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RESEARCH ARTICLE

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

**Emma Gardner · Robert A. Robinson · Angela Julian · Katherine Boughey · Steve Langham · Jenny Tse-Leon · Sergei Petrovskii · David J. Baker · Chloe Bellamy · Andrew Buxton · Samantha Franks · Chris Monk · Nicola Morris · Kirsty J. Park · Silviu Petrovan · Katie Pitt · Rachel Taylor · Rebecca K. Turner · Steven J. R. Allain · Val Bradley · Richard K. Broughton · Mandy Cartwright · Kevin Clarke · Jon Cranfield · Elisa Fuentes-Montemayor · Robert Gandola · Tony Gent · Shelley A. Hinsley · Thomas Madsen · Chris Reading · John W. Redhead · Sonia Reveley · John Wilkinson · Carol Williams · Ian Woodward · John Baker · Philip Briggs · Sheila Dyason · Steve Langton · Ashlea Mawby · Richard F. Pywell · James M. Bullock**

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**Abstract**

*Context* Land-use change is a key driver of biodiversity loss. Models that accurately predict how biodiversity might be affected by land-use changes are urgently needed, to help avoid further negative impacts and inform landscape-scale restoration projects. To be effective, such models must balance model realism with computational tractability and must represent the different habitat and connectivity requirements of multiple species.

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

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E. Gardner (✉) · R. K. Turner · R. K. Broughton · S. A. Hinsley · C. Reading · J. W. Redhead · R. F. Pywell · J. M. Bullock
UK Centre for Ecology and Hydrology, Benson Lane, Wallingford OX10 8BB, UK
e-mail: emmgar@ceh.ac.uk

R. A. Robinson · S. Franks · I. Woodward
British Trust for Ornithology, The Nunnery, Thetford, Norfolk IP24 2PU, UK

A. Julian · C. Monk · N. Morris · K. Pitt · K. Clarke · S. Dyason
Amphibian and Reptile Groups of UK (ARG UK), 82 Gidley Way, Horspath, Oxford OX33 1TG, UK

K. Boughey · S. Reveley · C. Williams · P. Briggs
Bat Conservation Trust, Quadrant House, 250 Kennington Lane, London SE11 5RD, UK

S. Langham
Surrey Amphibian and Reptile Group, 'Panorama' Folly Hill, Farnham, Surrey GU9 0BD, UK

J. Tse-Leon · S. Petrovan · A. Mawby
Froglife, Brightfield Business Hub, Bakewell Road, Orton Southgate, Peterborough PE2 6XU, UK

S. Petrovskii
School of Computing and Mathematical Sciences and Institute for Environmental Futures, University of Leicester, Leicester LE1 7RH, UK

D. J. Baker
Environment and Sustainability Institute, University of Exeter, Cornwall, UK

C. Bellamy
Forest Research, Northern Research Station, Midlothian, UK

A. Buxton · S. J. R. Allain
Durrell Institute of Conservation and Ecology, School of Anthropology and Conservation, University of Kent, Marlowe Building, Canterbury, Kent CT2 7NR, UK

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*Methods* We developed a family of process-based models (*4pop) that simulate landscape use by birds, bats, reptiles and amphibians, derived from the well-established poll4pop model (designed to simulate bee populations). Given landcover data, the models predict spatially-explicit relative abundance by simulating optimal home-range foraging, reproduction, dispersal of offspring and mortality. The models were co-developed by researchers, conservation NGOs and volunteer surveyors, parameterised using literature data and expert opinion, and validated against observational datasets collected across Great Britain.
*Results* The models were able to simulate habitat specialists, generalists, and species requiring access to multiple habitats for different types of resources (e.g. breeding vs foraging). We identified model refinements required for some taxa and considerations for modelling further species/groups.
*Conclusions* We suggest process-based models that integrate multiple forms of knowledge can assist biodiversity-inclusive decision-making by predicting habitat use throughout the year, expanding the range of species that can be modelled, and enabling decision-makers to better account for landscape context and habitat configuration effects on population persistence.

**Keywords** Process-based modelling · Biodiversity · Foraging · Dispersal · Population dynamics · Land-use change

## Introduction

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

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

Process-based models that simulate underlying processes are expected to have greater predictive power than pattern-based models in novel situations (Dormann et al. 2012), making them potentially more suitable for exploring consequences of proposed land-use changes. Many are explicitly designed to

A. Buxton · M. Cartwright · T. Gent · J. Wilkinson · J. Baker
Amphibian and Reptile Conservation Trust, 744 Christchurch Road, Boscombe, Bournemouth, Dorset BH7 6BZ, UK

K. J. Park · E. Fuentes-Montemayor
Biological and Environmental Sciences, Faculty of Natural Sciences, University of Stirling, Stirling, UK

S. Petrovan
Department of Zoology, Conservation Science Group, University of Cambridge, Cambridge, UK

R. Taylor
British Trust for Ornithology Cymru, Thoday Building, Deiniol Road, Bangor, Gwynedd LL57 2UW, UK

V. Bradley
Brecon and Radnor Amphibian and Reptile Group, Amphibian and Reptile Groups of UK (ARG UK), 82 Gidley Way, Horspath, Oxford OX33 1TG, UK

J. Cranfield
Herpetologic Ltd, 38 Nursery Road, New Alresford, Winchester, Hampshire SO24 9JR, UK

R. Gandola
Herpetological Society of Ireland, Wicklow, Ireland

T. Madsen
Centre for Integrative Ecology, School of Life and Environmental Sciences, Deakin University, Geelong, VIC, Australia

