

Improving reintroduction success in large carnivores through individual-based modelling: how to reintroduce Eurasian lynx (*Lynx lynx*) to Scotland

Abstract

Globally, large carnivores have been heavily affected by habitat loss, fragmentation and persecution, sometimes resulting in local extinctions. With increasing recognition of top-down trophic cascades and complex predator-prey dynamics, reintroductions are of growing interest for restoration of ecosystem functioning. Many reintroductions have however failed, in part due to poor planning and inability to model complex eco-evolutionary processes to give reliable predictions. Using the case study of Eurasian lynx (*Lynx lynx*), a large predator being considered for reintroduction to Scotland, we demonstrate how an individual-based model that integrates demography with three distinct phases of dispersal (emigration, transfer and settlement) can be used to explore the relative suitability of three geographically-distant potential reintroduction sites, multi-site reintroductions and two founding population sizes. For a single-site reintroduction of 10 lynx, our simulation results show a clear hierarchy of suitability across all metrics. Reintroduction in the Kintyre Peninsula (west coast) consistently performed best, with a probability of population persistence at year 100 of 83%, and the Scottish component of Kielder Forest (southern Scotland) worst, with only a 21% chance of population persistence to year 100. Simultaneous two-site reintroduction in the Kintyre Peninsula and in Aberdeenshire (near the east coast) of 32 lynx gave a 96% persistence at 100 years. Our model was highly sensitive to survival, particularly of adults, highlighting this parameter's importance for reintroduction success. The results strongly indicate the potential viability of Eurasian lynx reintroduction to Scotland given the current cover of suitable woodland habitat. More generally, our work demonstrates how emerging modelling approaches incorporating increased realism in representing species' demography, ecology and dispersal can have high value for quick, inexpensive assessment of likely reintroduction success and for selection between alternative strategies.

Keywords: Individual based model – Reintroduction – Dispersal – Large carnivores – Eurasian lynx

Abbreviations

Individual Based Model: IBM

Least Cost Path: LCP

Stochastic Movement Simulator: SMS

Research highlights

- IBM approaches that integrate stochastic movement trajectories with population dynamics modelling across heterogeneous landscapes provide greater realism in reintroduction modelling.
- This modelling approach enables the quick and effective assessment of alternative reintroduction proposals and management scenarios.
- The contribution of this modelling approach could significantly improve the probability of reintroduction successes, especially of large carnivores.
- This case study demonstrates the suitability of existing habitat in Scotland for the reintroduction of Eurasian lynx but that appropriate site selection is key to success.

1. Introduction

47 Globally, many large carnivores have experienced drastic population declines linked to
48 habitat loss, persecution and decreases in prey abundance (Ceballos *et al.*, 2017; Ceballos
49 and Ehrlich, 2002; Di Minin *et al.*, 2016). Many continue to face the ever present threat of
50 extinction (Weber and Rabinowitz, 1996) or have already been extirpated from their native
51 ranges (Hayward and Somers, 2009). Interest in the role that apex predators play in trophic
52 cascades and the regulation of ecosystem structure and function has grown in recent years
53 (Estes *et al.*, 2011; Ordiz *et al.*, 2013). These interactions are however complex, unresolved
54 and far from uniformly observed, one recent review highlighting that such cascades have
55 only been documented in 7 out of 31 of the world's largest mammalian carnivores (Ripple *et al.*,
56 2014). Some authors caution against the broad applicability of trophic cascades based
57 on insufficient evidence (Allen *et al.*, 2017). This lack of uniformly applicable evidence,
58 coupled with the context-dependency of any reintroduction (Kuijper *et al.*, 2016), means this
59 motivation should not form the sole justification of any reintroduction argument. Nonetheless,
60 there is a growing interest in how the reintroduction of top-order predators can be applied to
61 ecosystem restoration (Ritchie *et al.*, 2012; Wolf and Ripple, 2018), reinforced by generally
62 positive and supportive public opinion and protective legislation (Huber *et al.*, 2014) linked to
63 a variety of socioeconomic drivers.

64 Modelling plays a key role in informing reintroduction decision making (Seddon *et al.*, 2007).
65 The International Union for Conservation of Nature specifies that modelling should be used
66 in scenario exploration to devise an optimal strategy, accounting for intraspecific variation
67 and dispersal as well as highlighting the fundamental importance of matching habitat
68 suitability and availability to the target species (IUCN/SSC, 2013). The spatial and metabolic
69 requirements of large predators, coupled with their prey selection and hunting tactics, often
70 result in human-wildlife conflict, especially through the depredation of livestock (Ripple *et al.*,
71 2014). The socio-ecological context, specifically human attitudes, is therefore fundamentally
72 important to the success of large carnivore reintroductions, and its importance cannot be
73 underestimated (Linnell *et al.*, 2009). It is equally necessary to establish and model the long-
74 term suitability of any reintroduction landscape, for neither of these considerations is
75 sufficient in isolation to justify and proceed with a reintroduction. Habitat suitability modelling
76 can be used as one of a suite of tools, contributing much needed information into the
77 broader, more complex decisions made by policy makers and conservation practitioners of
78 whether to proceed, a decision that is arguably outside the capabilities and remit of a single
79 model.

80 Spatially explicit models have been specifically advocated for the advantages they confer in
81 being able to cope with the complex interacting dynamics of species-specific behaviours in
82 spatially heterogeneous landscapes (DeAngelis and Yurek, 2016). Historically, least-cost
83 path (LCP) modelling has been a popular tool with ecologists and researchers to aid
84 understanding of connectivity between populations (Schadt *et al.*, 2002) and particularly to
85 identify migration and dispersal corridors (Larue and Nielsen, 2007; Li *et al.*, 2010). Partly,
86 this has been due to its implementation simplicity and accessibility (available in GIS
87 software), and the increasing availability of high-resolution habitat data (Adriaensen *et al.*,
88 2003). In essence, this approach highlights, using a cost grid, the "optimum route" for a
89 species to cross a heterogeneous landscape matrix through the accumulated costs
90 associated with the intervening habitat separating two suitable patches (Adriaensen *et al.*,
91 2003). This has led to LCP modelling being widely utilised to inform reintroduction strategies
92 (Ziółkowska *et al.*, 2012), especially for large carnivores (Hebblewhite *et al.*, 2011; Paquet *et al.*,
93 2001; Schadt *et al.*, 2002). However, Zeller *et al.*, (2012) caution against over-reliance on
94 expert opinion in models, and highlight the importance of distinguishing between movement
95 behaviour and resource use; such data on a species' ecology are not always readily
96 available for a proposed location or in a context relevant to a planned reintroduction

97 Least cost path modelling suffers from several inherent limitations, summarized by a few key
98 assumptions made in all LCP models: the implied omniscience of individuals, a lack of
99 stochasticity within a population, and an assumption that movement always occurs in the
100 direction of 'least resistance' (Coulon et al., 2015). In contrast, stochastic individual-based
101 models (IBM) can relax the key assumptions implicit in LCP modelling by incorporating step-
102 by-step movement decisions that are made based upon information available within an
103 organism's perceptual range. The stochastic movement simulator (SMS; Palmer et al. 2011)
104 provides such a model, and it has been demonstrated to outperform LCP and circuit theory
105 approaches when tested against spatial genetic data (Coulon et al., 2015). One limitation of
106 IBMs, however, is that they typically require more information to enable rigorous
107 parameterization (Kool et al., 2013), restricting their utility to species for which a significant
108 amount of demographic and dispersal knowledge exists. Notably, SMS has been developed
109 to require very few additional parameters than those already required for LCP, making its
110 application more straightforward than other potential movement models.

111 Dispersal is a complex, multi-phase process, which influences population dynamics,
112 distribution, abundance and ultimately persistence (Zimmermann et al., 2005). Commonly,
113 dispersal is now regarded as comprising three distinct phases: emigration, transfer and
114 settlement (Mathysen, 2012). Models such as LCP or SMS represent the transfer phase,
115 and it is vital that the other two phases are also well represented. Importantly, the costs
116 associated with each of these stages are both context-dependent and pose unique
117 challenges that vary between individuals, sexes and life stages (Delgado et al., 2010), as
118 well as across space and time (Samelius et al., 2012). Dispersal is an ecological
119 cornerstone of range expansion dynamics (Bocedi et al., 2014b), meaning that the failure to
120 represent this process accurately, as it is empirically understood to operate, could have
121 considerable implications for the efficacy of reintroduction planning. It is therefore essential
122 to incorporate dispersal as a multi-phase process when attempting to model how individuals
123 will use a landscape, to identify how well-connected functionally suitable habitat patches are,
124 to model likely patterns of range expansion and to predict accurately the probability of
125 population persistence following release. In one recent example, an IBM approach was used
126 to compare the relative success of alternative strategies for introducing the specialist
127 grassland butterfly, *Maniola jurtina*, ahead of its current range in Finland (Heikkinen et al.,
128 2015). While this study did incorporate some dispersal complexity by including density-
129 dependent emigration, for the transfer phase dispersal was modelled phenomenologically,
130 using a double-negative-exponential dispersal kernel, and thus the exercise did not
131 incorporate sensitivities of movement to landscape characteristics. For reintroductions into
132 heterogeneous landscapes, incorporating greater realism into movement behaviour will likely
133 be key to gaining fuller understanding of the possible success of alternative management
134 options.

