schmidt, K. (2015). Edge effect and influence of economic growth on Eurasian lynx mortality in the Białowieża Primeval Forest, Poland. *Mammal Research*, *60*(1), 3-8.

[112] Deredec, A., & Courchamp, F. (2007). Importance of the Allee effect for reintroductions. *Ecoscience*, *14*(4), 440-451.

[113] Armstrong, D. P., & Wittmer, H. U. (2011). Incorporating Allee effects into reintroduction strategies. *Ecological Research*, *26*(4), 687-695.

[114] Ryser-Degiorgis, M. P., Meli, M. L., Breitenmoser-Würsten, C., Hofmann-Lehmann, R., Marti, I., Pisano, S. R., & Breitenmoser, U. (2021). Health surveillance in wild felid conservation: experiences with the Eurasian lynx in Switzerland. *Cat News*, *14*, 64-75.

[115] Andrén, H., Linnell, J. D., Liberg, O., Andersen, R., Danell, A., Karlsson, J., ... & Segerström, P. (2006). Survival rates and causes of mortality in Eurasian lynx (Lynx lynx) in multi-use landscapes. *Biological conservation*, *131*(1), 23-32.

[116] Bath, A., Olszanska, A., & Okarma, H. (2008). From a human dimensions perspective, the unknown large carnivore: public attitudes toward Eurasian lynx in Poland. *Human Dimensions of Wildlife*, *13*(1), 31-46.

[117] Arlettaz, R., Chapron, G., Kéry, M., Klaus, E., Mettaz, S., Roder, S., ... & Braunisch, V. (2021). Poaching threatens the establishment of a lynx population, highlighting the need for a centralized judiciary approach. *Frontiers in conservation science*, 17.

[118] Smith, D., O'Donoghue, P., Convery, I., Eagle, A., & Piper, S. (2016). Reintroduction of the Eurasian Lynx to the United Kingdom: results of a public survey.

[119] Hawkins, S. A., Brady, D., Mayhew, M., Smith, D., Lipscombe, S., White, C., ... & Convery, I. (2020). Community perspectives on the reintroduction of Eurasian lynx (Lynx lynx) to the UK. *Restoration Ecology*, *28*(6), 1408-1418.

[120] Marques, F. F., Buckland, S. T., Goffin, D., Dixon, C. E., Borchers, D. L., Mayle, B. A., & Peace, A. J. (2001). Estimating deer abundance from line transect surveys of dung: sika deer in southern Scotland. *Journal of Applied Ecology*, 349-363.

[121] Schmidt, K. (2008). Behavioural and spatial adaptation of the Eurasian lynx to a decline in prey availability. *Acta Theriologica*, 53, 1-16.

[122] Maschinski, J. (2006). Implications of population dynamic and metapopulation theory for restoration. *Foundations of restoration ecology*, 59-87.

[123] Zimmermann, F., Breitenmoser-Würsten, C., & Breitenmoser, U. (2007). Importance of dispersal for the expansion of a Eurasian lynx Lynx lynx population in a fragmented landscape. *Oryx*, *41*(3), 358-368.

[124] Hewitt, G. M. (1999). Post-glacial re-colonization of European biota. *Biological journal of the Linnean Society*, *68*(1-2), 87-112.

[125] Allendorf, F. W. (1986). Genetic drift and the loss of alleles versus heterozygosity. *Zoo biology*, *5*(2), 181-190.

[126] Caballero, A., & García-Dorado, A. (2013). Allelic diversity and its implications for the rate of adaptation. *Genetics*, *195*(4), 1373-1384.

[127] Herdtfelder, M., Schraml, U., & Suchant, R. (2021). Steps towards a lynx population in the Black Forest. *Cat News Special*, (14), 45-46.

[128] Kirkland, H., Hare, D., Daniels, M., Krofel, M., Rao, S., Chapman, T., & Blossey, B. (2021). Successful deer management in Scotland requires less conflict not more. *Frontiers in Conservation Science*, *2*.

[129] Drouilly, M., & O'Riain, M. J. (2021). Rewilding the world's large carnivores without neglecting the human dimension. *Biodiversity and Conservation*, *30*(3), 917-923.