S. Langton
Hallgarth, Leavening, Malton, N Yorkshire YO17 9SA, UK

account for the joint effects of landscape composition and configuration (e.g. Bocedi et al. 2021) and they have greater flexibility to produce outputs at the spatio-temporal scales most relevant to species and decision-makers. This is because they don't have to aggregate to coarser resolution to control for observational biases, in contrast to most correlative models derived directly from species observations (e.g. Boyd et al. 2023). Finally, some process-based models can integrate multiple forms of data (Zipkin & Saunders 2018), which can broaden the range of species that can be modelled. For instance, for some species, there may be insufficient species records (either in terms of quantity or spatial coverage) to derive reliable correlative associations but a combination of discrete field measurements and expert opinion assessments may be available to parameterise a process-based model. Importantly, this combination of input data types also increases their ability to represent the needs of species with seasonal or life-cycle variation in habitat use. Species-landcover correlations will not always be sensitive to species' habitat use outside of the season/situations when species observations are typically collected. For example, amphibians are typically surveyed in aquatic breeding habitats but may spend the non-breeding season in terrestrial habitats, while bird and reptile surveys may likewise focus on times of peak detectability during which habitat use may differ from usage at other times. Expert opinion and other knowledge sources may provide this information and can potentially be integrated into a process-based simulation.

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

Population-level, rather than individual-level, process-based models offer a potential compromise between representing ecological processes and retaining the ability to model sufficiently large spatial extents, at fine enough spatial resolution, to be relevant to landscape decision-makers. Poll4pop (Häussler et al. 2017; Gardner et al. 2020) is an example of such an intermediate-complexity (i.e. population-level), process-based model. Instead of tracking the status and explicit movement paths/decisions of individuals, it simulates how multiple individuals might ultimately be distributed, given their general movement process (e.g. optimal foraging). Designed to simulate the central-place foraging, population growth and dispersal processes of bees, poll4pop has been used to explore the national-scale consequences of fine-scale land-use decisions on bumblebee and solitary bee population size and distributions in the UK, accounting for the importance of habitat configuration for these mobile species (Image et al. 2022).

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

The poll4pop model accounts for this small-scale, within-home-range connectivity by rating landcovers according to their relative provision of different types of resource (nesting vs foraging; see Gardner et al. 2020), allowing for seasonal variation in resource provision/use. The productivity of any given nest then depends on the amount of foraging resources that can be gathered from surrounding landcovers, ensuring sensitivity to the configuration of nesting and foraging resources on small scales (while a separate dispersal process accounts for longer-range inter-generational connectivity between nest site locations). In doing so, the model steps away from traditional island biogeographic ideas of discrete habitat patches within an inhospitable matrix (MacArthur & Wilson 1967) that are central to much spatial modelling in ecology and admits more flexible conceptualisations (Betts et al. 2014), where the actual combination of landcovers

used and 'inhabited' by a species may vary according to preference, availability and accessibility (given the species' movement range) in any given landscape. Instead of identifying a species' habitat with a landcover type, the model enables users to simulate how the 'utilised habitat' of a species in a given situation may be a bespoke combination of landcovers determined by the species' needs/preferences and the relative availability/accessibility of landcovers meeting those needs within the landscape. The poll4pop modelling approach therefore has potential to represent landscape use by a wide range of different species, including habitat specialists, generalists and those that use different habitats for different purposes or at different times. However, to date, the approach has only been used to simulate landscape use by bees.

In this study, we explore the potential to adapt the model to simulate other taxa of conservation concern. We develop adaptations for birds, bats, reptiles and amphibians and validate their predictions against species observations. Our aim is to test whether this model framework—shown to have potential to balance model realism and computational tractability to produce outputs relevant for decision-makers—can be extended to simulate species with diverse ecologies. We also test species-level versus guild-level parameterisations of the bird model to determine when it is necessary to model individual species versus groupings of similar species when extending the model framework. Finally, we discuss the extent to which the extended *4pop approach might fill a key gap in biodiversity-inclusive landscape decision-making.

## Methods

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

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

We use Great Britain as our study area for model development due to availability of detailed spatial and validation datasets.