135 Reintroductions, especially those of carnivores, are often complex and costly, making
136 efficiencies in planning highly attractive (Kramer-Schadt et al., 2005). As such, advances in
137 modelling can be disproportionately valuable compared with the cost of repeated
138 reintroduction failures. Examples of ecological restoration success stories following predator
139 reintroductions (Beschta and Ripple, 2009; Wilmers et al., 2012) coupled with the rise in
140 popularity of the rewilding movement (Navarro and Henrique, 2015) have seen the potential
141 reintroduction of the Eurasian lynx (*Lynx lynx*) become a focal point of recent discourse in
142 the UK (Hetherington et al., 2008; Milner and Irvine, 2015; Wilson, 2004). Indeed, a LCP
143 analysis conducted by Hetherington et al. (2008), which identified two distinct habitat
144 networks, one in the Highlands and one in the Southern Uplands (**Fig. 1**), is currently being
145 used as the foundation upon which proposals for lynx reintroduction in Scotland are being
146 based (Smith et al., 2015; White et al., 2016). There have, however, been significant
147 advances in modelling approaches since that study was conducted.

148 Since 1971, 15 reintroductions across eight European countries have involved over 170
149 Eurasian lynx individuals, but only five of these attempts are considered to be successful
150 (Linnell *et al.*, 2009). As a result, important lessons have been learnt, and a significant body
151 of knowledge about the species' ecology, demography (Breitenmoser-Würsten *et al.*, 2007;
152 Bagnard *et al.*, 2016; Jędrzejewski *et al.*, 1996), dispersal behaviour (Samelius *et al.*, 2012;
153 Schmidt, 1998; Zimmermann *et al.*, 2005), habitat requirements and use (Belotti *et al.*, 2013;
154 Filla *et al.*, 2017; Podgórski *et al.*, 2008; Rozyłowicz *et al.*, 2010; Zimmermann *et al.*, 2007b)
155 has been amassed. However, there is a particular need for tools that enable the synthesis of
156 this knowledge and incorporate recent progress in dispersal ecology theory, in order to
157 provide more reliable assessments of landscape suitability and inter-patch connectivity, and
158 to increase the probability of future reintroduction successes.

159 We use the potential reintroduction of the Eurasian lynx to Scotland as a case study to
160 explore how an IBM that explicitly accounts for spatial heterogeneity, individual stochasticity
161 and, crucially, dispersal in its three distinct phases can inform reintroduction decision
162 making. Specifically, we aim to use this model to address the following key questions:

- 163 a) How does reintroduction from three alternative proposed reintroduction sites
164 compare and what is the likelihood of long-term population persistence for each?
- 165 b) Are there distinct habitat networks and/or key areas of the landscape through which
166 dispersal is inhibited, preventing the colonisation of apparently suitable habitat?
- 167 c) How does a multi-site reintroduction and differences in the founding population affect
168 the probability of population persistence over time?

169 **2. Material and methods**

170 **2.1 Modelling Software**

171 We used a recently developed, spatially explicit, stochastic IBM, RangeShifter (Bocedi *et al.*,
172 2014a), to model the reintroduction of lynx in Scotland. RangeShifter is a freely available
173 software package that combines demographic models with the explicit modelling of the three
174 distinct phases of dispersal (emigration, transfer and settlement) (Travis *et al.*, 2012), and
175 provides the mechanistic stochastic movement simulator (SMS) (Palmer *et al.*, 2011) to
176 model the transfer phase through a heterogeneous landscape represented as a cost grid
177 akin to the LCP approach.

178 **2.2 Landscape**

179 We implemented a patch-based model, in which local groups of suitable breeding habitat
180 cells are aggregated into larger patches for the purpose of demographic modelling, whereas
181 dispersal is modelled at the scale of individual cells (Bocedi *et al.*, 2014a). Land Cover Map
182 2007 (Morton *et al.*, 2011) was used to derive a habitat classification grid across mainland
183 Scotland at a cell size of 100 m x 100 m. The broad habitat classes were amalgamated into
184 distinct habitat classes that were deemed to be different in their effect on lynx behaviour and
185 outcomes as indicated by the preference lynx show for different habitats (permeability) and
186 the resulting mortality risk, based on those used by Hetherington *et al.* (2008). Each 100 m x
187 100 m cell is represented by the dominant habitat class that occupied the greatest proportion
188 of that cell.

189 While Eurasian lynx are known to occasionally use other habitats (Filla *et al.*, 2017), they are
190 predominantly a forest-dwelling species (Belotti *et al.*, 2013; Breitenmoser-Würsten *et al.*,
191 2001; Podgórski *et al.*, 2008) (hereafter the term "woodland" will be used, as a synonym of
192 forest, to reflect the terminology more commonly used in UK). In addition to breeding, this
193 preferential selection of woodland habitat has been shown to be important for all stages of
194 lynx dispersal, woodland distribution heavily influencing its direction and distance (Schmidt,

195 1998). We therefore updated the distribution of woodland cells with more recent estimates of
196 woodland extent from the National Forest Inventory (2015) dataset, from which two
197 woodland habitat categories were derived. 'High Quality Woodland' (**Table 1**) included all
198 polygons categorised into the seven classes of assumed woodland, broadleaf, conifer,
199 coppice, coppice with standards, mixed mainly broadleaf or mixed mainly conifer; 'Low
200 Quality Woodland' (**Table 1**) included all polygons categorised into the eight classes of
201 cloud/shadow, failed, felled, ground preparation, low density, uncertain, windthrow or young
202 trees woodland. Areas classified as cloud/shadow are small and infrequent, covering only
203 37 ha across all of Scotland. These are known woodland areas, but where an alternative
204 woodland type was difficult to allocate due to insufficient detail. As such, these areas were
205 conservatively allocated to the 'Low Quality Woodland' category. This distinction between
206 'high' and 'low' quality woodland was to enable differentiation between the ease of
207 movement through taller mature forest and younger, dense or regenerating forest, reflected
208 by the different cost values in **Table 1**. Large, busy roads are known to present barriers to
209 lynx dispersal and movement (Zimmermann et al., 2007a) as well as posing a higher risk of
210 mortality than other habitats (Andren et al., 2006; Schmidt-Posthaus et al., 2002). As such,
211 all current dual carriageways and motorways in Scotland, along with the A9 and A96 roads
212 that are currently undergoing or planned for conversion to dual carriageways, were
213 incorporated as a further landscape class (Ordnance Survey, 2017) and were given priority
214 allocation in the cost grid, represented by an unbroken line of adjacent 100 m cells. Relative
215 habitat cost values (inversely related to permeability) and per-step mortality probabilities
216 were then derived or inferred from the relevant literature (Hetherington et al., 2008;
217 Podgórski et al., 2008; Schmidt, 1998; Zimmermann, 2004; Kramer-Schadt et al., 2004) and
218 applied to corresponding habitats (**Table 1**).

219 **2.3 Habitat Patches**

220 Lynx are primarily solitary animals, females and males predominantly coming together to
221 mate, and their home ranges are characterised by a high degree of intrasexual territoriality
222 (Mattisson et al., 2013). This is especially true in females, with one study showing < 10%
223 overlap between neighbouring adult female ranges (Schmidt et al., 1997). Female home
224 ranges appear to be dictated more by prey availability, whilst male home ranges are
225 governed more by the presence of females (Schmidt et al., 1997). Home ranges have been
226 shown to vary greatly across different regions, but commonly smaller home territories are
227 observed in areas of high prey density (Breitenmoser-Würsten et al., 2001; Herfindal et al.,
228 2005; Sunde et al., 2000b). Hetherington & Gorman (2007) used this relationship, in
229 conjunction with data on the occurrence of four deer species (*Cervus elaphus*, *Capreolus*
230 *capreolus*, *Cervus nippon* and *Dama dama*), to forecast the potential population density of
231 lynx in the Southern Uplands of Scotland (0.83/100 km²) and the Scottish Highlands
232 (2.63/100 km²). The latter estimate was adopted for use in this study as, in the absence of
233 top-down predator-prey regulation, deer numbers have continued to increase during the last
234 decade and are predicted to continue to rise across the UK (Palmer, 2014). In order to
235 identify the location and extent of all habitat patches of sufficient size to support at least one
236 female lynx home range, the criteria and thresholds previously used by Hetherington et al.
237 (2008) for lynx in Scotland were applied to the 2015 National Forest Inventory dataset
238 (Forestry Commission, 2016).

