

## A family of process-based models to simulate landscape use by multiple taxa

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50 **Abstract**

51

52 Context.

53 Land-use change is one of the primary drivers of biodiversity loss. There is an urgent need for models  
54 that accurately predict how biodiversity might be affected by land-use changes, to help avoid further  
55 negative impacts and inform landscape-scale restoration projects. In order to be effective, such  
56 models must represent the different habitat and connectivity requirements of multiple species.

57

58 Objectives.

59 We explored the extent to which process-based modelling might fulfil this role, examining feasibility  
60 for different taxa and potential for informing real-world decision-making.

61

62 Methods.

63 We developed a family of process-based models (\*4pop) that simulate landscape use by birds, bats,  
64 reptiles and amphibians, derived from the well-established poll4pop model (designed to simulate  
65 bee populations). Given landcover data, the models predict spatially-explicit relative abundance by  
66 simulating optimal home-range foraging, reproduction, dispersal of offspring and mortality. The  
67 models were co-developed by researchers, conservation NGOs and volunteer surveyors,  
68 parameterised with a combination of literature data and expert opinion, and validated against  
69 observational datasets collected across Great Britain.

70

71 Results.

72 The models were able to simulate habitat specialists, generalists, and species requiring access to  
73 multiple habitats for different types of resources (e.g. breeding vs foraging). We identified model  
74 refinements required for some taxa and considerations for modelling further species/groups.

75

76 Conclusions.

77 We suggest process-based models that integrate multiple forms of knowledge can assist  
78 biodiversity-inclusive decision-making by predicting habitat use throughout the year, expanding the  
79 range of species that can be modelled, and enabling decision-makers to better account for landscape  
80 context and habitat configuration effects on population persistence.

81

82

83

84 **Keywords:** process-based modelling, biodiversity, foraging, dispersal, population dynamics, land-use  
85 change.

86

87 **1. Introduction**

88

89 Human-driven land-use changes have caused habitat loss, fragmentation, degradation and  
90 homogenisation, leading in turn to biodiversity declines (Newbold et al. 2019). Reversing these  
91 declines and restoring ecosystems requires transformative change – not only in the way we use land  
92 (Leclère et al. 2020) but also in the way we represent and account for the needs of other species  
93 when we make land use decisions.

94

95 Enabling decision-makers to better take the needs of non-human species into account requires  
96 models and tools that can predict how species may be affected by proposed land-use changes. Such  
97 models must realistically reflect species' responses to landscape composition and configuration,  
98 over spatio-temporal scales that are relevant to both species and decision-makers. Many models are  
99 available for relating species occurrence or abundance to landscape properties. These range from  
100 process-based models, which use mechanistic understanding to simulate ecological processes, to  
101 pattern-based models, which use correlative methods to relate observed species  
102 occurrence/abundance to environmental variables (Zurell et al. 2022).

103

104 Process-based models that simulate underlying processes are expected to have greater predictive  
105 power than pattern-based models in novel situations (Dormann et al. 2012), making them  
106 potentially more suitable for exploring consequences of proposed land-use changes. Many are  
107 explicitly designed to account for the joint effects of landscape composition and configuration (e.g.  
108 Bocedi et al. 2021) and they have greater flexibility to produce outputs at the spatio-temporal scales  
109 most relevant to species and decision-makers. This is because they don't have to aggregate to  
110 coarser resolution to control for observational biases, in contrast to most correlative models derived  
111 directly from species observations (e.g. Boyd et al. 2023). Finally, some process-based models can  
112 integrate multiple forms of data (Zipkin & Saunders 2018), which can broaden the range of the  
113 species that can be modelled. For instance, for some species, there may be insufficient species  
114 records (either in terms of quantity or spatial coverage) to derive reliable correlative associations but  
115 a combination of discrete field measurements and expert opinion assessments may be available to  
116 parameterise a process-based model. Importantly, this combination of input data types also  
117 increases their ability to represent the needs of species with seasonal or life-cycle variation in  
118 habitat use. Species-landcover correlations will not always be sensitive to species' habitat use  
119 outside of the season/situations when species observations are typically collected. For example,  
120 amphibians are typically surveyed in aquatic breeding habitats but may spend the non-breeding  
121 season in terrestrial habitats, while bird and reptile surveys may likewise focus on times of peak  
122 detectability during which habitat use may differ from usage at other times. Expert opinion and  
123 other knowledge sources may provide this information and can potentially be integrated into a  
124 process-based simulation.

125

126 Modelling complex processes typically results in large numbers of parameters that must be set,  
127 calibrated or estimated. Highly detailed Individual-Based Models (IBM) are popular in ecology and  
128 involve tracking many individuals over potentially complex landscapes. This is computationally  
129 demanding and time consuming, especially if multiple scenarios are to be explored and/or large  
130 extents are to be modelled. While increases in computing power can help to offset these issues, they  
131 do constrain the utility of IBMs for large-scale landscape decision-making (Isaac et al 2018),  
132 especially if the aim is simply to get population-level predictions.

133

134 Population-level, rather than individual-level, process-based models offer a potential compromise  
135 between representing ecological processes and retaining the ability to model sufficiently large  
136 spatial extents, at fine enough spatial resolution, to be relevant to landscape decision-makers.  
137 Poll4pop (Gardner et al. 2020; Häussler et al. 2017) is an example of such an intermediate-

138 complexity (i.e. population-level), process-based model. Instead of tracking the status and explicit  
139 movement paths/decisions of individuals, it simulates how multiple individuals might ultimately be  
140 distributed, given their general movement process (e.g. optimal foraging). Designed to simulate the  
141 central-place foraging, population growth and dispersal processes of bees, poll4pop has been used  
142 to explore the national-scale consequences of fine-scale land-use decisions on bumblebee and  
143 solitary bee population size and distributions in the UK, accounting for the importance of habitat  
144 configuration for these mobile species (Image et al. 2022).

145  
146 A key advantage of this model is that it simulates both intergenerational dispersal behaviour and  
147 day-to-day foraging behaviour. This sets it apart from other process-based models (e.g. Rangeshifter;  
148 Bocedi et al. 2021) and most connectivity-focused tools (e.g. Condatis; Hodgson et al. 2012), which  
149 focus on the intergenerational connectivity needed for meta-population dynamics and climate-  
150 induced range shifting. Yet, the optimum habitat configuration for facilitating such large-scale  
151 dispersal movements can be very different to the optimum configuration for satisfying the day-to-  
152 day connectivity requirements necessary for local population persistence (Hodgson et al. 2011).  
153 Therefore, models that account for both are likely needed for supporting in-situ nature recovery.

154  
155 The poll4pop model accounts for this small-scale, within-home-range connectivity by rating  
156 landcovers according to their relative provision of different types of resource (nesting vs foraging;  
157 see Gardner et al. 2020), allowing for seasonal variation in resource provision/use. The productivity  
158 of any given nest then depends on the amount of foraging resources that can be gathered from  
159 surrounding landcovers, ensuring sensitivity to the configuration of nesting and foraging resources  
160 on small scales (while a separate dispersal process accounts for longer-range inter-generational  
161 connectivity between nest site locations). In doing so, the model steps away from traditional island  
162 biogeographic ideas of discrete habitat patches within an inhospitable matrix (MacArthur & Wilson  
163 1967) that are central to much spatial modelling in ecology and admits more flexible  
164 conceptualisations (Betts et al. 2014), where the actual combination of landcovers used and  
165 'inhabited' by a species may vary according to preference, availability and accessibility (given the  
166 species' movement range) in any given landscape. Instead of identifying a species' habitat with a  
167 landcover type, the model enables users to simulate how the 'utilised habitat' of a species in a given  
168 situation may be a bespoke combination of landcovers determined by the species'  
169 needs/preferences and the relative availability/accessibility of landcovers meeting those needs  
170 within the landscape. The poll4pop modelling approach therefore has potential to represent  
171 landscape use by a wide range of different species, including habitat specialists, generalists and  
172 those that use different habitats for different purposes or at different times. However, to date, the  
173 approach has only been used to simulate landscape use by bees.

174  
175 In this study, we explore the potential to adapt the model to simulate other taxa of conservation  
176 concern. We develop adaptations for birds, bats, reptiles and amphibians and validate their  
177 predictions against species observations. Our aim is to test whether the model framework can  
178 simulate species with diverse ecologies. We also test species-level versus guild-level  
179 parameterisations of the bird model to determine when it is necessary to model individual species  
180 versus groupings of similar species when extending the model framework. Finally, we discuss the  
181 extent to which the extended \*4pop approach might fill a key gap in biodiversity-inclusive landscape  
182 decision-making.

183

184 **2. Methods**

185

186 Modelling and data analysis was carried out using R version 4.2.0 (R Core Team 2022) with QGIS  
187 used for additional spatial data processing (QGIS Development Team, 2022).

188

189 All the \*4pop models require an input landcover map in raster format – we first describe the  
190 generation of this driving landcover data, followed by the model development, parameterisation and  
191 validation approaches.

192

193 We use the UK as our study area for model development due to availability of detailed spatial and  
194 validation datasets.

195

196

197 **2.1 Landcover data**

198

199 We generate a base landcover map for Great Britain by combining the UKCEH Landcover Map  
200 (Morton et al. 2020) and crop map (Land Cover Plus: Crops; Upcott et al. 2023) for the year 2019 and  
201 overlaying the locations of priority habitats given in the Natural England Priority Habitat Inventory  
202 (Natural England 2014), followed by urban green spaces from OS Open Greenspace Map, surface  
203 water features from OS Open Rivers and OS District Map, multi-carriageway roads from OS Open  
204 Roads, and railways from OS District Map (Ordnance Survey 2022). In addition, we separate semi-  
205 natural grasslands and heathlands into upland (>300m) and lowland sub-categories using the OS  
206 Terrain 50 dataset (Ordnance Survey 2022). Table S7 details how the landcover classification systems  
207 of these datasets are aligned with the landcover classification system for which the models are  
208 parameterised. This combined vector dataset is then rasterised with 10x10m pixel resolution.