### Landcover data

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

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

### Original model structure designed to simulate bees (poll4pop)

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

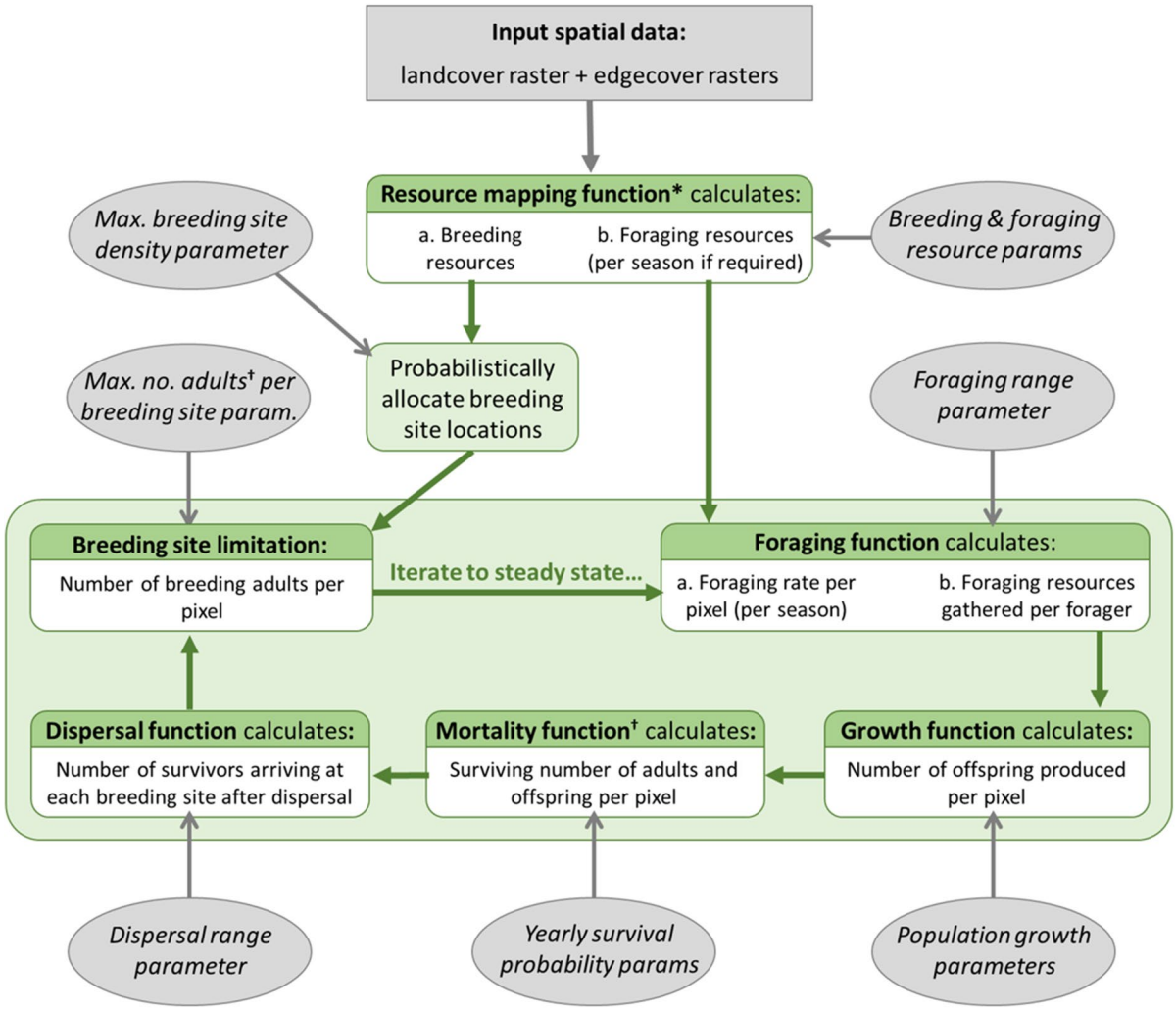
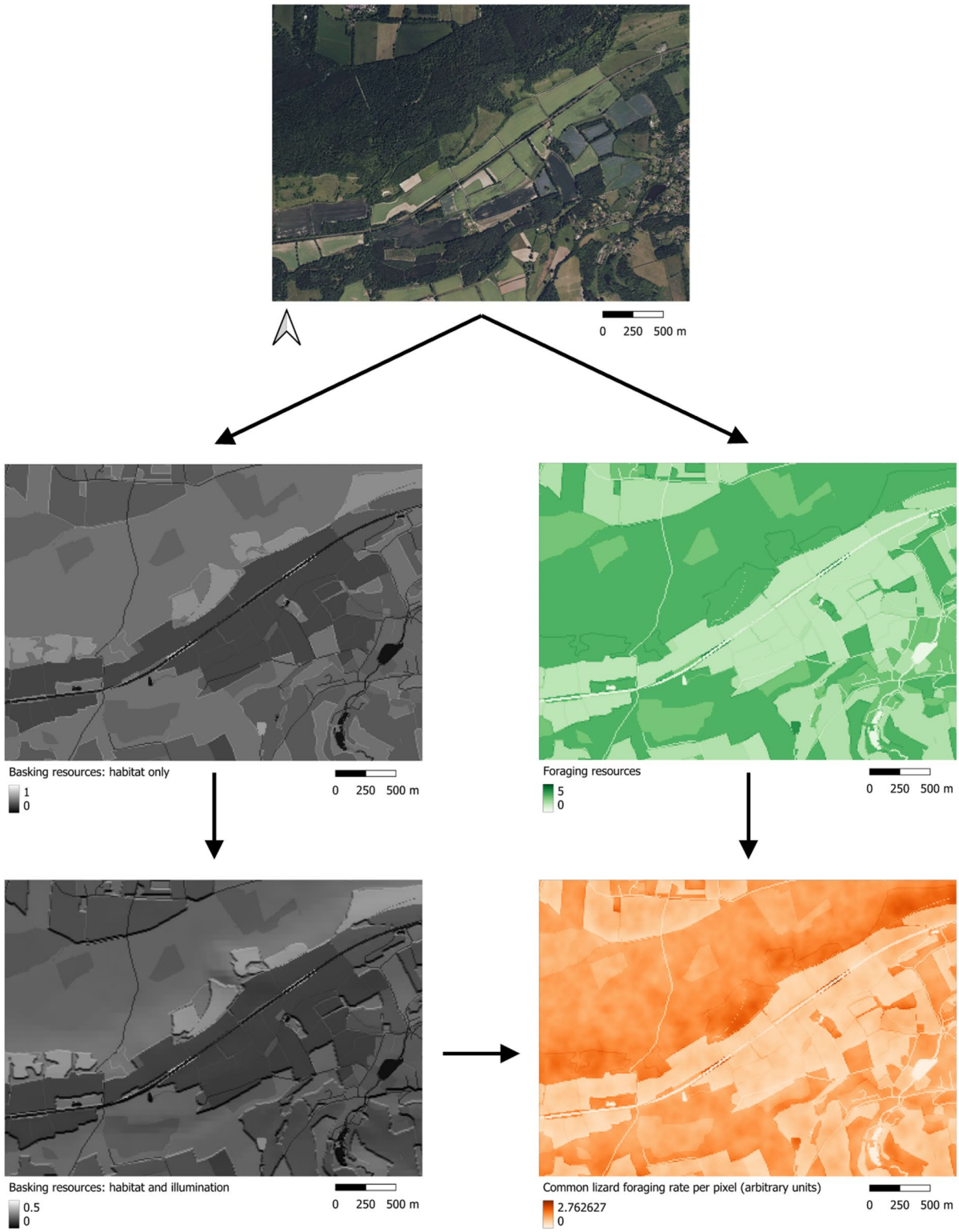



**Fig. 1** Schematic of generic *4pop model structure that was adapted for each taxon, showing its simulation of two movement scales (foraging and dispersal) plus probabilistic age-dependent survival, and its ability to separately account for effects of breeding resource limitation and foraging resource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

The model allows for the fact the modelled guild may preferentially nest in certain habitats while preferring to forage in others; each landcover therefore has separate parameters representing its attractiveness as a nesting resource and its attractiveness as a foraging resource, for each guild. This parameterisation makes the model highly suitable for adaptation to other taxa that use different habitats for different purposes (e.g. breeding vs foraging). A **resource mapping function** uses these parameters to convert the input landscape into separate maps representing the distribution of nesting resources and the distribution of foraging resources (seasonally resolved, as needed).