239 One limitation of RangeShifter is that during the reproduction phase, juveniles are assigned
240 an initial location within the same patch but not necessarily the same cell as the mother. This
241 issue can potentially result in a juvenile commencing dispersal from the opposite end of the
242 natal patch to the mother's nominal location, giving a potentially false impression of
243 dispersal, but this is only of substantial concern when habitat patches are large in extent or
244 very elongated. To circumvent this issue, such patches were further subdivided to ensure no
245 single habitat patch was greater in extent than 700 km². This ultimately resulted in a total of

246 53 habitat patches considered suitable for female lynx home ranges across mainland
247 Scotland (**Fig. 1**).

248 **2.4 Demography and Dispersal Parameters**

249 We specified a demographic model comprising three stages: juveniles (0 - 12 months), non-
250 breeding sub-adults (12 - 24 months) and breeding adults (> 24 months). The timing of
251 sexual maturation in males can be variable (Kvam, 1991) so the sensitivity of our model to a
252 delayed sexual maturity of males to three years was also tested. Survival rate is highly
253 variable across the literature and regions of Europe for all three life stages (Andren *et al.*,
254 1997; Breitenmoser-Würsten *et al.*, 2001; Breitenmoser-Würsten *et al.*, 2007; Jędrzejewski
255 *et al.*, 1996), and will likely be influenced by factors independent of habitat. As no data for
256 Scotland yet exist, and considering this variability, survival values considered broadly
257 representative of each life stage were used to reflect the observed general increase in
258 survival probability with age in lynx, and were informed by the pessimistic and intermediate
259 survival rates used by Hetherington (2005) in his minimum viable population analysis of lynx
260 for Scotland (**Table 2**).

261 Whilst lynx are generally considered to be poor dispersers (Zimmermann *et al.*, 2005,
262 2007a), modelling their dispersal is complicated owing to, amongst other things, a lack of
263 studies identifying the relative emigration probabilities of the sexes. One study found little
264 evidence of a significant sex bias in dispersing lynx, but highlighted the relative tendency of
265 females to establish home ranges proximate to their natal patch or even to take over
266 maternal home ranges (Zimmermann *et al.*, 2005), whereas another found that 100% of
267 males dispersed but 35% of females remained philopatric (Samelius *et al.*, 2012). However,
268 population spread is considered to be dependent on the more generally conservative
269 dispersal patterns of females (Molinari-Jobin *et al.*, 2017). To reflect this, the absences of
270 context-specific dispersal data for lynx in Scotland and the inability of sub-adult lynx to
271 disperse readily across anthropogenic landscapes (Zimmermann, 2004), we chose to model
272 female maximum emigration probability conservatively and as being substantially lower than
273 that of males, and as density-dependent for both sexes (**Table 2**).

274 **2.5 Modelling reintroduction**

275 **2.5.1 Site Selection**

276 The three locations recently shortlisted for potential lynx reintroduction in Scotland (White *et al.*,
277 2016) were selected as model scenarios in the present study. The first is located in the
278 south at Kielder Forest, the second near the east coast in Aberdeenshire and the third near
279 the west coast on the Kintyre Peninsula (**Fig. 1**., patches 39, 45 and 46 respectively). The
280 chosen patches were thus located in widely-separated regions of Scotland. For the purposes
281 of this study, the political boundary of Scotland was treated as a 'hard border', preventing
282 individuals from crossing into England. This boundary condition meant that individuals that
283 reached this political border were retained within the population, being 'reflected' back into
284 mainland Scotland.

285 **2.5.2 Single-site reintroduction**

286 As almost all successful lynx reintroductions elsewhere involved 10 or more individuals
287 (Linnell *et al.*, 2009), a founding population of 10 lynx was adopted for the modelling of
288 single-site reintroductions. Each founding lynx individual and its subsequent progeny had an
289 equal probability of being male or female. Each reintroduction was modelled for
290 100 replicates of 100 years to reflect timescales previously used for modelling lynx (Wilson,
291 2004). Knowing the variability in lynx home range size documented elsewhere in Europe, we
292 also carried out a supplementary analysis in which we amalgamated where possible smaller

293 patches with neighbouring larger patches to test the sensitivity of model predictions to patch
294 size.

295 **2.5.3 Multi-site reintroduction**

296 Some authors have suggested that multi-site lynx reintroductions may represent a better
297 strategy for reintroduction success or recovery programmes in fragmented landscapes
298 (Zimmermann et al., 2007a). Equally, others have suggested that 10 lynx may be too small a
299 founding population for Scotland, and have advocated that 32 would present a more realistic
300 chance of success (Hetherington, 2005). To assess the relative effect of these two variables,
301 we also modelled reintroductions at the same prospective locations in Aberdeenshire and
302 the Kintyre Peninsula, both independently with a founding population of 32 lynx in each and
303 with 18 lynx released in the Kintyre Peninsula and 14 released in Aberdeenshire (released
304 simultaneously). The relative number released in each location in the latter case was
305 proportional to the relative size of the habitat patch area (533 km² and 395 km² respectively).

306 **2.6 Analysis**

307 **2.6.1 Metrics of success**

308 Four main metrics of reintroduction success were derived from the output files generated by
309 RangeShifter: a) the number of replicates that reached year 100; b) the mean number of
310 habitat patches occupied at year 100 for replicates that reached year 100; c) the mean
311 number of individuals at year 100 for those replicates that reached year 100; d) the
312 extinction probability over time. Differences between reintroduction sites were compared by
313 ANOVA.

314 **2.6.2 Sensitivity Analysis**

315 Survival probability was selected for sensitivity analysis owing to its variability amongst
316 previous studies for all three lynx life stages and the prior identification of its importance in
317 model sensitivity testing in other IBM studies of Eurasian lynx (Kramer-Schadt et al., 2005).
318 Equally, uncertainty regarding the maximum emigration probability of the sexes through a
319 lack of empirical data, coupled with its probable importance to population expansion, led us
320 also to select this variable for sensitivity testing. The tested values of these two variables
321 were chosen to differ from the selected values by +/- 5% to test the model's sensitivity to
322 minor perturbations. Each scenario was averaged over 100 model runs for 100 years. In line
323 with other assessments of model sensitivity to survival probability in lynx (Kramer-Schadt et
324 al., 2005), the model was deemed to be sensitive should a deviation of $\geq 20\%$ from those
325 obtained with the standard values be realised for any of the calculated model outputs.

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Table 1 - Habitat classes and their associated cost and mortality values for a stochastic movement simulator model with habitat-dependant per-step mortality. Cost values were derived from Hetherington et al. (2008) while per-step mortality values and rank order were inferred from relevant literature (Hetherington et al., 2008; Podgórski et al., 2008; Schmidt, 1998; Zimmermann, 2004; Kramer-Schadt et al., 2004).

Habitat Number	Habitat Name	Cost value	Per-step mortality probability
1	Salt Water	100000	0.9999
2	Arable & Horticulture	30	0.0002
3	All Freshwater (incl. lochs, rivers, etc.)	100	0.0005
4	Built up Areas & Gardens	1000	0.007
5	Inland Rock	1000	0.00001
6	Previously Woodland	7	0.000001
7	Montane Habitats	10	0.00001
8	Grassland	10	0.00001
9	High Quality Woodland	1	0
10	Low Quality Woodland	2	0
11	Supra/Littoral Sediment & Rock	10	0.00001
12	Bog, Marsh, Fen Swamp	10	0.00001
13	Dwarf, Shrub, Heath	7	0.00001
14	Motorways & Dual Carriageways	120	0.07