209

210 The models can also ingest information on landcovers that occupy only a fraction of a pixel  
211 (additional ‘edge features’), where the widths of these features are input parameters. We therefore  
212 generate edge feature rasters denoting the presence/absence of the following ecologically  
213 important features: woodland edges, woody linear features (e.g. hedgerows), arable field margins,  
214 single carriageway roads, waterbody margins and watercourses (see Table S8 for details).

215

216

217 **2.2 Original model structure designed to simulate bees (poll4pop)**

218

219 Poll4pop (Gardner et al. 2020; Häussler et al 2017) is a process-based model that simulates the  
220 central-place foraging, population growth and dispersal processes of bees. It predicts spatially  
221 explicit, seasonally-resolved bee abundance and foraging activity for a given rasterised landscape. It  
222 can be run using parameters that represent an individual bee species or (more frequently) a ‘guild’  
223 of bees with similar behaviour. Gardner et al. (2020) parameterised and validated poll4pop for four  
224 UK bee guilds: ground-nesting bumblebees, tree-nesting bumblebees, ground-nesting solitary bees  
225 and cavity-nesting solitary bees.

226

227 The model allows for the fact the modelled guild may preferentially nest in certain habitats while  
228 preferring to forage in others; each landcover therefore has separate parameters representing its  
229 attractiveness as a nesting resource and its attractiveness as a foraging resource, for each guild. This  
230 parameterisation makes the model highly suitable for adaptation to other taxa that use different  
231 habitats for different purposes (e.g. breeding vs foraging). A **resource mapping function** uses these

232 parameters to convert the input landscape into separate maps representing the distribution of  
233 nesting resources and the distribution of foraging resources (seasonally resolved, as needed).

234

235 The model initially seeds nests (i.e. reproductive females) in the landscape according to the  
236 distribution of nesting resources. A **foraging function** distributes foragers from all the nests across  
237 the foraging resources, assuming foragers spend more time in proximate and better-quality foraging  
238 areas. This is done by convolving the number of foragers at each nest site location with the  
239 distribution of foraging resources, using an attractiveness-weighted distance-decay kernel defined  
240 by the input foraging distance. This step calculates the foraging rate to each pixel in the landscape  
241 and the number of foraging resources gathered by each nest.

242

243 If simulating short-lived solitary bees, there is foraging by the reproductive female only, during a  
244 single foraging season. The three-season approach used for longer-lived, colony-nesting bees is  
245 described in the supplementary material.

246

247 A **growth function** relates the number of bees produced by each nest to the amount of foraging  
248 resources gathered, so enabling amount/accessibility of foraging resources to influence population  
249 size.

250

251 The new reproductive females produced by each nest are dispersed across the landscape. This is  
252 done by convolving the number of dispersers at each nest site location with the distribution of  
253 nesting resources, using an attractiveness-weighted distance-decay kernel defined by the input  
254 dispersal distance. Availability of nesting resources limits the number of new reproductive females  
255 that survive to found their own nests the following year. This **dispersal function** enables availability  
256 of nesting resources and metapopulation dynamics to influence population sizes/distributions.

257

258 The model iterates over multiple successive years until the steady-state population size for the  
259 landscape is reached.

260

261

## 262 2.3 Adapting model structure to simulate other taxa (\*4pop model family)

263

264 We used the core functions from poll4pop (resource mapping function, foraging/dispersal functions  
265 and population growth function) to build adaptations of the model for other taxa: birds, bats,  
266 reptiles and amphibians, chosen to represent a variety of taxa of conservation concern. This involved  
267 redefining the central place (e.g. as a basking site in rept4pop) and movement timescales (e.g.  
268 foraging movements around the nest during the breeding season are represented in bird4pop,  
269 whereas longer-timescale seasonal foraging movements around a breeding pond are represented in  
270 amph4pop).

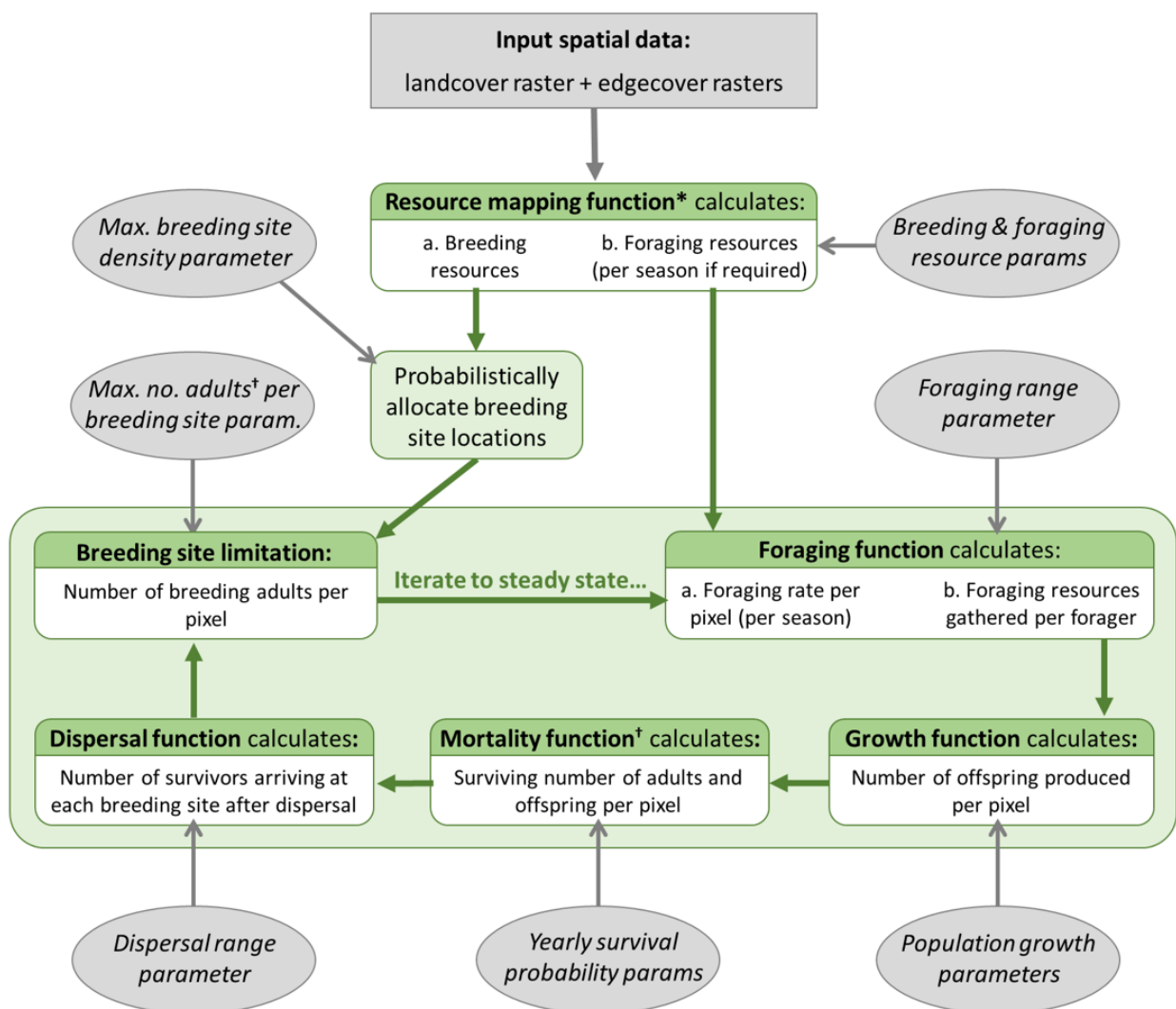
271

272 Probabilistic yearly survival was also introduced to account for these taxa, unlike bees, living for  
273 multiple years. This gives the models increased sensitivity to species' minimum resource  
274 requirements (equivalent to 'minimum area requirements' when modelling a habitat specialist). If  
275 there is only a small amount of forage-rich landcover within foraging range, this limits the amount of  
276 foraging resources a forager can gather and therefore the amount of offspring they produce. If the  
277 rate of offspring production falls below the yearly mortality rate, the population will die out locally  
278 and that particular patch of otherwise 'suitable' habitat will be unoccupied.