The model initially seeds nests (i.e. reproductive females) in the landscape according to the distribution of nesting resources. A **foraging function** distributes foragers from all the nests across the foraging resources, assuming foragers spend more time in proximate and better-quality foraging areas. This is done by convolving the number of foragers at each nest site location with the distribution of foraging


0 250 500 m
Basking resources: habitat only
1
0
0 250 500 m
Foraging resources
5
0
0 250 500 m
Basking resources: habitat and illumination
0.5
0
0 250 500 m
Common lizard foraging rate per pixel (arbitrary units)
2.762627
0
0 250 500 m

◂**Fig. 2** Schematic illustrating how common lizard foraging rates predicted by rept4pop are a function of availability of foraging and basking resources in the landscape, where the basking resources are in turn a function of both the landcovers present and the level of solar illumination of those landcovers. Note the inverted scale for the basking resource maps to ensure darker areas in the bottom left panel indicate more shading and/or less suitable landcover for basking activity. Aerial image obtained through QGIS from Microsoft's Bing Map Services. Example landscape is located within Surrey, UK

resources, using an attractiveness-weighted distance-decay kernel defined by the input foraging distance. This step calculates the foraging rate in each pixel in the landscape and the number of foraging resources gathered by each nest.

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

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

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

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

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

We used the core functions from poll4pop (resource mapping function, foraging/dispersal functions and population growth function) to build adaptations of the model for other taxa: birds, bats, reptiles and amphibians, chosen to represent a variety of taxa of conservation concern. This involved redefining the central place (e.g. as a basking site in rept4pop) and movement timescales (e.g. foraging movements around the nest during the breeding season are represented in bird4pop, whereas longer-timescale seasonal foraging movements around a breeding pond are represented in amph4pop). These decisions, along with decisions around which processes should be modelled, were the result of discussions between researchers, conservation NGOs and conservation volunteers with experience of the modelled taxa.

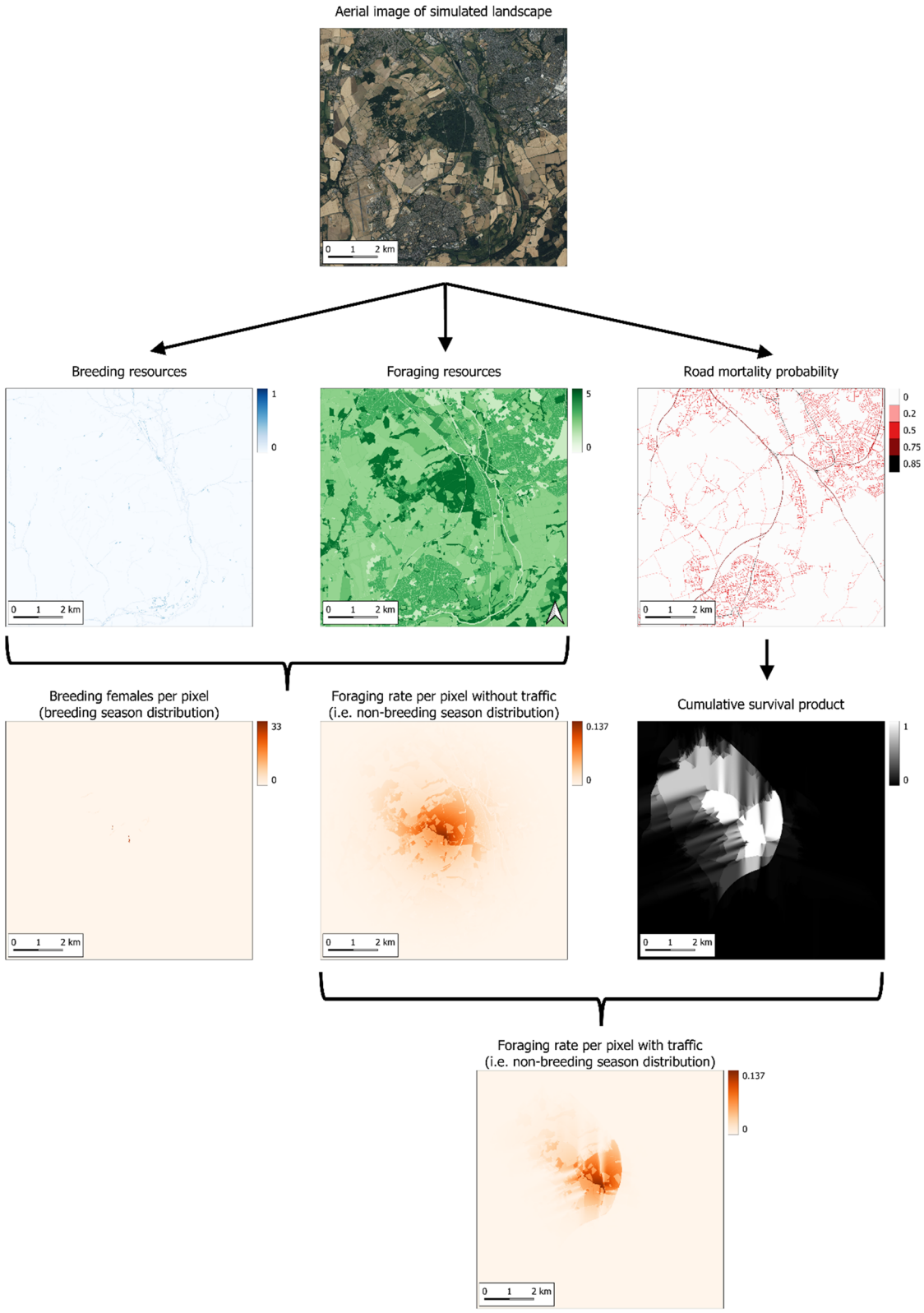
Probabilistic yearly survival was also introduced to account for these taxa, unlike bees, living for multiple years (Fig. 1). This gives the models increased sensitivity to species' minimum resource requirements (equivalent to 'minimum area requirements' when modelling a habitat specialist). If there is only a small amount of forage-rich landcover within foraging range, this limits the amount of foraging resources a forager can gather and therefore the amount of offspring they produce. If the rate of offspring production falls below the yearly mortality rate, the population will die out locally and that particular patch of otherwise 'suitable' habitat will be unoccupied.