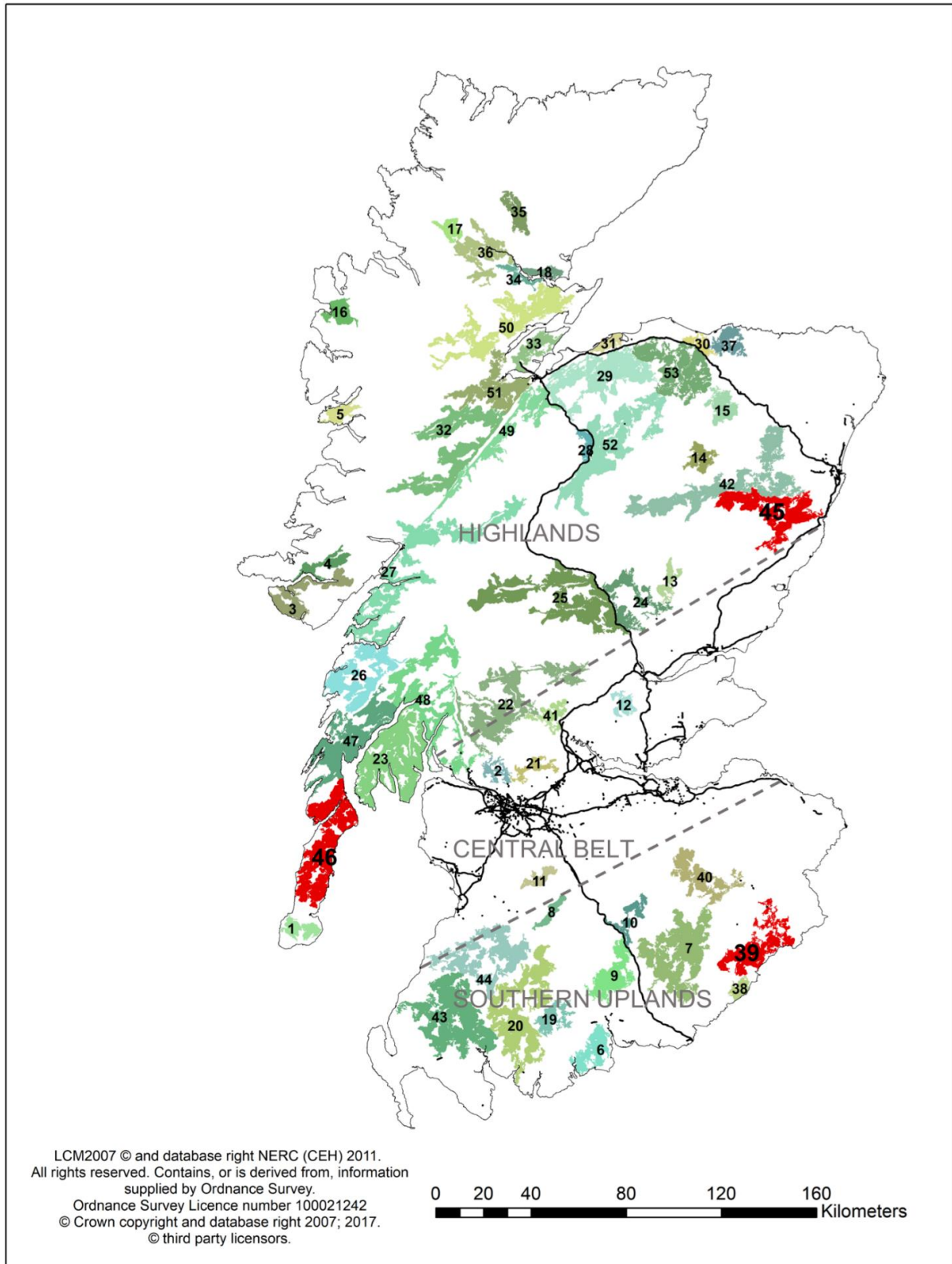
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Table 2 - Parameter values and settings applied in the RangeShifter stage-structured simple sexual model with overlapping generations.

(a) Breitenmoser-Würsten *et al.* (2007), (b) Andren *et al.* (1997), (c) Breitenmoser-Würsten *et al.* (2001), (d) Jędrzejewski *et al.* (1996) (e) Vandel *et al.* (2006), (f) von Arx *et al.* (2004), (g) Gaillard *et al.* (2014), (h) Schmidt *et al.* (1997), (i) Zimmermann *et al.* (2005), (j) White *et al.* (2015), (k) Hetherington & Gorman (2007), (l) Samelius *et al.* (2012), (m) Vandel *et al.* (2006), (n) Schmidt (1998), Supplementary material: (o) Fig. S1, (p) Fig. S2, (q) Fig. S3, (r) SMS parameters.

Demographic Parameter	Value
Number of life stages ^(a)	3
- Juvenile (kitten) survival probability ^(a, b, c, d, m)	53%
- Sub-adult survival probability ^(a, b, c, d, m)	63%
- Adult survival probability ^(a, b, c, d, m)	80%
Maximum age (years) ^(f)	17
Maximum fecundity at low density ^(f)	5
Mean fecundity at equilibrium density / year ^(a, c, g)	2
Number of reproductive seasons / year ^(h, i)	1
Probability of being male in founding population and at birth ^(c, d)	50%
Probability of reproducing annually ^(a, j)	100%
Number of years after reproduction before subsequent reproduction ⁽ⁿ⁾	0
Habitat-specific strength of density dependence in fecundity (1/b) (individuals / ha):	
High Quality Woodland and Low Quality Woodland ^(k, o)	0.000285
All other habitats	0
Emigration Parameters ^(p)	Value
Juvenile female maximum emigration probability ^(i, l)	0.4
Juvenile male maximum emigration probability ^(i, l)	0.9
Sub-adult maximum emigration probability (male & female) ^(a)	0
Adult maximum emigration probability (male & female) ^(a)	0
Alpha (slope of density-dependent function)	10
Beta (relative inflection point of density-dependent function)	1
Stochastic Movement Simulator Settings ^(r)	Value
Perceptual range	500 m
Perceptual range method	2
Directional persistence	5.0
Memory size (steps)	5
Goal type	0
Settlement Parameters ^(q)	Value
Female	Find a suitable patch + density dependence
Male	Find a suitable patch + density dependence + mating requirements
Maximum settlement probability (male & female)	1.0
AlphaS (slope of density-dependent function)	-10
BetaS (relative inflection point of density-dependent function)	1
Maximum number of steps	5000



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Fig. 1. - The distribution of suitable habitat patches in mainland Scotland derived from the National Forest Inventory 2015 data (Forestry Commission, 2016) are shown in various shades of green and blue to distinguish adjacent patches. The three potential reintroduction sites tested in the present study are shown in red and with larger font text (Kielder Forest - 39, Aberdeenshire - 45 and Kintyre Peninsula - 46). All motorways and dual carriageways in Scotland, including those currently undergoing or planned for conversion to dual carriageways, are shown in black. Three geographical regions are shown in grey separated by dashed lines.

344 3. Results

345 3.1 Single Site Reintroduction

346 A population reintroduced on the Kintyre Peninsula was predicted to survive for 100 years in
347 83% of replicates, much higher than those in either Aberdeenshire (35%) or Kielder Forest
348 (21%). Similarly, the mean number of patches occupied at year 100 differed between sites
349 and was highest for the Kintyre Peninsula and lowest for Kielder Forest, as was the final
350 population size (**Table 3**). A complete breakdown by habitat patch for each metric and each
351 reintroduction site averaged across all 100 replicates is presented in **Table S1**. A large
352 increase in the probability of population extinction occurs between 10 and 30 years post-
353 release, after which it tended to stabilise in all three sites (**Fig. 2**). The increase was much
354 less for reintroduction in the Kintyre Peninsula than in the other two sites..Subsequent
355 analysis of the first 30 years post release shows that for one of the three release sites,
356 Kintyre, this is linked to both number of females in the initial population and low birth rate in
357 the first year (**Fig. S5**) and, for all three sites, lower rates of patch colonisation (**Fig. S6**).. On
358 average there was a decline in the number of individuals in the reintroduction patch across
359 all sites (**Fig. S7**). However, in surviving replicates the decline was arrested after 5-10 years,
360 whereas in extinct replicates this arrest was much less apparent (**Fig. S7**). This same figure
361 shows that in surviving replicates, the equilibrium population size was less than the
362 10 released individuals for all release sites, and was on average below 6 for Aberdeenshire
363 and Kielder.

364 Hetherington *et al.* (2008) suggested there were two geographically distinct habitat networks
365 for lynx in Scotland, one in the Southern Uplands and one in the Highlands (**Fig. 1**).
366 Reintroduction in the Kintyre Peninsula only ever resulted in lynx reaching the Southern
367 Uplands in 12% of replicates, with only 3 of the 13 Southern Uplands woodland habitat
368 patches being reached (**Fig. 3**). Across all replicates, reintroduction in Aberdeenshire never
369 resulted in any patch being colonised in the Southern Uplands (**Fig. 3**). With reintroduction in
370 Kielder Forest, only a single patch was ever reached in the Highlands habitat network
371 (**Fig. 3.**) and then only in 9% of replicates. While this single patch was capable of being
372 reached, its mean occupancy probability, averaged over 100 years and 100 replicates was
373 still <1% (**Fig. S4**). Equally, no lynx was found to be alive in the Highlands habitat network in
374 year 100 in any of the 100 model replicates following reintroduction in Kielder Forest
375 (**Fig. 4**).

376 The rank order between sites was maintained following the amalgamation of smaller patches
377 into neighbouring larger ones, the model proving to be robust to minimum patch size
378 (**Table S2**). Similarly, while an expected reduction across all three metrics was realised
379 following a delay in the sexual maturation of males to 3 years, the same rank order for the
380 three sites was again maintained (**Table S3**).

381 Ten additional simulations from each site for which individual-level output was generated
382 were also conducted to establish mean dispersal distance for both successful and
383 unsuccessful dispersers, both male and female (**Fig. S8**). There was very little difference
384 between the sexes in mean dispersal distance, and unsuccessful dispersers showed a
385 greater mean dispersal distance than successful dispersers. Dispersal distance was greatest
386 for both successful and unsuccessful dispersers from the Kintyre release site compared with
387 the other two sites.

388 As there are no direct data available for lynx in Scotland, alternative values for several
389 demographic parameters observed in Europe were also tested. When running the model
390 with alternative values for maximum age, maximum litter size and annual female
391 reproduction probability, the rank order of site suitability was unaltered (**Table S4**).