279

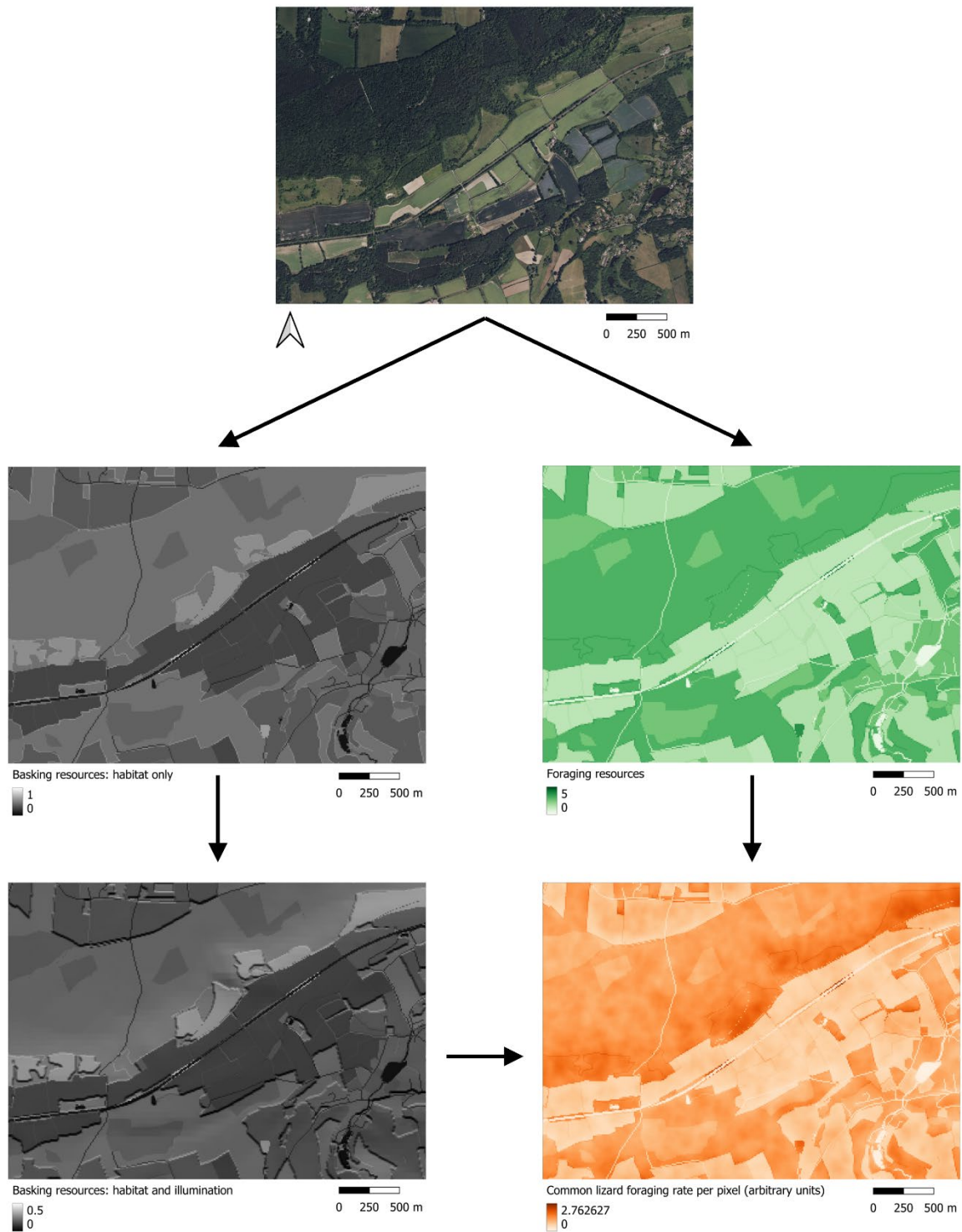
280 For reptiles, we also incorporated the effects of habitat shading (Fig. 2) by multiplying the landcover-  
 281 based basking site availability scores by the mean level of solar illumination received by each pixel.  
 282 For amphibians, we included the effects road mortality (Fig. 3), since this can limit access to foraging  
 283 habitat (Eigenbrod et al. 2008) and our validation dataset is specifically associated with amphibian  
 284 road crossings (see Section 2.4). This was done by multiplying the predicted foraging distribution  
 285 without road mortality by the cumulative probability of amphibians successfully reaching pixels  
 286 occurring beyond roads, based on their expected traffic levels. This reduces the number of  
 287 amphibians returning to breed within the model's iterations towards steady state.

288  
 289 Fig. 1 summarises the basic model structure. Table 1 summarises the adaptations made for each  
 290 taxon, with full descriptions of each adaptation given in the supplementary material. All models are  
 291 written in R and freely available (Gardner et al. 2023).  
 292



293  
 294 Fig. 1. Schematic of generic \*4pop model structure that was adapted for each taxon, showing its  
 295 simulation of two movement scales (foraging and dispersal) plus probabilistic age-dependent  
 296 survival, and its ability to separately account for effects of breeding resource limitation and foraging  
 297 resource limitation on population size. Asterisk and dagger indicate where additions/alterations are  
 298 made within rept4pop and amph4pop respectively (see supplementary material). The raster outputs  
 299 of the model are described in white boxes beneath the functions that generate them.

300



302  
 303 *Fig. 2. Schematic illustrating how common lizard foraging rates predicted by rept4pop are a function*  
 304 *of availability of foraging and basking resources in the landscape, where the basking resources are in*  
 305 *turn a function of both the habitats present and the level of solar illumination of those habitats. Note*  
 306 *the inverted scale for the basking resource maps to ensure darker areas in the bottom left panel*  
 307 *indicate more shading and/or less suitable landcover for basking activity. Example landscape is*  
 308 *located within Surrey, UK.*



Table 1. Summary of \*4pop model adaptations.

Model	Taxon	Central place	Foraging by	Foraging timescale	Offspring production dependent on	Dispersal of offspring	Inter-year survival	Parameterised for
poll4pop	bees	nest	reproductive females (and workers, if social)	seasonally resolved: - early spring - late spring - summer	<ul style="list-style-type: none"> <li>foraging resources gathered</li> <li>max. bee production parameter</li> </ul>	yes	<ul style="list-style-type: none"> <li>none for existing reproductive females</li> <li>nest site limitation for new reproductive female offspring</li> </ul>	<ul style="list-style-type: none"> <li>ground-nesting bumblebees</li> <li>tree-nesting bumblebees</li> <li>ground-nesting solitary bees</li> <li>cavity-nesting solitary bees</li> </ul>
bird4pop	nidicolous birds	nest	breeding pairs	breeding season	<ul style="list-style-type: none"> <li>foraging resources gathered</li> <li>max. no. of chicks per year</li> </ul>	yes	<ul style="list-style-type: none"> <li>probabilistic survival of adults and offspring</li> <li>nest site limitation</li> </ul>	<ul style="list-style-type: none"> <li>woodland specialists</li> <li>woodland generalists</li> <li>edge-nesting farmland passerines</li> <li>nuthatch</li> <li>robin</li> <li>yellowhammer</li> <li>skylark</li> </ul>
bat4pop	bats	maternity roost	breeding females	breeding season	<ul style="list-style-type: none"> <li>foraging resources gathered</li> <li>assumes max. one pup per female</li> </ul>	no <sup>1</sup>	<ul style="list-style-type: none"> <li>probabilistic survival of adults and offspring</li> <li>roost site and roost size limitation</li> </ul>	common pipistrelle

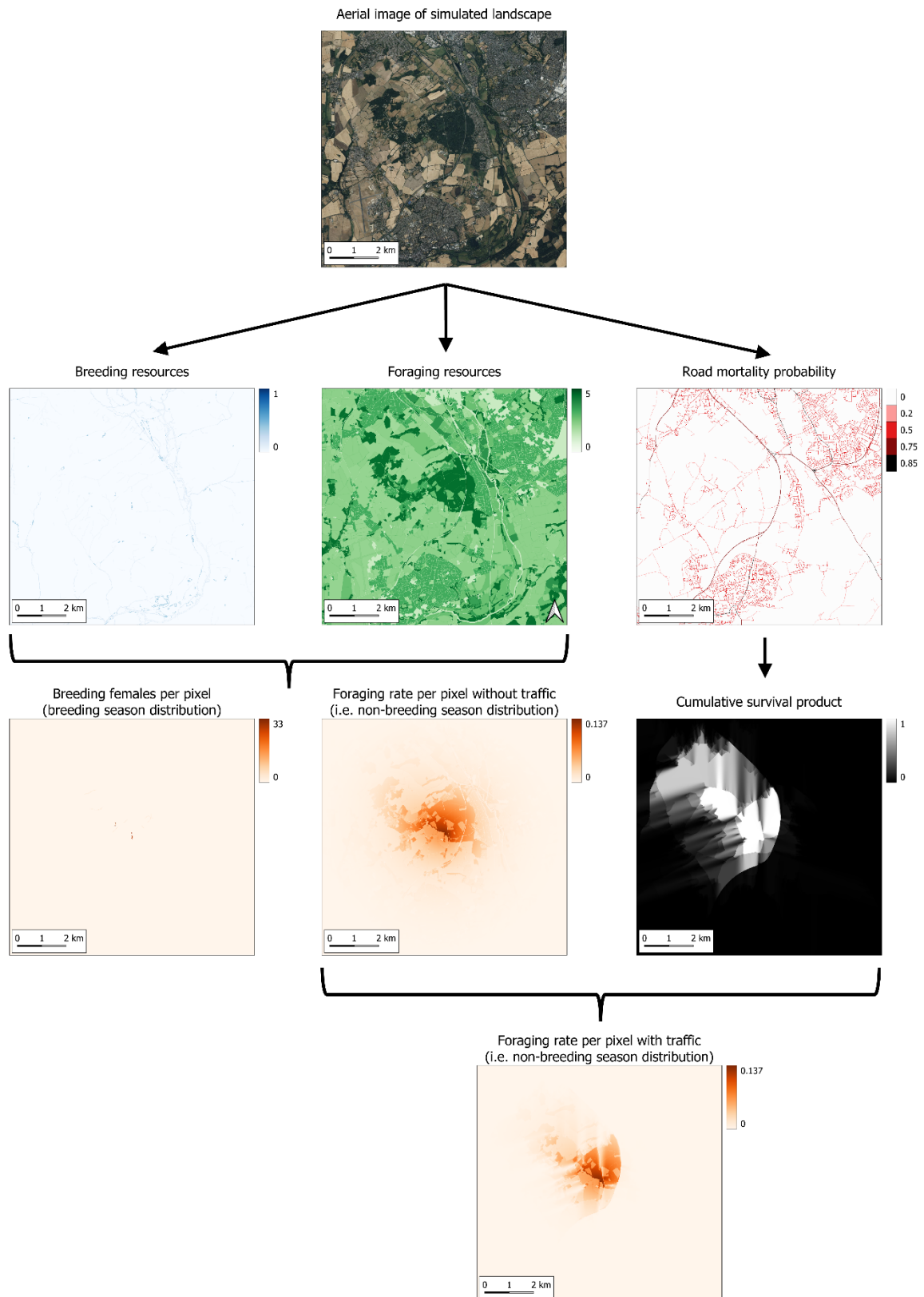
rept4pop	site-faithful reptiles	basking site <i>(accounting for habitat shading)</i>	breeding females	active season	<ul style="list-style-type: none"> <li>• foraging resources gathered</li> <li>• max. clutch size</li> </ul>	yes	<ul style="list-style-type: none"> <li>• probabilistic survival of adults and offspring</li> <li>• basking site limitation</li> </ul>	common lizard
amph4pop	amphibians	breeding pond	breeding females	active season	<ul style="list-style-type: none"> <li>• foraging resources gathered</li> <li>• max. clutch size</li> <li>• max. tadpole density</li> </ul>	yes	<ul style="list-style-type: none"> <li>• probabilistic survival of adults and offspring</li> <li>• road mortality</li> </ul>	common toad

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310 <sup>1</sup>due to high female philopatry shown by bats (Fornůsková et al. 2014).