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

Figure 1 summarises the basic model structure and Table 1 summarises the adaptations made for each taxon, with full descriptions of each adaptation given in the supplementary material. All models are written in R and freely available.

### Model parameterisation

Bird4pop was parameterised for three guilds of birds, representing groups with similar habitat preferences:


Aerial image of simulated landscape
0 1 2 km
Breeding resources
1
0
0 1 2 km
Foraging resources
5
0
0 1 2 km
Road mortality probability
0
0.2
0.5
0.75
0.85
0 1 2 km
Breeding females per pixel
(breeding season distribution)
33
0
0 1 2 km
Foraging rate per pixel without traffic
(i.e. non-breeding season distribution)
0.137
0
0 1 2 km
Cumulative survival product
1
0
0 1 2 km
Foraging rate per pixel with traffic
(i.e. non-breeding season distribution)
0.137
0
0 1 2 km

◂**Fig. 3** Schematic illustrating how incorporating road mortality curtails the toad foraging distributions output by amph4pop. Aerial image obtained through QGIS from Microsoft's Bing Map Services. Example landscape is located within Oxfordshire, UK

woodland specialists, woodland generalists and edge-nesting farmland passerines. It was also parameterised for four individual species: nuthatch (*Sitta europaea*), robin (*Erithacus rubecula*) and yellowhammer (*Emberiza citrinella*), chosen as widespread representative species for the three guilds, respectively, and skylark (*Alauda arvensis*), chosen as an example of an open-nesting farmland passerine. Bat4pop was parameterised for common pipistrelle (*Pipistrellus pipistrellus*), being a widespread bat species with the largest structured observational dataset available for validation (see Sect. "Model validation"). Rept4pop was parameterised for common lizard (*Zootoca vivipara*), chosen to represent a widespread reptile with limited mobility, while amph4pop was parameterised for common toad (*Bufo bufo*), since, of the UK's widespread amphibians, this is the most terrestrial (Sinsch 1988).

An expert opinion questionnaire (n = 4 experts; see supplementary material) was used to set the nesting and foraging resource parameters per landcover type used by bird4pop for each bird guild (the same parameters were also used for the representative species) and for skylark. Expert opinion was chosen because we required estimates of resource provision for distinct uses (nesting vs foraging etc., rather than general habitat associations) and robustness could be introduced by combining the judgements of multiple experts, each integrating their own literature knowledge and field experience of our specific mapped habitat categories. Similar expert opinion questionnaires were used to set the roosting and foraging resource parameters used in bat4pop (n = 3 experts), the basking and foraging resource parameters used in rept4pop (n = 10 experts), and the breeding and foraging resource parameters used in amph4pop (n = 10 experts). Within each questionnaire, the experts rated 77 landcover types (based on those available in the input mapping data and distinctions considered to be ecologically meaningful for the modelled taxa) on an integer scale from 0 = 'not used/no resources' to 5 = 'very high resource provision' and rated how certain they were of their answers on a similar 6-point scale from 'no confidence' to 'high confidence'. We then calculated the mean resource scores per landcover type across all experts, weighted by their certainty scores, following the procedure described in Gardner et al. (2020). A 0–5 scale was retained for the mean foraging resource scores, while the mean nesting, roosting, basking and breeding scores (for the bird4pop, bat4pop, rept4pop and amph4pop models, respectively) were renormalised onto a 0–1 scale (as required for model calculations; see supplementary material for details). Copies of the questionnaires are provided in the supplementary material and final parameter values are given in Tables S2-S5.

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

## Model validation

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

Bird4pop and bat4pop were both validated against national recording scheme data collected by volunteers for the British Trust for Ornithology and the Bat Conservation Trust, respectively. To test the model's

**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:<br>- early spring<br>- late spring<br>- summer | • Foraging resources gathered<br>• Max. bee production parameter | Yes | • None for existing reproductive females<br>• Nest site limitation for new reproductive female offspring | • Ground-nesting bumblebees<br>• Tree-nesting bumblebees<br>• Ground-nesting solitary bees<br>• Cavity-nesting solitary bees |
| Bird4pop | Nidicolous birds | Nest | Breeding pairs | Breeding season | • Foraging resources gathered<br>• Max. no. of chicks per year | Yes | • Probabilistic survival of adults and offspring<br>• Nest site limitation | • Woodland specialists<br>• Woodland generalists<br>• Edge-nesting farmland passerines<br>• Nuthatch<br>• Robin<br>• Yellowhammer<br>• Skylark |
| Bat4pop | Bats | Maternity roost | Breeding females | Breeding season | • Foraging resources gathered<br>• Assumes max. one pup per female | No[1] | • Probabilistic survival of adults and offspring<br>• Roost site and roost size limitation | Common pipistrelle |
| Rept4pop | Site-faithful reptiles | Basking site *(accounting for habitat shading)* | Breeding females | Active season | • Foraging resources gathered<br>• Max. clutch size | Yes | • Probabilistic survival of adults and offspring<br>• Basking site limitation | Common lizard |
| Amph4pop | Amphibians | Breeding pond | Breeding females | Active season | • Foraging resources gathered<br>• Max. clutch size<br>• Max. tadpole density | Yes | • Probabilistic survival of adults and offspring<br>• Road mortality | Common toad |

[1]Due to high female philopatry shown by bats (Fornusková et al. 2014)

ability to reproduce context-dependent habitat use, we also investigated whether the yellowhammer parameterisation of bird4pop could reproduce the interaction observed by Robinson et al. (2001), who found that yellowhammer abundance depends more strongly on area of arable habitat in pasture-dominated landscapes than in arable-dominated landscapes.