392 **3.2 Founding Population Size and Multi-Site Reintroduction**

393 When comparing the likelihood of population persistence after release of 32 individuals
394 between two release sites, Aberdeenshire notably underperformed compared with the
395 Kintyre Peninsula. The multi-site reintroduction of 18 lynx released in the Kintyre Peninsula
396 and 14 released in Aberdeenshire gave marginally the greatest chance of population
397 persistence after 100 years (**Table 3**). However, the difference between this two-site
398 reintroduction and the modelled reintroduction of the same number of lynx solely in the
399 Kintyre Peninsula was not significant for the number of patches occupied, nor the number of
400 individuals in the population at year 100 (ANOVA: $F_{1,187} < 1.22$, $P > 0.271$ in both cases).

401 Interestingly, the reintroduction of 32 lynx in the Kintyre Peninsula gave a 10% greater
402 population persistence probability over 100 years than that of a release of only 10 lynx in the
403 same location. Otherwise, this increase in the founding population size had little effect on
404 patch occupancy or population size. Equally, releasing 32 lynx in Aberdeenshire still
405 appeared to perform worse across all metrics than a 10-lynx release in the Kintyre
406 Peninsula.

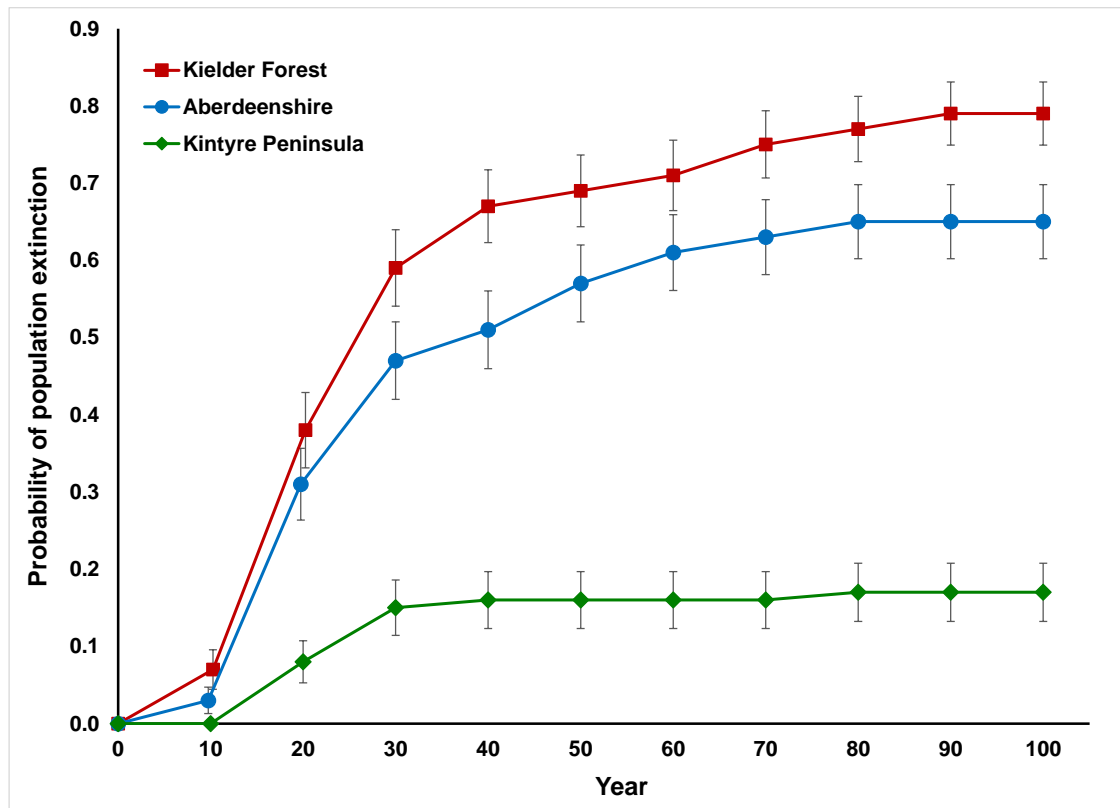
407 **3.3 Sensitivity Analysis**

408 **3.3.1 Survival Probability**

409 The model was sensitive to a 5% decrease in adult survival for every response metric and
410 sensitive to an increase of adult survival for the number of occupied patches and the mean
411 number of individuals in the population at year 100. Similarly, the model was sensitive to a
412 decrease in sub-adult survival of 5% for all metrics, but not to an increase of 5%. The only
413 metrics that appeared to be sensitive to changes in juvenile survival were the number of
414 patches occupied and the mean number of individuals at year 100, both of which were
415 sensitive to a reduction of 5% in juvenile survival (**Table 4**).

416 **3.3.2 Emigration Probability**

417 Across all three outputs the model was not sensitive to $\pm 5\%$ modifications to either male or
418 female maximum emigration probability (**Table 4**). However, there was a disproportionate
419 reduction in population persistence when maximum emigration probability of females was
420 reduced, as too few young females were emigrating to found new populations. Equally,
421 when the emigration probability of males was increased, a similar disproportionate effect
422 occurred, this time likely to be due to there being too few philopatric males to maintain
423 existing populations if the adult male(s) died. It has been suggested that lynx may display
424 negative density-dependent dispersal behaviour (Zimmermann et al., 2007a), but we found
425 that our model showed little sensitivity to whether emigration was modelled as density-
426 dependent or -independent (**Table S5**).



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Fig. 2 - Cumulative extinction probability averaged across 100 replicates for each decade over 100 years following release of 10 adult lynx at one of three single reintroduction sites in Scotland. Error bars show 1 standard error.

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Table 1 - Predicted success of reintroduction at three sites in Scotland: means of 100 replicate simulations following the release of 10 individuals in a single site, or 32 individuals in a single site, or 32 individuals split between two sites. Kielder Forest (Kiel), Aberdeenshire (Aber), the Kintyre Peninsula (Kint), Aberdeenshire (14 lynx) + the Kintyre Peninsula (18 lynx) (Aber + Kint).

	10 lynx			32 Lynx		
	Kiel (\pm SE)	Aber (\pm SE)	Kint (\pm SE)	Aber (\pm SE)	Kint (\pm SE)	Aber + Kint (\pm SE)
Number of replicates reaching year 100	21	35	83	45	93	96
Mean number of patches occupied at year 100.	10.2 (0.41)	18.9 (1.38)	27.1 (0.41)	17.9 (1.17)	26.0 (0.55)	26.8 (0.85)
Mean number of individuals at year 100	55.0 (3.39)	97.8 (8.15)	150 (2.01)	88.4 (6.67)	143 (2.84)	147 (4.37)