311

312



313  
 314 *Fig. 3. Schematic illustrating how incorporating road mortality curtails the toad foraging distributions*  
 315 *output by amph4pop. Example landscape is located within Oxfordshire, UK.*  
 316

317  
 318

## 319 2.4 Model parameterisation

320

321 Bird4pop was parameterised for three guilds of birds, representing groups with similar habitat  
322 preferences: woodland specialists, woodland generalists and edge-nesting farmland passerines. It  
323 was also parameterised for four individual species: nuthatch (*Sitta europaea*), robin (*Erithacus*  
324 *rubecula*) and yellowhammer (*Emberiza citrinella*), chosen as widespread representative species for  
325 the three guilds, respectively, and skylark (*Alauda arvensis*), chosen as an example of an open-  
326 nesting farmland passerine. Bat4pop was parameterised for common pipistrelle (*Pipistrellus*  
327 *pipistrellus*), being a widespread bat species with the largest structured observational dataset  
328 available for validation (see Section 2.5.2). Rept4pop was parameterised for common lizard (*Zootoca*  
329 *vivipara*), chosen to represent a widespread reptile with limited mobility, while Amph4pop was  
330 parameterised for common toad (*Bufo bufo*), since, of the UK's widespread amphibians, this is the  
331 most terrestrial (Sinsch 1988).

332

333 An expert opinion questionnaire (n=4 experts; see supplementary material) was used to set the  
334 nesting and foraging resource parameters per landcover type used by bird4pop for each bird guild  
335 (the same parameters were also used for the representative species) and for skylark. Expert opinion  
336 was chosen because we required estimates of resource provision for distinct uses (nesting vs  
337 foraging etc., rather than general habitat associations) and robustness could be introduced by  
338 combining the judgements of multiple experts, each integrating their own literature knowledge and  
339 field experience of our specific mapped habitat categories. Similar expert opinion questionnaires  
340 were used to set the roosting and foraging resource parameters used in bat4pop (n=3 experts), the  
341 basking and foraging resource parameters used in rept4pop (n=10 experts), and the breeding and  
342 foraging resource parameters used in amph4pop (n=10 experts). Within each questionnaire, the  
343 experts rated 77 landcover types (based on those available in the input mapping data and  
344 distinctions considered to be ecologically meaningful for the modelled taxa) on an integer scale from  
345 0 = 'not used/no resources' to 5= 'very high resource provision' and rated how certain they were of  
346 their answers on similar 6-point scale from 'no confidence' to 'high confidence'. We then calculated  
347 the mean resource scores per landcover type across all experts, weighted by their certainty scores,  
348 following the procedure described in Gardner et al. (2020). Copies of the questionnaires are  
349 provided in Supplementary Material and final parameter values are given in Tables S2-S5.

350

351 Movement ranges, productivity and survival parameter values were based on available literature  
352 data, with abundance-weighted mean values calculated for the bird guilds (Table 2; Table 3).  
353 Population growth parameters regulate the conversion of arbitrary forage units gathered into  
354 offspring production and were set to reproduce observed responses to habitat fragmentation  
355 (Hinsley et al. 1996) in the case of bird4pop (Fig. S1) and the observed range of roost sizes (Mathews  
356 et al. 2018) in the case of bat4pop (Fig. S2). Due to lack of equivalent calibration datasets, we chose  
357 the population growth parameters that produced the maximum  $R^2$  in the model-data fit for  
358 rept4pop (see Section 2.5.3; Fig. S3), and the maximum possible number of validation sites (see  
359 Section 2.5.4) with steady-state non-zero population sizes when including road mortality effects for  
360 amph4pop (Fig.S4).

361

362

363 *Table 2. Movement ranges, population growth and survival parameters used in bat4pop, rept4pop and amph4pop models.*

Species	Parameter	Units	Value	Source
Common pipistrelle (bat4pop)	Foraging range	km	2	Bat Conservation Trust (2016)
	Maximum roost density	km <sup>-2</sup>	2.25	Value from Mathews et al. (2018) increased by order of magnitude to minimise spatial stochasticity in model predictions when comparing with (already highly stochastic) observational data.
	Maximum roost size	breeding females	80	Set to reproduce range of roost sizes given in Mathews et al. (2018); see Fig. S2.
	Adult survival probability		0.8	Sendor & Simon (2003)
	Juvenile survival probability		0.53	Sendor & Simon (2003)
	Growth parameter a		1.5	Set to reproduce range of roost sizes given in Mathews et al. (2018); see Fig. S2.
	Growth parameter b		3	Set b = 2a, following Häussler et al. (2017).
	Common lizard (rept4pop)	Foraging range	m	30
Dispersal range		m	60	Set to twice foraging range; Léna, Fraipont & Clobert (2000) classify dispersers as those moving >30m.
Maximum basking density		ha <sup>-1</sup>	625	Sorci, Clobert & Belichon (1996)
Adult survival probability			0.53	Sorci, Clobert & Belichon (1996)
Juvenile survival probability			0.2	Sorci, Clobert & Belichon (1996)
Maximum offspring per female			9	Inns (2009)
Growth parameter a			3.1	Set to value producing maximum R <sup>2</sup> in the model-data fit; see Fig. S3.
Growth parameter b			6.2	Set b = 2a, following Häussler et al. (2017).
Common toad (amph4pop)	Foraging range	m	1000	Typical mid-range value within wide range of measured values cited in Salazar et al. (2016).
	Maximum clutch size	eggs per female	1500	Banks & Beebee (1986); Gittins, Kennedy, & Williams (1984)

Maximum tadpole density	$m^{-2}$	38	Reading & Clarke (1999) measured a maximum of $\sim 1.3 \times 10^5$ tadpoles in 0.34 ha pond (i.e. 38 tadpoles $m^{-2}$ ) where there were suggestions of density dependence effects ( $b=0.819$ with 95% confidence limits 0.63-1.02 using Bartlett's three-group method test).
Fraction of tadpoles surviving to metamorphosis		0.1	based on Fig 4 in Reading & Clarke (1999)
Metamorph survival to breeding age probability		0.08	Reading (1991) marked 5158 metamorphs in 1984 and recorded 41 returning as breeding adults over the subsequent 6 year period (due to the unknown sex ratio of the metamorphs, we combine their data for both male and female returners and use the data from their earlier 1984 cohort only, as this reduces the number of surviving females omitted through not having matured enough to commence breeding before the end of their study period). This gives a metamorph survival fraction of 0.008. However, we find an order of magnitude increase on this is necessary to achieve sustainable populations across the majority of our validation sites when road traffic effects are included, hence we use a value of 0.08 in order to obtain foraging distributions for comparison with the observational data.
Adult female yearly survival probability		0.4	Gittins (1983)
Growth parameter a		0.01	Set to enable sustainable populations when traffic effects are included across maximum achievable number of validation sites (>80%); see Fig. S4.
Growth parameter b		0.02	Set $b = 2a$ , following Häussler et al. (2017).
Mortality probability on motorway		1.00	Set using Fig. 5 in Hels & Buchwald (2001) and 2020 statistics on motor vehicle flow (thousand vehicles per day) by road class from UK Department for Transport (2021).
Mortality probability on urban A road		0.85	As above
Mortality probability on rural A road		0.75	As above
Mortality probability on urban minor road		0.50	As above
Mortality probability on rural minor road		0.20	As above

364

365 *Table 3. Movement ranges, population growth and survival parameters used in bird4pop model. Survival probabilities and number of chicks produced per*  
 366 *year are derived from Robinson (2005), where chicks per year is calculated as the number of broods multiplied by the mean clutch size. Dispersal ranges are*  
 367 *taken from Paradis et al. (1998). Guild-level values are the abundance-weighted mean of the values for the constituent species listed in Table S6, weighted*  
 368 *by the number of breeding territories of each species nationally given in Robinson (2005). Maximum nest density is derived from data in Batten (1976; see*  
 369 *Supplementary Material for details). Foraging range and growth parameter a were set using Fig. 1 of Hinsley et al. (1996) and Fig. S1, with the same values*  
 370 *used for all guilds/species (to ensure proportionally equivalent forage units to chicks conversion rates and due to lack of species-specific breeding season*  
 371 *foraging range estimates for many species). Growth parameter b set to be twice the value of growth parameter a, following Häussler et al. (2017).*

Parameterisation	Growth param a	Growth param b	Foraging range (m)	Dispersal range (m)	Maximum nest density (ha <sup>-1</sup> )	Chicks produced per year	Adult survival probability	Juvenile survival probability
Woodland Specialist	0.2	0.4	250	10000 ± 2000	5	12 ± 1	0.45 ± 0.02	0.13 ± 0.06
Woodland Generalist	0.2	0.4	250	5800 ± 800	5	9.2 ± 0.8	0.47 ± 0.04	0.40 ± 0.04
Farmland Passerine	0.2	0.4	250	9000 ± 2000	5	9.2 ± 0.8	0.41 ± 0.04	0.38 ± 0.06
Skylark	0.2	0.4	250	6000 ± 4000	5	8.73 ± 0.04	0.513 ± 0.024	0.513 ± 0.024
Nuthatch	0.2	0.4	250	7000 ± 2000	5	6.66 ± 0.05	0.51	0.51
Robin	0.2	0.4	250	6000 ± 1000	5	9.74 ± 0.03	0.419 ± 0.014	0.41
Yellowhammer	0.2	0.4	250	8000 ± 3000	5	6.88 ± 0.03	0.536 ± 0.028	0.529

372

373 2.5 Model validation

374

375 Table 4 summarises the observational datasets and statistical tests used for model validation, with  
376 full methodological details given in the supplementary material. Wherever possible, we used  
377 standardised, systematically collected datasets that allowed for control of observational biases.  
378 Since our mapping data relates predominantly to the year 2019, data was restricted to ~5 year  
379 period to enable averaging over year-to-year variation while minimising the effects of land-use  
380 changes and long-term abundance trends.