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

No comparable measures of common toad abundance across multiple sites were available to validate amph4pop's relative abundance predictions. Instead, we attempted to validate the model's predictions for common toad habitat use. The Toads on Roads

**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 | $km^{-2}$ | 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 | Upper limit; Léna et al. (2000) |
| | Dispersal range | m | 60 | Set to twice foraging range; Léna et al. (2000) classify dispersers as those moving > 30 m |
| | Maximum basking density | $ha^{-1}$ | 625 | Sorci et al. (1996) |
| | Adult survival probability | | 0.53 | Sorci et al. (1996) |
| | Juvenile survival probability | | 0.2 | Sorci et al. (1996) |
| | Maximum offspring per female | | 9 | Inns (2009) |
| | Growth parameter a | | 3.1 | Set to value producing maximum $R^2$ 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 et al. (1984) |
| | Maximum tadpole density | $m^{-2}$ | 38 | Reading & Clarke (1999) measured a maximum of ~ $1.3 \times 10^5$ 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) |

**Table 2** (continued)

| Species | Parameter | Units | Value | Source |
|---|---|---|---|---|
| | 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 |

Project, run by Froglife, supports a network of volunteer Toad Patrols, who assist toads across roads to reduce road mortality during the spring migration from terrestrial habitats to aquatic breeding habitats. We sent a questionnaire to Froglife's Toad Patrols in May 2021 to collect information on which types of terrestrial habitats migrating toads were observed to be travelling from and their breeding locations. We then used amph4pop to simulate the foraging distributions (i.e. the predicted spatial distribution of foraging rates) of these breeding populations. We ranked habitats from those that were predicted to be most

**Table 3** Movement ranges, population growth and survival parameters used in bird4pop model

| Parameterisation | Growth param a | Growth param b | Foraging range (m) | Dispersal range (m) | Maximum nest density ($ha^{-1}$) | Chicks produced per year | Adult survival probability | Juvenile survival probability |
|---|---|---|---|---|---|---|---|---|
| Woodland specialist | 0.2 | 0.4 | 250 | 10,000 ± 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 |

Survival probabilities and number of chicks produced per 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 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 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 supplementary material for details of the calculation and the use of a uniform value across parameterisations). Foraging range and growth parameter a were set using Fig. 1 of Hinsley et al. (1996) and Fig. S1, with the same values used for all guilds/species (to ensure proportionally equivalent forage units to chicks conversion rates and due to lack of species-specific breeding season foraging range estimates for many species). Growth parameter b is set to be twice the value of growth parameter a, following Häussler et al. (2017)

used to those predicted to be least used across all the sites and compared this to the relative habitat usage reported by the Toad Patrols (see supplementary material for details).

## Results

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

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

The yellowhammer relative abundance predictions showed a positive association with area of arable, whose slope was significantly steeper for more arable dominated landscapes (Table 6). Since this interaction is not consistent with those found by Robinson et al. (2001), we repeated the analysis with model predictions from an alternative parameterisation (Yellowhammer_n; Table 6), where the yellowhammer nesting resource score was set to zero for all landcovers except for arable field margins and hedgerows. This produced a context-dependent trend that becomes significantly less steep as the wider landscape transitions to arable-dominated, in better agreement with observations (Robinson et al. 2001). This alternative parameterisation still showed a significant positive relationship with the surveyors' counts across the BBS squares but with lower $R^2$ (Table 5).

Bat4pop's common pipistrelle foraging activity predictions showed a significant positive relationship with the total number of common pipistrelle passes

**Table 4** Observational datasets and statistical tests used for *4pop model validation

| Model | Observational dataset(s) | Spatial coverage | Temporal coverage | n | Statistical test |
|---|---|---|---|---|---|
| Bird4pop | British Trust for Ornithology's Breeding Bird Survey (BBS) | Great Britain | 2016–2020 | 4874 1km survey squares | Generalised linear model with a Poisson error distribution of the form:<br>$\ln(A_i) = \beta_0 + \beta_1 B_i$<br>where:<br>$A_i$ = mean relative abundance in survey square $i$ during the 5 year period, rounded to nearest integer<br>$B_i$ = mean number of breeding pairs per pixel predicted within survey square $i$ by bird4pop<br>$\beta_x$ = fitted coefficients, where a statistically significant positive value of $\beta_1$ indicates successful validation |
| Bird4pop (yellowhammer parameterisation only) | Robinson et al. (2001) | Great Britain | - | 4874 1km squares | Linear model with a Gaussian error distribution of the form:<br>$B_i = \beta_0 + (\beta_{1,G1}, \beta_{1,G2}, \beta_{1,G3}) G\ C_i$<br>where:<br>$B_i$ = mean number of breeding pairs of yellowhammers predicted within BBS square $i$ by bird4pop<br>$C_i$ = arable area within the BBS square (units = 1000ha)<br>$G$ = the group (factor) that the 33 × 33km tile surrounding the BBS square is assigned to, where groups are based on the arable:grass ratio ($R$) within the 33 × 33km tile and group 1 tiles have $R < 0.5$ (representing grassland-dominated landscapes), group 2 have $0.5 \leq R < 2.5$ (mixed), group 3 have $R \geq 2.5$ (arable-dominated)<br>$\beta_x$ = fitted coefficients, where $\beta_{1,x}$ interaction terms consistent with those found by Robinson et al. (2001) indicate successful validation |