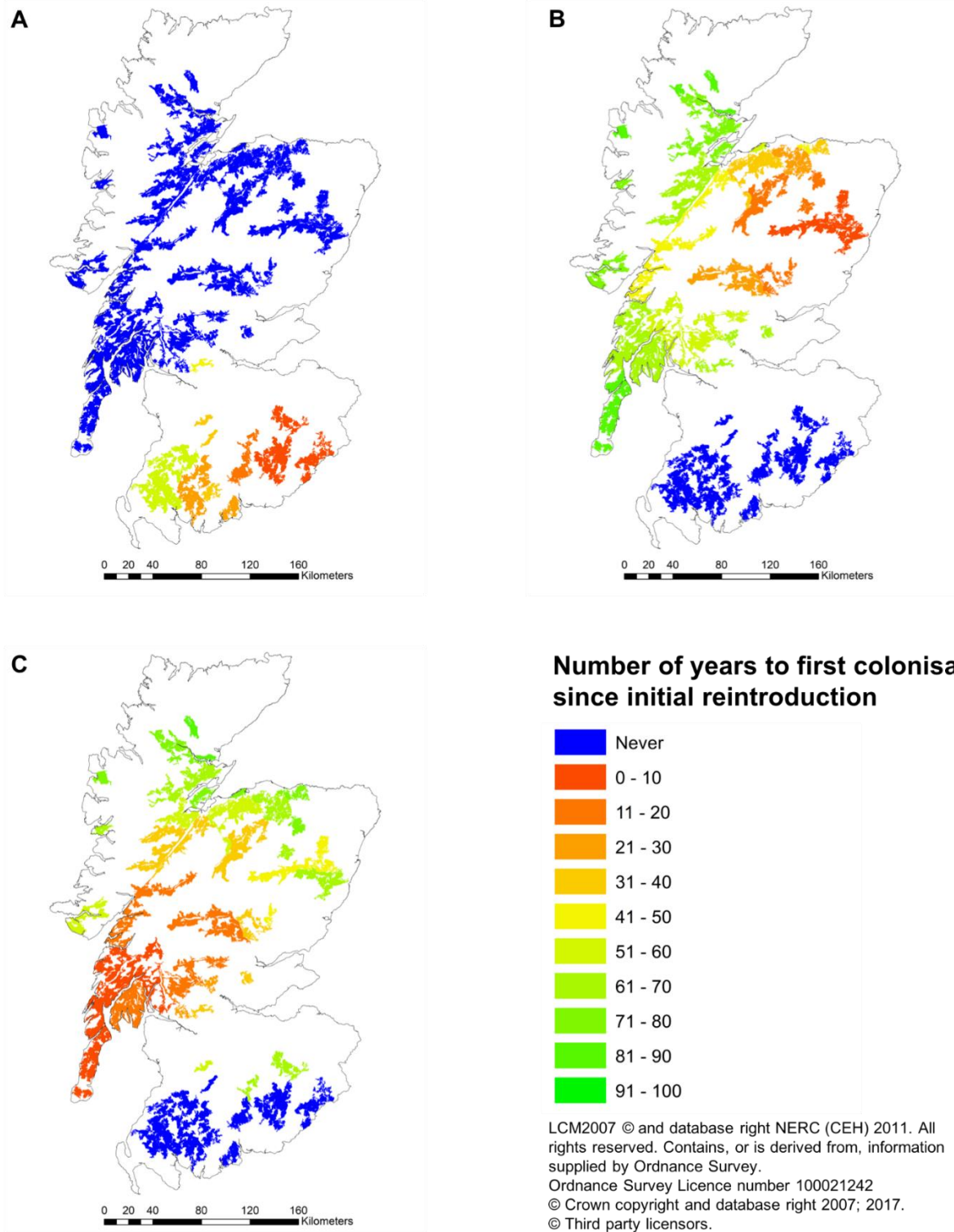
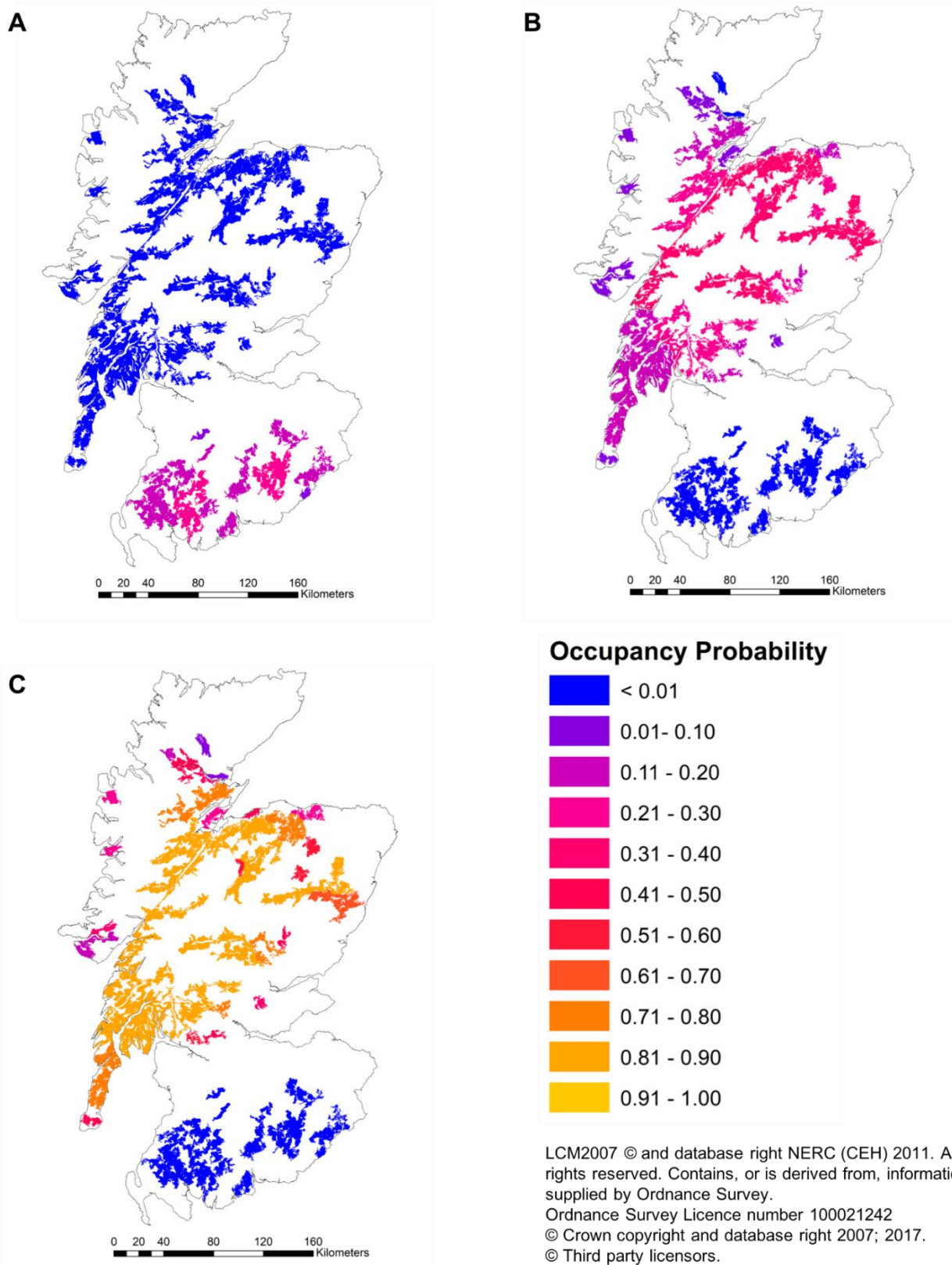


Fig. 3 - Predicted mean year of first colonisation for every woodland patch across mainland Scotland following reintroduction in (A) Kielder Forest, (B) Aberdeenshire and (C) the Kintyre Peninsula.

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Fig. 4 – Mean occupancy probability for each woodland patch at year 100, calculated as the average across all 100 replicates for the occupancy probability in the 100th year only, following reintroduction in (A) Kielder Forest, (B) Aberdeenshire and (C) the Kintyre Peninsula.

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Table 2 - Model sensitivity to juvenile, sub-adult and adult survival probability, and male and female maximum emigration probabilities (D0), for reintroductions in the Kintyre Peninsula averaged for 100 model runs over 100 years. The percentage positive or negative directional change from the model run with the standard parameters (juvenile survival = 53%, sub-adult survival = 63%, adult survival = 80%, female D0 = 0.4, male D0 = 0.9) is rounded and given in the table in parentheses. The model is considered sensitive should a deviation of $\geq 20\%$ be found from the standard parameters.

	Control	Survival Probability					Emigration Probability				
		Juvenile Survival		Sub-adult Survival		Adult Survival		Female		Male	
		48%	58%	58%	68%	75%	85%	D0 = 0.35	D0 = 0.45	D0 = 0.85	D0 = 0.95
Population persistence probability at year 100 (%)	83	70 (-16%)	88 (+6%)	62 (-25%)	83 (0%)	39 (-53%)	96 (+16%)	71 (-14%)	88 (+6%)	85 (+2%)	73 (-12%)
Mean number of patches occupied at year 100 for replicates reaching year 100	27.1	20.3 (-25%)	29.9 (+10%)	21.5 (-20%)	30.2 (+12%)	14.8 (-45%)	33.4 (+23%)	25.9 (-4%)	27.8 (+3%)	27.2 (+1%)	26.8 (-1%)
Mean number of individuals at year 100	150	106 (-29%)	170 (+14%)	116 (-22%)	171 (+14%)	73.6 (-51%)	199 (+33%)	148 (-2%)	150 (+0%)	152 (+1%)	149 (-1%)

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4. Discussion

448 By adopting a modelling approach in which stage-structured population dynamics are
449 incorporated and transfer is represented by a mechanistic movement model, we have
450 demonstrated how spatially detailed modelling predictions can be produced, which will
451 inform the process of site selection for the introduction of a large carnivore. By integrating a
452 stochastic model of dispersal with a representation of spatial population dynamics, our
453 approach has shown how critical the choice of introduction site can be to the potential
454 success of a reintroduction programme for a large carnivore. In this case study of the lynx in
455 Scotland, across all of the metrics we used to investigate the relative performance of the
456 three proposed single-site reintroductions, there was a clear hierarchy of suitability. Kielder
457 Forest repeatedly underperformed across all metrics, offering an unacceptably low
458 probability of long-term population persistence. The Aberdeenshire site performed notably
459 better, but the Kintyre Peninsula reintroduction site consistently proved to be the most
460 suitable across all metrics. Our model indicated that reintroduction in this location could
461 result in an 83% probability that a population of 150 lynx can become established by
462 year 100, occupying over half of the number of available woodland habitat patches in
463 mainland Scotland.

464 Identifying and accounting for both short- and long-term post-release effects is important
465 when attempting to predict population persistence (Armstrong et al., 2017). Additional
466 modelling and analysis in this study showed that following release in any one of the three
467 sites, on average the death of the last founding individual occurred in the eleventh year
468 (**Supplementary material**). The population of founding individuals, however, only remained
469 viable (at least one male and one female still alive but all juveniles having died or dispersed)
470 on average until half way through the sixth year and there was an indication that the size of
471 the release patch has an effect on the probability of establishment (**Fig. S7**).