381

382 Bird4pop and bat4pop were both validated against national recording scheme data collected by  
383 volunteers for the British Trust for Ornithology and the Bat Conservation Trust, respectively. To test  
384 the model's ability to reproduce context-dependent habitat use, we also investigated whether the  
385 yellowhammer parameterisation of bird4pop could reproduce the interaction observed by Robinson  
386 et al. (2001), who found that yellowhammer abundance depends more strongly on area of arable  
387 habitat in pasture-dominated landscapes than in arable-dominated landscapes.

388

389 Rept4pop's common lizard foraging rate predictions were compared to observational data collected  
390 in Surrey, UK, since national-level recording schemes for reptiles are still under development in GB  
391 and this county currently holds the largest and most detailed digitised datasets from long-term  
392 standardised reptile surveys, collected by members of Surrey Amphibian and Reptile Group (SARG).  
393 Volunteer surveyors enter their data into SARG's online ARGWEB system, which includes the facility  
394 for surveyors to record exact sighting locations. Consequently, validation was carried out at two  
395 spatial scales, testing the model's ability to reproduce variations in relative abundance between sites  
396 as well as its ability to predict the exact locations of lizard sightings within sites.

397

398 No comparable measures of common toad abundance across multiple sites were available to  
399 validate amph4pop's relative abundance predictions. Instead, we attempted to validate the model's  
400 predictions for common toad habitat use. The Toads on Roads Project, run by Froglife, supports a  
401 network of volunteer Toad Patrols, who assist toads across roads to reduce road mortality during the  
402 spring migration from terrestrial habitats to aquatic breeding habitats. We sent a questionnaire to  
403 Froglife's Toad Patrols in May 2021 to collect information on which types of terrestrial habitats  
404 migrating toads were observed to be travelling from and their breeding locations. We then used  
405 amph4pop to simulate the foraging distributions (i.e. the predicted spatial distribution of foraging  
406 rates) of these breeding populations. We ranked habitats from those that were predicted to be most  
407 used to those predicted to be least used across all the sites and compared this to the relative habitat  
408 usage reported by the patrols (see supplementary material for details).

409



410 *Table 4. Observational datasets and statistical tests used for \*4pop model validation. See supplementary material for a full description of data preparation*  
 411 *and validation methodologies.*

Model	Observational dataset(s)	Spatial coverage	Temporal coverage	n	Statistical test
bird4pop	British Trust for Ornithology's Breeding Bird Survey	GB	2016-2020	4874 1km survey squares	<p>Generalised linear model with a Poisson error distribution of the form:</p> $\ln(A_i) = \beta_0 + \beta_1 B_i$ <p>where:  <math>A_i</math> = mean relative abundance in survey square <math>i</math> during the 5 year period, rounded to nearest integer  <math>B_i</math> = mean number of breeding pairs per pixel predicted within survey square <math>i</math> by bird4pop  <math>\beta_x</math> = fitted coefficients, where a statistically significant positive value of <math>\beta_1</math> indicates successful validation.</p>
bird4pop	Robinson et al. (2001)	GB	-	4874 1km squares	<p>Linear model with a Gaussian error distribution of the form:</p> $B_i = \beta_0 + (\beta_{1,G1}, \beta_{1,G2}, \beta_{1,G3}) G C_i$ <p>where:  <math>B_i</math> = mean number of breeding pairs of yellowhammers predicted within BBS square <math>i</math> by bird4pop  <math>C_i</math> = arable area within the BBS square (units = 1000ha)  <math>G</math> = the group (factor) that the 33x33km tile surrounding the BBS square is assigned to, where groups are based on the arable:grass ratio (R) within the 33x33km tile and group 1 tiles have <math>R &lt; 0.5</math> (representing grassland-dominated landscapes), group 2 have <math>0.5 \leq R &lt; 2.5</math> (mixed), group 3 have <math>R \geq 2.5</math> (arable-dominated)  <math>\beta_x</math> = fitted coefficients, where <math>\beta_{1,x}</math> interaction terms consistent with those found by Robinson et al. (2001) indicate successful validation.</p>

bat4pop	Bat Conservation Trust's National Bat Monitoring Programme Field Survey	GB	2016-2020	401 1km survey squares; 1778 surveys	<p>Generalised linear model with a Poisson error distribution of the form:</p> $\ln(A_i) = \beta_0 + \beta_1 F_i + \beta_2 S_i + \beta_3 T_i + \beta_4 C_i + \beta_5 W_i + \beta_6 R_i + \beta_7 S_i + \beta_8 E_i + \beta_9 D_i$ <p>where:</p> <p><math>A_i</math> = total number of common pipistrelle passes (a measure of bat activity) across all spots surveyed on visit <math>i</math> to a given survey square</p> <p><math>F_i</math> = mean common pipistrelle foraging rate per pixel predicted within the survey square by bat4pop</p> <p><math>S_i</math> = number of spots surveyed on visit <math>i</math></p> <p><math>T_i</math> = temperature (units = degrees Celsius)</p> <p><math>C_i</math> = cloud cover (factor)</p> <p><math>W_i</math> = wind strength (factor)</p> <p><math>R_i</math> = rainfall (factor)</p> <p><math>S_i</math> = volunteer skill level (factor)</p> <p><math>E_i</math> = volunteer experience levels (factor)</p> <p><math>D_i</math> = detector type (factor)</p> <p><math>\beta_x</math> = fitted coefficients, where a statistically significant positive value of <math>\beta_x</math> indicates successful validation.</p>
rept4pop	Surrey Amphibian and Reptile Group's Long-term reptile monitoring dataset	Surrey, England	2016-2021	83 sites; 1311 surveys	<p>Generalised linear model with a Poisson error distribution of the form:</p> $\ln(A_i/t_i) = \beta_0 + \beta_1 F_i + \beta_2 T_i + \beta_3 H_i + \beta_4 Y_i + \beta_5 D_i + \beta_6 D_i^2 + \beta_7 D_i^3 + \beta_8 S$ <p>where:</p> <p><math>A_i</math> = total number of adult common lizards recorded on survey <math>i</math></p> <p><math>t_i</math> = survey duration (units = minutes)</p> <p><math>F_i</math> = mean common lizard foraging rate per pixel within a 750m buffer of survey site centroid, as predicted by rept4pop</p> <p><math>T_i</math> = air temperature during survey (units = degrees Celsius)</p> <p><math>H_i</math> = relative humidity during survey</p> <p><math>Y_i</math> = year survey was conducted</p> <p><math>D_i</math> = the day of the year (where D=1 for 1<sup>st</sup> Jan)</p> <p><math>S</math> = surveyor skill level</p>

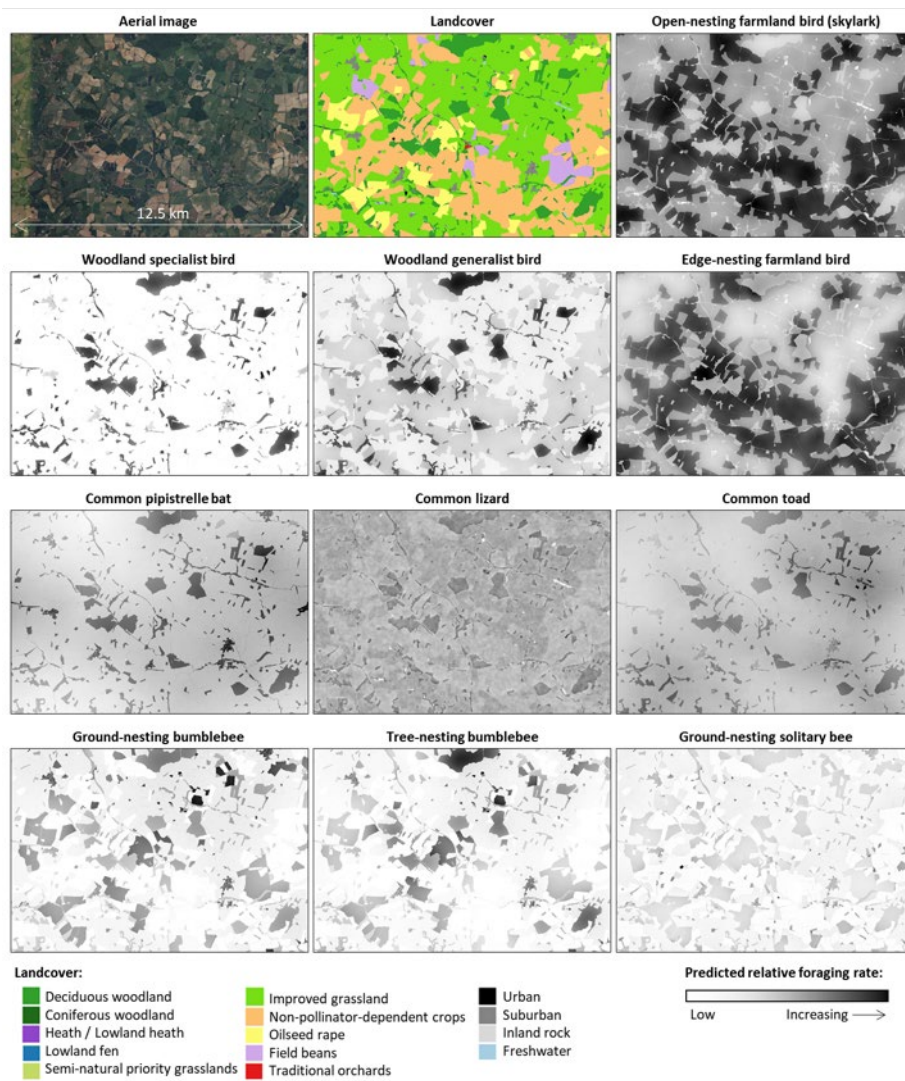
$\beta_x$  = fitted coefficients, where a statistically significant positive value of  $\beta_i$  indicates successful validation.