**Table 4** (continued)

| Model | Observational dataset(s) | Spatial coverage | Temporal coverage | n | Statistical test |
|---|---|---|---|---|---|
| Bat4pop | Bat Conservation Trust's National Bat Monitoring Programme Field Survey | Great Britain | 2016–2020 | 401 1km survey squares; 1778 surveys | Generalised linear model with a Poisson error distribution of the form:<br>$\ln(A_i) = \beta_0 + \beta_1 F_i + \beta_2 s_i + \beta_3 T_i + \beta_4 C_i + \beta_5 W_i + \beta_6 R_i + \beta_7 S_i + \beta_8 E_i + \beta_9 D_i$<br>where:<br>$A_i$ = total number of common pipistrelle passes (a measure of bat activity) across all spots surveyed on visit $i$ to a given survey square<br>$F_i$ = mean common pipistrelle foraging rate per pixel predicted within the survey square by bat4pop<br>$s_i$ = number of spots surveyed on visit $i$<br>$T_i$ = temperature (units = degrees Celsius)<br>$C_i$ = cloud cover (factor)<br>$W_i$ = wind strength (factor)<br>$R_i$ = rainfall (factor)<br>$S_i$ = volunteer skill level (factor)<br>$E_i$ = volunteer experience level (factor)<br>$D_i$ = detector type (factor)<br>$\beta_x$ = fitted coefficients, where a statistically significant positive value of $\beta_1$ indicates successful validation |

**Table 4** (continued)

| Model | Observational dataset(s) | Spatial coverage | Temporal coverage | n | Statistical test |
|---|---|---|---|---|---|
| Rept4pop | Surrey Amphibian and Reptile Group's Long-term Reptile Monitoring dataset | Surrey, England | 2016–2021 | 83 sites; 1311 surveys | Generalised linear model with a Poisson error distribution of the form: $\ln(A_i/t_i) = \beta_0 + \beta_1 F_i + \beta_2 T_i + \beta_3 H_i + \beta_4 Y_i + \beta_5 D_i + \beta_6 D_i^2 + \beta_7 D_i^3 + \beta_8 S$ where: $A_i$ = total number of adult common lizards recorded on survey $i$ $t_i$ = survey duration (units = minutes) $F_i$ = mean common lizard foraging rate per pixel within a 750m buffer of survey site centroid, as predicted by rept4pop $T_i$ = air temperature during survey (units = degrees Celsius) $H_i$ = relative humidity during survey $Y_i$ = year survey was conducted $D_i$ = the day of the year (where D = 1 for 1st Jan) S = surveyor skill level $\beta_x$ = fitted coefficients, where a statistically significant positive value of $\beta_1$ 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 |

**Table 4** (continued)

| Model | Observational dataset(s) | Spatial coverage | Temporal coverage | n | Statistical test |
|---|---|---|---|---|---|
| Amph4pop | Toad patroller responses to 'Your toads and their habitats' questionnaire | Great Britain | 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 10 × 10km around the validation sites. A stronger correlation with amph4pop's predictions than with simple habitat availability indicates successful validation |

See supplementary material for a full description of data preparation and validation methodologies

recorded by surveyors, although the $R^2$ for the model-data fit was low (Table 5).

Rept4pop's common lizard foraging rate predictions showed a significant positive relationship with the total number of adult lizards recorded by surveyors (Table 5). The median predicted number of foraging lizards across the sighting locations was also significantly higher than the median predicted number of foraging lizards across the randomly selected locations within the 750m survey site buffer zones (Wilcoxon rank sum test; $W = 2{,}847{,}391$; $P < 0.001$; Fig. 6).

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

## Discussion

### Validation

The validation results suggest that the general form and conceptualisation of the *4pop model family is relevant for a wide range of species. All models' predictions showed positive relationships with the observational data, although $R^2$ values were generally low. This emphasises the continued need for complementary, field-based, ecological surveys before any on-the-ground land-use decisions are actually made. It's likely that process-based models will always struggle to match the evaluation metrics of SDMs, which are by definition fitted to the data, because the act of simulating (often plastic) foraging/population processes adds additional noise. However, good evaluation metrics when matching to current/present-day observational datasets are not always indicative of good predictive power in novel/future situations