472 An empirical study of the survival rate of wild-caught adult lynx from the Carpathian
473 mountains that were reintroduced to the Vosges region of France, found that nine out of
474 21 individuals across 11 operations died within the first three years, eight of which were
475 within the first year (Vandel et al., 2006). Similarly, of 30 lynx originating from zoos in
476 Germany, Sweden and Finland that were released in Poland between 1993 and 2000, 13
477 died within the first three years (Linnell et al., 2009). These studies imply that there is a
478 period of vulnerability after reintroduction consistent with elevated mortality during an
479 acclimation period (Hamilton et al., 2010). Interestingly in our model, success in this early
480 period was found to be linked in part to the rate of patch colonisation (**Fig. S6**) and the
481 number of kittens born in the first breeding season (**Fig. S5B**). Initial mortality will however
482 be highly situation-dependent and potentially linked to the source of the founding individuals
483 or translocation stress, which can be mitigated through good practice, and need not result in
484 reintroduction failure (Dickens et al., 2010). The practice of using captive animals for
485 reintroductions can be controversial and requires careful handling having resulted in both
486 starvation and the need to recapture animals that were too habituated to people (Linnell et
487 al., 2009).

488 *Our results suggest that a period of vulnerability could be expected at a later stage, but they*
489 *do not provide definitive evidence about the cause of the increase in modelled extinction*
490 *probability around 10-30 years post-release. We can, however, infer that it is likely to be*
491 *linked to rates of patch colonisation, inadequate reproduction, patch size and levels of inter-*
492 *patch connectivity for the following reasons. . Immediately following release, smaller release*
493 *patches would become saturated more quickly, reducing fecundity and increasing male*
494 *emigration probability in our model. Where neighbouring patches are more fragmented with*
495 *greater intervening distances, this will likely result in a broadly distributed population whose*
496 *individuals are less likely to find a mate and are unable to re-disperse due to the emigration*

497 model implemented in this study. This implies that both the location of neighbouring patches
498 and critically the size of the reintroduction patch and its neighbouring patches have an effect
499 on the probability of population establishment. This is reflected in our results, with Kintyre
500 being the biggest and best connected of the three reintroduction patches.

501 We were not able to test the influence of patch shape or edge effects in our model. Their
502 influence is complicated for lynx partly due to its variability in microhabitat selection for
503 different purposes (Podgórski et al., 2008). Forest edge habitat, particularly adjacent to
504 farmland, was found to provide optimal cover for stalking their preferred prey species, roe
505 deer (*Capreolus capreolus*) in Scandinavia (Sunde et al., 2000a). However, other work has
506 demonstrated an increased risk of human-induced mortality associated with habitat edges
507 compared to core areas (Kowalczyk et al., 2015). While it is possible that the shape and
508 location of the Kintyre Peninsula influenced the suitability of this reintroduction location, the
509 west coast still outperformed other regions when alternative local patches were tested
510 (**Table S6**). An additional important factor (not included in the model) is the spatial and
511 temporal variation in the risk of lynx persecution, but no such data currently exist for
512 Scotland, nor do representative long-term studies of lynx reintroductions in Europe exist for
513 robust comparison with our predicted period of vulnerability (Linnell et al., 2009).

514 Currently, proposals advocating a reintroduction of lynx to the UK (Smith et al., 2015; White
515 et al., 2016) have placed substantial emphasis on the work conducted by Hetherington et al.
516 (2008). In contrast to Hetherington et al. (2008), our case study was confined geographically
517 to the political boundary of Scotland. This was to reflect the devolution of environmental
518 policy and decision making to the Scottish Government, along with the recent development
519 of a non-statutory Scottish Code for Conservation Translocations (National Species
520 Reintroduction Forum, 2014). As such, it is of note that the true extent of Kielder Forest was
521 underrepresented in our model, as contiguous woodland areas within England were omitted
522 and lynx were prevented from crossing into potentially suitable habitat in England. Should a
523 modelling exercise be conducted for the purpose of providing the evidence to justify a
524 specific imminent planned reintroduction to Scotland, it is likely that the full extent of Kielder
525 Forest would be included. Future versions of RangeShifter will enable the modelling of an
526 “absorbing” rather than a “reflective” boundary. This would allow for the more accurate
527 representation of contrasting policies in separate political regions, for example where lynx
528 could be protected by legislation in Scotland but not in England, resulting in potentially
529 higher rates of mortality in England through persecution.

530 Despite this, our results are of importance for assessing the suitability of Kielder Forest for
531 the long-term success of a full reintroduction and therefore as an appropriate site for a trial
532 reintroduction of lynx (White et al., 2016). The low scoring of this release site across all
533 metrics considered here raises concerns, and suggests that further modelling is needed to
534 investigate the appropriateness of this site relative to others. While this contrast between the
535 findings from our modelling and current proposals is worthy of further investigation, our study
536 has illustrated only a snapshot of the model’s potential. More detailed data on the
537 demography and dispersal behaviour of lynx in a context similar to Scotland, coupled with
538 further analysis of additional metrics, would be highly valuable, and is needed before any
539 definitive conclusions are drawn. For example, further analyses could explore sensitivities of
540 model outputs to sex-biased dispersal behaviours that might include sex-specific density
541 dependence in emigration and settlement decisions. It could also include extensions to allow
542 for potential demographic impacts of inbreeding to be included and a version of
543 RangeShifter that will allow for this will be available soon (Palmer et al. in prep). Importantly,
544 the modelling tools now exist that make it possible to establish robustly to which
545 demographic, landscape and even genetic factors potential reintroduction success is most
546 sensitive, and this can help to prioritise future data collection to reduce model uncertainties
547 iteratively. As permission for a reintroduction of lynx appears to be a possibility in Scotland,
548 an opportunity now exists to develop this modelling approach further and then validate its

549 accuracy by assessing the outcomes of any trial reintroductions as they develop against the
550 model's predictions.

551 Both Kramer-Schadt et al. (2005) and Hetherington (2005) defined predicted success as a
552 95% probability of population persistence following a lynx reintroduction after 50 and
553 100 years respectively. If this threshold is used, the only reintroduction scenario of those we
554 modelled that offers an acceptable chance of success after 100 years is a multi-site
555 reintroduction to both the Kintyre Peninsula and Aberdeenshire using 32 lynx split between
556 them. These preliminary results are however encouraging and give a strong indication as to
557 the broad potential for the long-term viability of a reintroduction of lynx to Scotland, given the
558 current availability of woodland habitat cover. This study has laid a strong foundation upon
559 which future modelling can now build to identify specifically the most appropriate course of
560 action for the reintroduction of lynx to Scotland, and it demonstrates the power such
561 modelling approaches have in informing reintroduction decision making of large carnivores
562 generally.

563 With landscape fragmentation and habitat loss noted as being among the most important
564 factors restricting the long-term success of Eurasian lynx reintroductions across Europe
565 (Linnell et al., 2009), being implicated in failed reintroduction attempts (Kramer-Schadt et al.,
566 2005) and threatening other species of lynx (Ferrerias, 2001), establishing the level of
567 connectivity between suitable habitat patches is key. Hetherington et al. (2008) proposed
568 two geographically distinct habitat networks across Scotland (one in the Highlands and one
569 in the Southern Uplands) to which our habitat patch landscape roughly corresponds (**Fig. 1**).
570 These authors used a LCP analysis to conclude that there was a low probability that
571 sufficient numbers of lynx would cross the intervening landscape to establish successfully in
572 the other network from where they were released. Using data on current woodland cover
573 and distribution, our results support this finding as they show extremely low occupancy
574 probabilities, both on average (**Fig. S4**) and at year 100 (**Fig. 4**), of patches in the other
575 habitat network from where the reintroduction took place, regardless of release site. Our
576 results thus emphasise how estimates quantifying habitat availability alone are insufficient to
577 inform reintroduction proposals. Without careful consideration of how functionally connected
578 the habitat is through the interactions of demography and dispersal characteristics with the
579 landscape, there is a danger of overestimating the appropriateness of a reintroduction.

580 Bateman & Fleming (2012) describe how, on average, large felids are often unable to
581 coexist comfortably in close proximity to humans. The response of lynx to the presence of
582 humans and human-modified landscapes varies, but they are often found to adjust their
583 home ranges to reduce exposure to increasing human disturbance (Bouyer et al., 2015).
584 The intervening matrix between the Highlands and Southern Uplands habitat networks
585 corresponds geographically to the Central Belt of Scotland (**Fig. 1**). This region supports the
586 two biggest cities and the highest human population densities in Scotland, while being at its
587 narrowest point a natural bottleneck approximately 38 km wide. It has been suggested that
588 targeted efforts could be made to expand the amount of suitable habitat in this region to
589 increase connectivity between the two habitat networks (Hetherington et al., 2008).
590 However, roads and areas of high human population density are known to pose formidable
591 barriers through vehicle collisions (Schmidt-Posthaus et al., 2002), persecution and
592 poaching (Andren et al., 2006), making the efficacy of such efforts questionable.