rept4pop	Surrey Amphibian and Reptile Group's Long-term reptile monitoring dataset	Surrey, England	2016-2021	1971 sightings across 62 sites	Wilcoxon rank sum test to compare the median predicted foraging rate at exact sighting locations (excluding those associated with refugia) with the median predicted foraging rate at random locations within a 750m buffer of survey site centroid, where a statistically significant higher median at sighting locations indicates successful validation.
amph4pop	Toad patroller responses to 'Your toads and their habitats' questionnaire	GB	2021	70 toad crossings	Spearman's rank test to compare observed habitat usage rankings with amph4pop's predicted habitat usage rankings and with habitat usage rankings based solely on the mean percentage area of each habitat available within 10x10km around the validation sites. A stronger correlation with amph4pop's predictions than with simple habitat availability indicates successful validation.

412

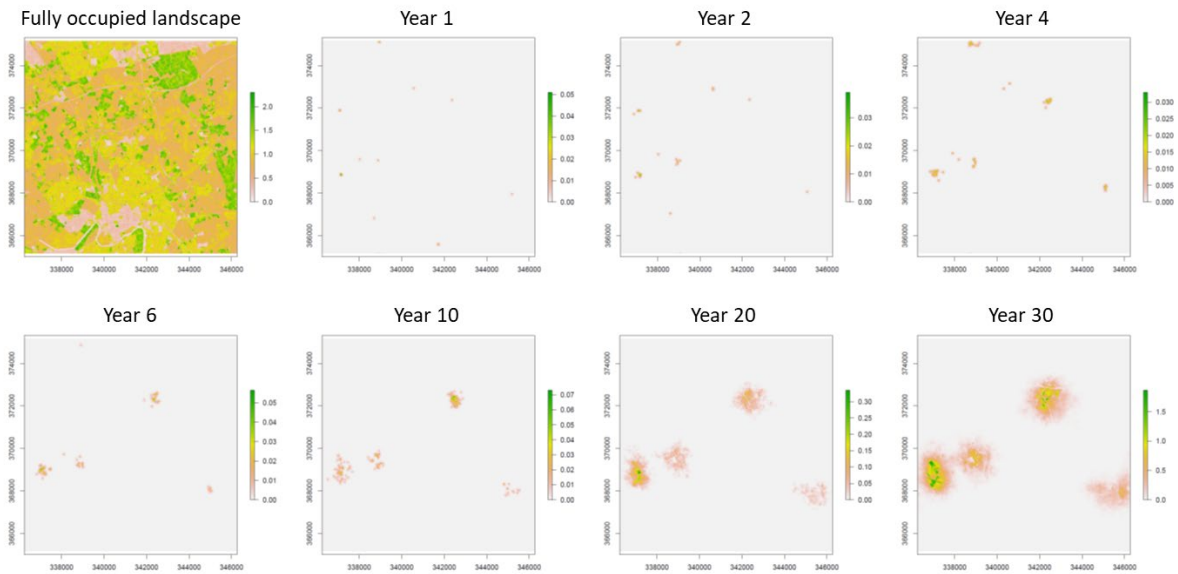
413

414 **3. Results**  
 415



416  
 417 *Fig. 4. Foraging rate predictions output by \*4pop models (poll4pop, bird4pop, bat4pop, rept4pop and*  
 418 *amph4pop) for a single agricultural landscape. Simulations were run at 10x10m resolution. Foraging*  
 419 *rate units are arbitrary, with scales individual to each panel and shades therefore not comparable*  
 420 *between taxa. Note that the landcover map shown has grouped some landcovers for ease of*  
 421 *visualisation and does not show the fine-scale edge habitats (e.g. hedgerows, field margins) also*  
 422 *input into the models. Example landscape is located on Leicestershire/Rutland border, UK.*  
 423

424 Fig. 4 shows the fully parameterised \*4pop models run on a single example landscape,  
 425 demonstrating their ability to illustrate fine-scale habitat use by species with different ecologies. The  
 426 dynamic nature of the models is shown in fig. 5, which uses an underoccupied landscape to illustrate  
 427 the foraging, population growth and dispersal processes underpinning the predictions.  
 428



429  
 430 *Fig. 5. Rept4pop simulations demonstrating the dynamic spatio-temporal behaviour of the models.*  
 431 *First panel shows predicted distribution of common lizard foraging activity within a 10x10km*  
 432 *landscape that is fully occupied and subsequent panels show the ability of common lizard to disperse*  
 433 *and recolonise the landscape over time if reduced to just ten randomly chosen populations in year 1.*  
 434 *Local resource availability and inherent stochasticity in the model result in loss of some of these*  
 435 *remnant populations while others expand. From year 30 onwards, the rescue effect of*  
 436 *metapopulations results in more stable growth and population expansion. Within this simulation, the*  
 437 *lizards' foraging and dispersal kernels are 30m and 60m, respectively.*

438  
 439  
 440 Bird4pop's predicted number of breeding pairs within the BBS survey squares showed a significant  
 441 positive relationship with the surveyors' counts and this was the case for all guilds and species  
 442 parameterised (Table 5). The model-data fit for the woodland specialist guild showed the highest  $R^2$   
 443 and the (edge-nesting) farmland passerine guild the lowest. The  $R^2$  was generally higher for the  
 444 single-species parameterisations than the guild-level parameterisations (compare woodland  
 445 generalist vs robin; farmland passerine vs yellowhammer), except for the woodland specialist guild  
 446 (cf. nuthatch).

447  
 448 The yellowhammer relative abundance predictions showed a positive association with area of  
 449 arable, whose slope was significantly steeper for more arable dominated landscapes (Table 6).  
 450 Repeating the analysis with model predictions from an alternative parameterisation  
 451 (Yellowhammer\_n; Table 6), where the yellowhammer nesting resource score was replaced with  
 452 zero for all landcovers except for arable field margins and hedgerows, produced a context-  
 453 dependent trend that becomes significantly less steep as the wider landscape transitions to arable-  
 454 dominated, in better agreement with observations (Robinson et al. 2001). This alternative  
 455 parameterisation still showed a significant positive relationship with the surveyors' counts across the  
 456 BBS squares but with lower  $R^2$  (Table 5).

457  
 458 Bat4pop's common pipistrelle foraging activity predictions showed a significant positive relationship  
 459 with the total number of common pipistrelle passes recorded by surveyors, although the  $R^2$  for the  
 460 model-data fit was low (Table 5).

461

462 Rept4pop’s common lizard foraging rate predictions showed a significant positive relationship with  
 463 the total number of adult lizards recorded by surveyors (Table 5). The median predicted number of  
 464 foraging lizards across the sighting locations was also significantly higher than the median predicted  
 465 number of foraging lizards across the randomly selected locations within the 750m survey site buffer  
 466 zones (Wilcoxon rank sum test;  $W = 2847391$ ;  $P < 0.001$ ; Fig. 6).

467

468 *Table 5. Relationships between model predictions (m) and observed counts (c) of relative abundance*  
 469 *or activity for those taxa fitted with a functional relationship of the form  $\ln c \propto \beta_1 \ln m$ . See methods*  
 470 *section for details of taxa-specific control variables.*

Model	Parameterisation	Coefficient ( $\beta_1$ )	Standard error	P value	R <sup>2</sup>
bird4pop	Woodland specialist	93.2	0.9	<0.001	0.365
	Woodland generalist	36.5	0.3	<0.001	0.165
	Farmland passerine	15.8	0.8	<0.001	0.010
	Nuthatch	94	2	<0.001	0.192
	Robin	49.1	0.7	<0.001	0.205
	Yellowhammer	102	2	<0.001	0.154
	Yellowhammer_n	1420	40	<0.001	0.059
	Skylark	71.3	0.8	<0.001	0.284
bat4pop	Common pipistrelle	6	2	<0.01	0.102
rept4pop	Common lizard	0.69	0.03	<0.001	0.183

471

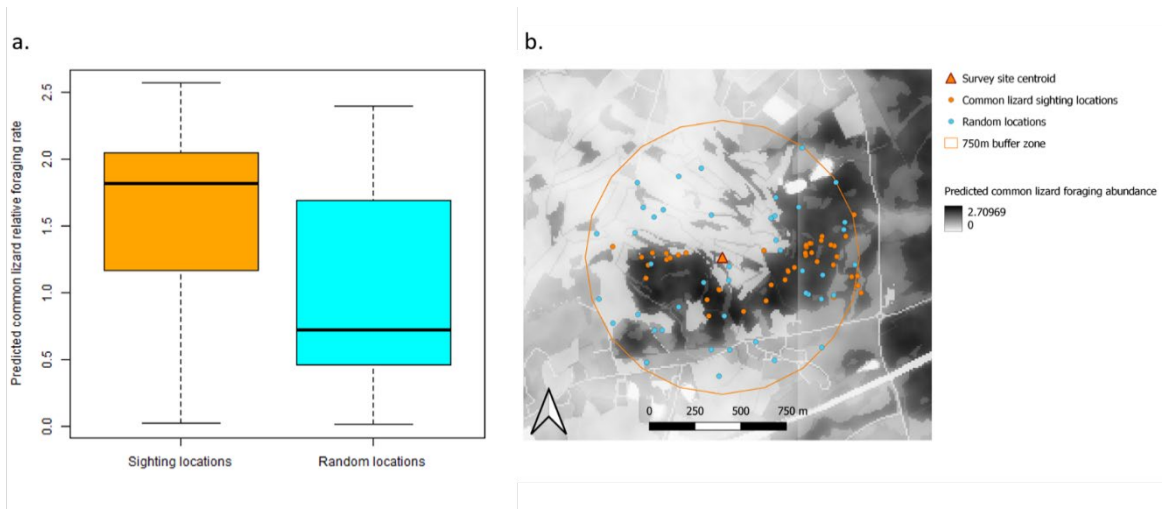
472 *Table 6. Results from regressing mean number of breeding yellowhammer pairs predicted by*  
 473 *bird4pop in each 1km BBS square ( $B_i$ ) against the arable area within the BBS square ( $C_i$ ; units =*  
 474 *1000ha), allowing an interaction with the arable:grass ratio group ( $G$ ) of the 33x33km tile within*  
 475 *which the BBS square falls, i.e. from fitting  $B_i = \beta_0 + (\beta_{1,G1}, \beta_{1,G2}, \beta_{1,G3})GC_i$  assuming a Gaussian error*  
 476 *distribution. Results are shown for the original yellowhammer model parameterisation and for a*  
 477 *second parameterisation (Yellowhammer\_n), where yellowhammer nesting resource score is*  
 478 *replaced with zero for all landcovers except for arable field margins and hedgerows. All  $\beta_{1,G1}$  are*  
 479 *significantly different from zero ( $P < 0.001$ ) and all  $\beta_{1,G2}$  and  $\beta_{1,G3}$  coefficients are significantly different*  
 480 *from their corresponding  $\beta_{1,G1}$  coefficient ( $P < 0.001$ ).*

Parameterisation	$\beta_{1,G1}$	$\beta_{1,G2}$	$\beta_{1,G3}$	R <sup>2</sup>
Yellowhammer	$(9.3 \pm 0.5) \times 10^{-2}$	$(14.8 \pm 0.8) \times 10^{-2}$	$(16.0 \pm 0.9) \times 10^{-2}$	0.464
Yellowhammer_n	$(5.6 \pm 0.2) \times 10^{-3}$	$(2.5 \pm 0.4) \times 10^{-3}$	$(1.1 \pm 0.5) \times 10^{-3}$	0.208

481

482 Amph4pop’s predicted habitat-use rankings showed a significant positive correlation with the  
 483 observed habitat-use rankings derived from the Toad Patrols’ questionnaire responses (Table 7).  
 484 These correlations were stronger than correlations between the observed habitat-use rankings and  
 485 rankings based solely on the mean percentage area of each habitat available within the 10x10km  
 486 validation landscapes (Table 7). For the subset of sites that sustained common toad populations  
 487 after road mortality effects were included in the simulations, including these limitations on habitat  
 488 accessibility due to presence of roads further strengthened the correlation between observed and  
 489 predicted habitat-use rankings (Table 7).

490



491  
 492 *Fig. 6. a) Distribution of rept4pop’s predicted common lizard foraging rates (arbitrary units) at*  
 493 *common lizard sighting locations recorded by surveyors during visits to SARG’s long-term reptile*  
 494 *survey sites compared to its predicted common lizard foraging rates at a matched sample of random*  
 495 *locations within 750m of the survey site centroids. b) Map of one survey site illustrating its sighting*  
 496 *locations and randomly selected locations superimposed over rept4pop’s common lizard foraging*  
 497 *rate predictions.*

498

499 *Table 7. Spearman’s  $\rho$  values for correlations between observed habitat-use rankings derived from*  
 500 *the Toad Patrols’ questionnaire responses and habitat-use rankings predicted by amph4pop, as well*  
 501 *as habitat rankings based on the mean percentage area of each habitat available within the*  
 502 *10x10km validation landscapes. Results are shown using data from all sites and for an analysis*  
 503 *restricted to data from only those sites showing non-zero toad population predictions when road*  
 504 *mortality effects are included. All correlations are statistically significant at  $P < 0.01$ .*

Observed habitat-use rankings	N	Landscape-level habitat availability rankings	Predicted habitat-use rankings	
			Omitting road mortality effects	Including road mortality effects
All sites	70	0.785	0.840	-
Non-zero population sites when including road mortality	58	0.738	0.793	0.815

505

506 **4. Discussion**

507

508 4.1 Validation

509

510 The validation results suggest that the general form and conceptualisation of the \*4pop model  
511 family is relevant for a wide range of species. All models' predictions showed positive relationships  
512 with the observational data, although  $R^2$  values were generally low. This emphasises the continued  
513 need for complementary, field-based, ecological surveys before any on-the-ground land-use  
514 decisions are actually made. It's likely that process-based models will always struggle to match the  
515 evaluation metrics of SDMs, which are by definition fitted to the data, because the act of simulating  
516 (often plastic) foraging/population processes adds additional noise. However, good evaluation  
517 metrics when matching to current/present-day observational datasets are not always indicative of  
518 good predictive power in novel/future situations (Irturbide et al. 2018; Warren et al. 2020),  
519 suggesting that modelling these ecological processes and compromising on predictive power over  
520 current data may be acceptable if achieving greater predictive confidence in unfamiliar future  
521 scenarios is the aim. What is considered sufficient predictive power will likely vary according to the  
522 decision-maker and the situation, and it is unlikely (and generally inadvisable) for decisions to be  
523 made based on model predictions alone. Importantly, we have shown these models have the  
524 potential to make ecologically meaningful predictions, which could be used to inform discussions  
525 within a decision-making process that also integrates information from other sources.

526

527 Our explorations demonstrate there are multiple opportunities to test the realism of process-based  
528 models. We validated their species activity predictions at different spatial scales (1km, 750m and  
529 species presence at 1m resolution; Table 5; Fig. 6), checked their ability to reproduce context-  
530 dependent interactions derived from statistical model fits to observational data (Table 6) and  
531 quantified their ability to reproduce observed habitat preferences of species (Table 7). We also  
532 ensured the models reproduced observed distributions of roost sizes and minimum area responses  
533 to habitat fragmentation (Fig. S1; Fig. S2). These additional checks help assess performance of the  
534 models' underlying processes and we suggest those developing process-based models could be  
535 imaginative in finding multiple approaches to validate their functionality.

536

537 Our model validations made much use of widespread systematic monitoring data collected by  
538 volunteers, since this offers large numbers of geolocated measurements of relative  
539 abundance/activity collected using a systematic survey methodology (to minimise noise from  
540 observational biases) in a wide variety of landcover types and contexts (to maximise measurement  
541 range and leverage) across a large spatial extent (to increase applicability). The fine resolution of  
542 \*4pop model outputs gave flexibility to resample predictions to match the spatial extent of the  
543 observational sampling units used across different schemes. However, more intensive field study  
544 data (from mark-recapture, radio-tracking and other detailed studies, as appropriate for each taxon)  
545 was used in model parameterisation (see Tables 2 & 3). This emphasises that, although models may  
546 provide a powerful tool, there is a continued need to support large-scale monitoring and detailed  
547 field/experimental studies in order to obtain the observational measurements necessary to underpin  
548 this modelling.

549

550 4.2 Species-level versus guild-level approaches

551

552 We compared species-level versions of the bird models with guild-level versions, which collectively  
553 model a group of species with similar life histories, habitat usage and movement ranges. The guild-



554 level parameterisation outperformed the species-level parameterisation for woodland specialists,  
555 but not for farmland passerines.

556

557 Woodland specialist species (not only of birds but also of other taxa e.g. bats) often depend on the  
558 presence of specific woodland vegetation structures (Hewson et al. 2011), which are generally not  
559 mapped, making it difficult to accurately predict the observed abundance of an individual woodland  
560 specialist species, but easier to predict the observed abundance of woodland specialists as a group.  
561 For this guild, grouping averages over these individual species peculiarities to produce a guild-level  
562 response that aligns better with the coarser habitat distinctions present in the spatial input data. For  
563 the farmland guild, the poorly/un-mapped effects of farmland management practices are likely  
564 being confounded with the varied needs of this smaller guild (Vickery et al. 2004; Baker et al. 2012)  
565 such that aggregating to guild level only increases variability.