593 Mortality from hunting and poaching is often high, especially in adult lynx (Andren et al.,
594 2006) and is still thought to be one of the biggest challenges facing lynx populations
595 reintroduced in mainland Europe more than 25 years on (Breitenmoser, 1998). Indeed
596 recent work suggests the prevention of illegal hunting should be considered the highest
597 priority for the conservation of lynx in a reintroduced population in the Bohemian Forest
598 Ecosystem (Heurich et al., 2018). Our model's sensitivity to survival, particularly adult
599 survival, reflects the findings of previous studies (Vandel et al., 2006) and suggests that

600 increases in population persistence probability could be achieved through a reduction in
601 adult mortality. This is especially interesting as our sensitivity analysis demonstrated that a
602 5% increase in adult survival, well within the natural range of variability (Andren et al., 2006,
603 1997), could result in a 96% probability that the population would reach year 100 for a
604 reintroduction of only 10 lynx in the Kintyre Peninsula. As a result, safeguarding adequate
605 levels of adult survival appears to be a key area of focus to ensure any reintroduction is a
606 success. To ensure such levels of lynx survival are realised, we would advocate the use of
607 additional, socio-economic work to identify key stakeholder groups and areas of potential
608 conflict, whilst quantifying the levels of risk these would pose to animal welfare and broader
609 reintroduction success. We caution against the pursuit of a single decision-making tool,
610 instead supporting the combined use of multiple sources of evidence that can be used
611 collectively to inform effective decision making.

612 The apparent paucity of genetic variation within previously reintroduced populations of lynx
613 in Europe (Bull et al., 2016), their reported limited success, and the call from authors to learn
614 from the mistakes of previous failed lynx reintroduction attempts (Linnell et al., 2009), makes
615 the inclusion of sufficient population genetic variation an essential consideration. As such,
616 using survival rate as a surrogate for a larger founding population should be considered with
617 care and categorically cannot be considered in isolation from the need to secure the long-
618 term genetic viability of a population (IUCN/SSC, 2013). The upcoming release of
619 RangeShifter v2 enables the explicit modelling of genetic relatedness, which will allow these
620 fundamental considerations to be considered when interpreting model predictions. Future
621 modelling should thus aim to incorporate such genetic factors and further explore scenarios
622 where an initial population of lynx is subsequently bolstered by a second introduction.

623 Phased reintroductions of this nature may also help to reduce any pressure on the source
624 populations from which the animals are obtained. For the three reintroduction sites
625 considered in this study, we found that modelling of a phased reintroduction had a negligible
626 impact on any of the three metrics of success across all sites (**Fig. S9**). Owing to the
627 quantity of potential phased release combinations, this modelling approach would likely be
628 best suited to investigating the performance of separately identified, feasible alternatives
629 rather than searching for an 'optimum' scenario. Equally our model could be adapted to
630 explore further the hypothesis that a single-site reintroduction is sub-optimal, but "population
631 nuclei" should be introduced in neighbouring patches in a fragmented landscape (Kramer-
632 Schadt et al., 2005; Zimmermann et al., 2007a). Scenarios of this nature will help to identify
633 key areas that could benefit from population enrichment due to their isolation or during
634 periods in time where the population may be more vulnerable to extinction, such as those
635 already demonstrated here.

636 Often overlooked, but of particular importance for reintroductions of species with large
637 spatial requirements, is the dynamic nature of modern landscapes and the lack of constancy
638 in resource availability (Osborne and Seddon, 2012). As the lynx is a woodland-dwelling
639 species, the impact that modern forestry practice has on the continuity of woodland cover
640 could be substantial. In a country like Scotland, a large proportion of the total woodland
641 cover is managed on a short rotation clearfell system (Macdonald and Hubert, 2002). This
642 has the potential to change rapidly the suitability and location of core habitat, leaving some
643 populations isolated. Conversely, new woodland creation continues to be a focus of the
644 Scottish Government (Forestry Commission Scotland, 2006), and current policy means that
645 once forestry has become the dominant land use in an area it often remains as such, with
646 tree restocking obligations on harvested sites. As lynx have been found to use a variety of
647 woodland types and successional stages at different periods in their life cycle (Podgórski et
648 al., 2008), and show a preference for habitat heterogeneity (Rozyłowicz et al., 2010), the
649 impact this will have on a reintroduced population is uncertain.

650 Lynx are a specialist predator of roe deer (Jobin et al., 2000), meaning the abundance of roe
651 deer could have a profound impact on habitat suitability and modelled output for lynx.
652 Female lynx home ranges are dictated primarily by prey availability (Schmidt et al., 1997),
653 with a prevailing consensus that smaller home territories are linked to higher prey density
654 (Linnell et al., 2007; Sunde et al., 2000b). A comparison of four separate areas across
655 Europe revealed a “highly significant relationship between lynx density and the density of
656 ungulate biomass” (Hetherington and Gorman, 2007). As a result of this tight coupling and
657 the uncertainty surrounding prey abundance, especially under future conditions, care should
658 be taken in interpreting long-term model projections. Attempts to modify habitat patch
659 suitability based on roe deer density could be a productive avenue for future modelling,
660 particularly as there is some evidence that roe deer densities have historically been lower in
661 the west of Scotland than further east (Latham et al., 1996; Palmer and Truscott, 2003).
662 However, the mobility of deer and uncertainty about the impacts lynx reintroduction would
663 have on prey behaviour make this a challenging task. Nevertheless, attempting to
664 incorporate how a landscape and prey communities will change over time into predictions
665 should be a key focus of future reintroduction modelling, as they have the potential to alter
666 site suitability drastically or even the efficacy of wider reintroduction proposals.

667 Models themselves cannot make decisions, but instead help us to understand the complex
668 interacting dynamics of species with their environment whilst creating a framework around
669 which realistic objectives can be set (Osborne and Seddon, 2012). We have demonstrated
670 how the use of an IBM that specifically accounts for a species’ demography, ecology and
671 dispersal can be used to assess quickly and inexpensively the likelihood of reintroduction
672 success. Notably, the modelling approach we have adopted explicitly incorporates several
673 processes that we understand to have substantial impact on the establishment and spread
674 of introduced species. Density-dependent emigration, stochastic individual movement
675 trajectories and stochastic demography are all key components of the inherently uncertain
676 course of any given introduction (Melbourne & Hastings, 2009; Bocedi *et al.*, 2014b). By
677 integrating these processes in a modelling exercise it becomes possible to identify the range
678 of likely outcomes (Cuddington et al., 2013) and to establish how sensitive these are to
679 uncertainties in model structure and to parameter values. This can in turn help to target
680 limited conservation funds and can subsequently be used in an adaptive approach as data
681 emerge from reintroductions conducted on the focal species, or even on closely related
682 species.

683 For lynx reintroduction to Scotland, we recommend that future research should focus on
684 assessing the sociological components of lynx reintroduction and a spatially explicit
685 quantification of any resultant risk. Specifically, this should involve a comprehensive
686 assessment of key stakeholder perceptions and the potential for wildlife conflict, with
687 particular consideration given to the risk of livestock depredation, hunting and persecution.
688 Such an assessment should also reflect roe deer and sheep densities and their respective
689 seasonal variation alongside the spatial arrangement and temporal variability of pasture and
690 woodland. We recommend that decision-makers should use as evidence such independent
691 modelling of the spatial variation in the socio-economic components of risk, alongside the
692 individual-based species models demonstrated in the present study, to assess the relative
693 suitability of alternative reintroduction strategies for both lynx in Scotland and large carnivore
694 reintroduction programmes generally. In the future we envisage coupled individual-based
695 models of the ecological system and agent-based models representing human actors (see
696 Synes et al., 2018) being of considerable utility in understanding and managing the spatio-
697 temporal dynamics of potential human-wildlife conflicts.

698 In a global context, planning of large carnivore reintroductions fundamentally needs to
699 consider how individuals will disperse through a complex landscape and how this drives the
700 spread of a colonising population. This requires modelling of dispersal as a complex, multi-
701 phased process such that the realised distances travelled by dispersers becomes a function

702 of their behavioural rules, the landscape structure and also the structure of the current
703 population. Notably, while recent theory has highlighted how the incorporation of moderate
704 complexity in the modelling of individual dispersal can result in strikingly different population
705 spread dynamics across complex landscapes (Bocedi et al. 2014b), this approach has very
706 rarely been taken in applied ecological studies. Thus, the modelling approach demonstrated
707 here, which uses RangeShifter to incorporate explicitly the three phases of dispersal,
708 including a mechanistic representation of individual movements across spatially
709 heterogeneous landscapes, can provide an indispensable tool for delivering more spatially
710 realistic and species-specific predictions of landscape suitability and reintroduction viability,
711 especially for large carnivores.

712 **Conflicts of Interest**

713 The authors have no actual or potential conflicts of interest to declare.

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