566

567 Comparing bird4pop's woodland specialist and woodland generalist parameterisations (Table 5)  
568 shows that the activity patterns of stricter habitat specialists (whose broad habitat types are  
569 reasonably well mapped) are more easily reproduced than those of more flexible species. This may  
570 be due to a number of factors: i. a generalist may utilise small patches of habitat (e.g. isolated  
571 shrubs) that may not appear in remote-sensed mapping data and/or may not even be considered by  
572 human observers to be 'habitat' (Franklin et al. 2009); ii. the more generalist the species is, the more  
573 likely the locations utilised in reality will be due to some small positive difference of one habitat  
574 patch over another that again will not appear in mapping data (e.g. Petrovan et al. 2013); iii.  
575 opportunistic generalist species may show large plasticity in foraging processes (e.g. Guerrero-  
576 Sanchez et al. 2022; Ceia et al. 2014); iv. although generalists as a group use a greater range of  
577 habitats, each individual species may use a different subset of habitats (Hinsley et al. 1995; Fuller et  
578 al. 2001), such that the group as a whole is less homogeneous and therefore harder to predict  
579 accurately (Chetcuti et al. 2019). The generalist behaviour of common pipistrelle may therefore be a  
580 contributing factor to the relatively low  $R^2$  for the bat4pop model.

581

#### 582 4.3 Supporting biodiversity-inclusive landscape decision-making

583

584 Mobile species that require access to multiple habitat types are often not well catered for by  
585 decision-making approaches that fail to take into account habitat configurations and species'  
586 movement ranges (e.g. habitat accounting; Gardner et al. 2022). In contrast, our model adaptations  
587 show poll4pop's highly flexible framework can represent multi-habitat use over a wide range of taxa,  
588 spatial and temporal scales. From originally simulating seasonally-resolved short-range foraging of  
589 bees around their nests and longer-range dispersal of their reproductives to new nest sites, we have  
590 adapted the model to simulate analogous behaviour by birds, with probabilistic yearly survival  
591 included for these longer lived species. Other adaptations simulate the home range behaviour of  
592 lizards, core activity zones of bats resulting from separation of roosting and foraging habitat and the  
593 seasonally distinct distributions of amphibians due to migration from aquatic to terrestrial habitats.  
594 This enables the models to identify situations where population sizes may be limited by availability  
595 of one particular resource despite ample supply of another. For example, they indicate the changing  
596 relationship between yellowhammer abundance and arable cover can be explained by populations  
597 being forage resource limited in pasture-dominated landscapes and nest site limited in arable-  
598 dominated landscapes. Their outputs could therefore help decision-makers take on board the  
599 requirements of multiple taxa and ensure proposed landscape changes do not cause imbalances that  
600 force landscapes into a resource-limited state for any particular species (Pöysä & Pöysä 2002;  
601 Desaegher et al. 2021).

602

603 SDMs are already being used to value locations for supporting species within decision-making (e.g.  
604 via biodiversity credit schemes; Simpson et al. 2021), but these correlative models are often driven  
605 by observational data collected when the species is most detectable and may not capture species-  
606 habitat associations outside of the peak survey period. If these other habitats are essential for  
607 population persistence, then the species may still be lost, despite data-driven efforts to conserve  
608 habitat with which it is associated (Runge et al. 2014). Process-based models that simulate habitat  
609 use throughout the year, integrating expert knowledge of behaviour outside traditional survey  
610 seasons where needed, could help to avoid such inadvertent negative outcomes. For instance,  
611 amph4pop predicts breeding season activity levels in aquatic habitats, where this taxon is most  
612 commonly surveyed, as well as patterns of terrestrial habitat use during the non-breeding season  
613 (Fig. 3). The original poll4pop model is temporally resolved into three seasons each able to show a  
614 different pattern of habitat use, and other adaptations, such as bird4pop, could be easily extended  
615 to simulate non-breeding season habitat use in addition to the breeding season habitat-use  
616 simulated here, as required.

617

618 Sedentary species in particular often show patchy underoccupancy of habitat due to local extinctions  
619 and inability to recolonise (Dorrough & Ash 1999). Fig 5 shows how simulations can be run where  
620 only some suitable habitat patches are initially seeded and the population processes run over  
621 multiple years to probabilistically assess the species' ability to (re)colonise other areas. This  
622 functionality could enable decision-makers to move away from assumptions that habitat presence  
623 equals species presence and help estimate potential success of landscape-scale restoration plans  
624 (Brudvig & Catano 2021) for species with different habitat preferences and dispersal abilities.

625

626 Within the original poll4pop model, straight-line travel paths are implicitly assumed and there are no  
627 barriers to movement. The amph4pop adaptation introduced road mortality effects, since roads  
628 represent significant barriers for amphibians (Beebee 2013), and this improved agreement with  
629 observed toad habitat use (Table 7). This suggests incorporating barrier effects into the framework is  
630 worthwhile and possible, but further work is needed to implement this without significantly  
631 increasing run times. Likewise, making the models sensitive to availability of commuting habitat (as  
632 distinct from foraging habitat) for species such as bats (Pinaud et al. 2018) may also be beneficial.  
633 Incorporating other key factors (e.g. artificial lighting effects, hibernation site/winter food limitation  
634 etc.) could be done using existing functionality and would increase the models' ability to represent  
635 species' interests in decision-making.

636

637 A key challenge when building any biodiversity models is discrepancies between the habitat  
638 distinctions available in (usually remote-sensed) input landcover data and habitat distinctions of  
639 relevance to the modelled species. The \*4pop models can account for small-scale habitat features  
640 (see §2.1) and be parameterised for a finely-graded habitat classification system (§2.4) to capture  
641 the needs of species and of decision-makers investigating future scenarios. However, their  
642 operationalisation in the present day (and the set of species to which they can be confidently  
643 applied) may be limited in practice by the coarser spatial and thematic resolution of current  
644 landcover datasets (Betts et al. 2014). This is particularly problematic if poorly detected, small or  
645 ephemeral habitat features are essential resources for seeding populations in the digitised landscape  
646 but missing from input landcover data. Incorporating on-the-ground survey information, structural  
647 descriptors from LiDAR data and future advances in very high resolution remote-sensing may help to  
648 address this issue and increase predictive power (Bradter et al. 2020; Price et al. 2023).

649

650 Initial discussions and trials with UK decision-makers (those already supported by/collaborating with  
651 the model co-developers' various organisations) have highlighted a number of ways these models  
652 could be integrated into decision-making. Decisionmakers attempting to target, tailor and co-  
653 ordinate conservation efforts can contrast the species activity predictions with the maps of relative  
654 habitat resource provision to identify high activity areas to protect and examine why other areas lack  
655 species activity (e.g. through a deficit of one or more types of resources). Those trying to motivate  
656 conservation action locally can use before-and-after simulations to demonstrate the potential  
657 consequences of proposed habitat interventions (as in Gardner et al. 2021). Decisionmakers  
658 balancing confidence and risk across multiple outcomes can make use of multiple simulations to  
659 propagate uncertainty in underlying ecological parameters through to model outputs (as in Image et  
660 al. 2022). We have shown that the models can be run at national extent (Fig. S5) and still produce  
661 fine (10m) resolution outputs, with the influence of individual field-level and sub-field-level habitats  
662 clearly recognisable; this means that local, regional and national decisionmakers could all make use  
663 of the same model, potentially making it easier to co-ordinate planning and assessment of national  
664 policy and local action. The relative abundance predictions from the models could potentially help  
665 decisionmakers assess how proposed landscape changes might impact targets to improve not only  
666 biodiversity but also bioabundance (e.g. The Environmental Targets (Biodiversity) (England)  
667 Regulations 2023). Finally, the models can act as a discussion aid among groups of decisionmakers  
668 and offer an opportunity to share ecological knowledge: engaging with model outputs could help  
669 decision-makers gain a deeper understanding of how species are using landscapes, which may  
670 increase their ability to intuitively make biodiversity-inclusive decisions. Further work is now needed  
671 to systematically explore the models' utility for different types of decision-makers.

672

673

## 674 **5. Conclusions**

675

676 With increasing ambitions towards large-scale redesigns of landscapes, of directing human-centric  
677 development away from areas of value to biodiversity and of increasing habitat provision to reverse  
678 species declines, there is a pressing need for models that account for species' varied responses to  
679 landscape and that can estimate the potential biodiversity consequences of landscape changes. Such  
680 models must take a holistic view of landscape use across species' lifecycles and integrate movement  
681 ecology, so that effects of habitat context and configuration are incorporated and any discrepancies  
682 between the spatial scale of human decision-making and spatial scales of importance to species are  
683 highlighted. If models are to support effective conservation actions, we must also ensure that  
684 consideration of biodiversity is not inadvertently biased towards the needs of easily modelled or  
685 commonly studied species. We propose that the \*4pop framework fills a gap by offering a flexible,  
686 process-based modelling approach, adaptable to the needs of multiple species, that can integrate  
687 different forms of knowledge (data from field studies, expert opinion, citizen science and  
688 standardised monitoring, alongside landcover data) to help address these challenges.

689

690

## 691 **6. References**

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## 948 **7. Statements & Declarations**

949

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954

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956 manuscript. The bird (bird4pop), herptile (rept4pop & amph4pop) and bat (bat4pop) models were  
957 co-developed with RAR, AJ and KB, respectively. Authors RAR to JT-L contributed to model  
958 parameterisation and validation, and provided access to and guided interpretation of observational  
959 datasets. SP helped develop the traffic mortality function for amph4pop. Authors DB to BKT  
960 provided additional input, which influenced model development and assisted with exploration of the  
961 real-world utility of the models. Authors SA to IW provided expert opinion for model  
962 parameterisation. Authors JB to AM assisted with provision, gathering and interpretation of  
963 observational datasets. RP and JMB oversaw the project and provided advice throughout. All authors  
964 were involved in revising the manuscript.

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966 Data availability: All models are freely available from the Environmental Information Data Centre  
967 (Gardner et al. 2023). Observational datasets used for model validation are available on request  
968 from British Trust for Ornithology, Bat Conservation Trust, Amphibian and Reptile Groups of UK,  
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