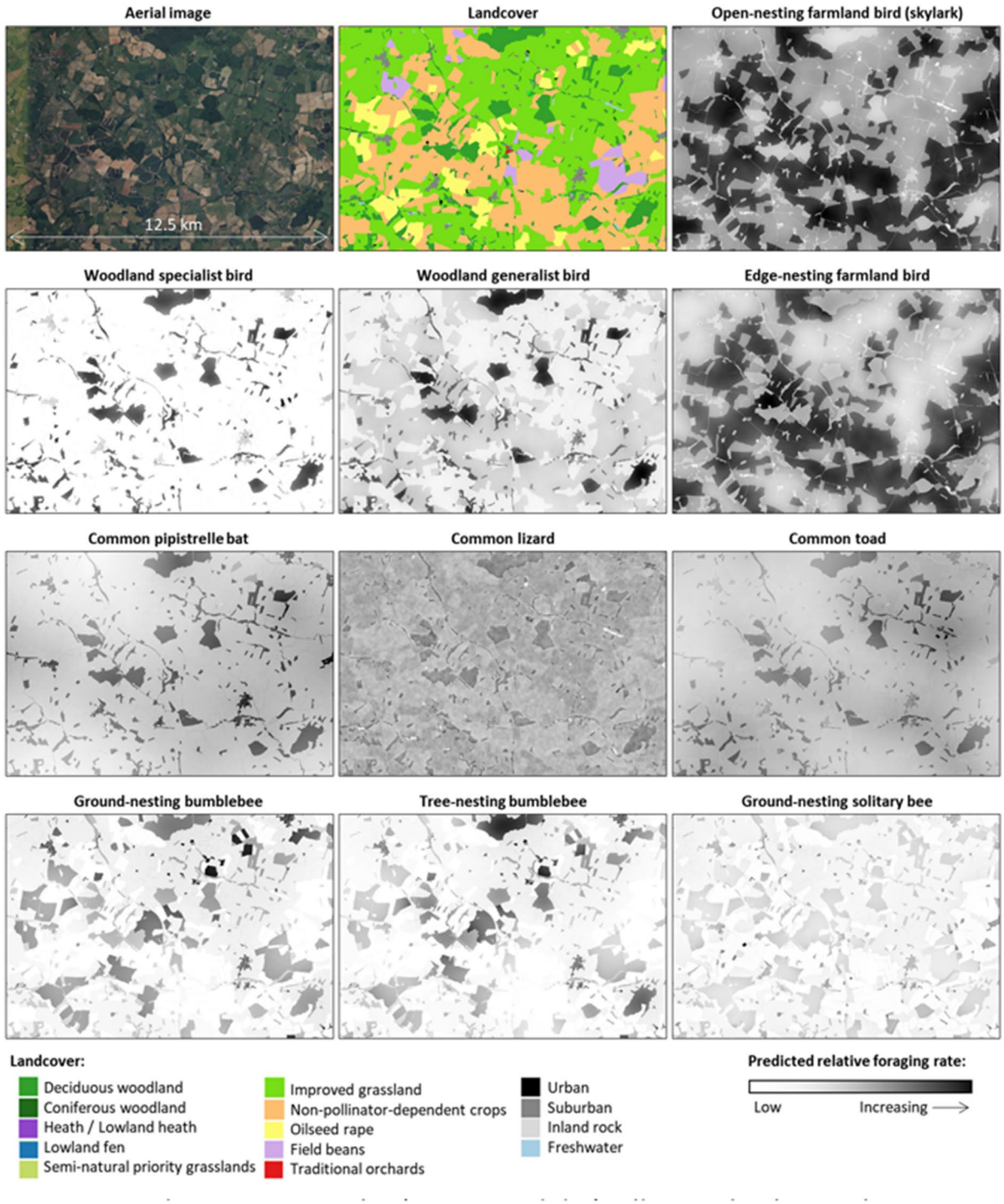



**Fig. 4** Foraging rate predictions output by *4pop models (poll4pop, bird4pop, bat4pop, rept4pop and amph4pop) for a single agricultural landscape. Simulations were run at 10 × 10m resolution. Foraging rate units are arbitrary, with scales individual to each panel and shades therefore not comparable between taxa. Note that the landcover map shown has grouped some landcovers for ease of visualisation and does not show the fine-scale edge habitats (e.g. hedgerows, field margins) also input into the models. Aerial image provided by QGIS from Microsoft's Bing Map Services. Example landscape is located on Leicestershire/Rutland border, UK

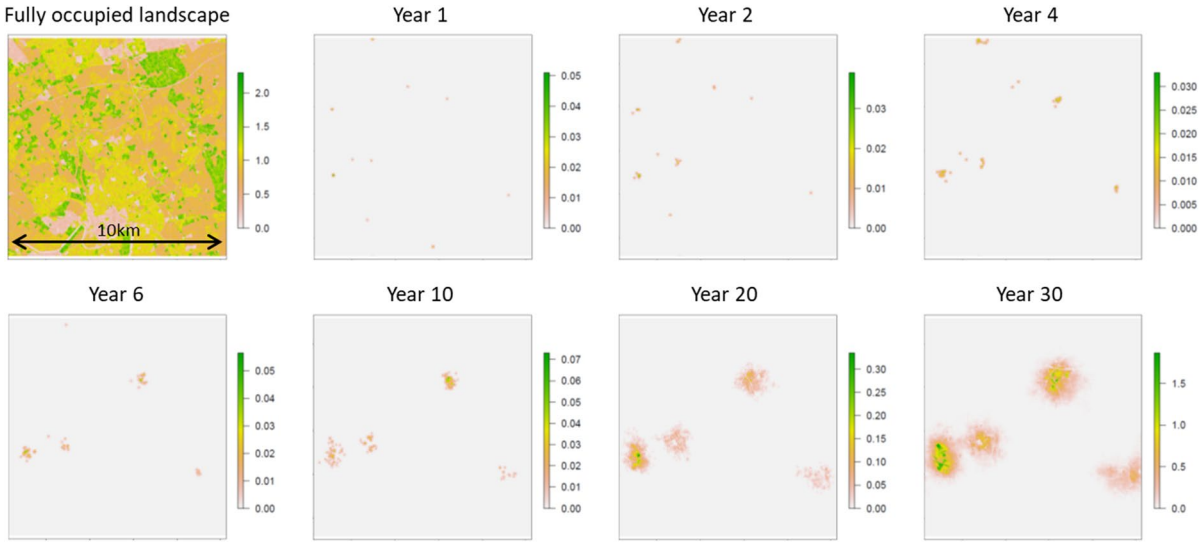



**Fig. 5** Rept4pop simulations demonstrating the dynamic spatio-temporal behaviour of the models. First panel shows predicted distribution of common lizard foraging activity within a 10 × 10km landscape that is fully occupied and subsequent panels show the ability of common lizard to disperse and recolonise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

**Table 5** Relationships between model predictions ($m$) and observed counts ($c$) of relative abundance or activity for those taxa fitted with a functional relationship of the form $\ln(c) \propto \beta_1 m$

| Model | Parameterisation | Coefficient ($\beta_1$) | Standard error | P value | $R^2$ |
|---|---|---|---|---|---|
| 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 |

See methods section for details of taxa-specific control variables

(Iturbide et al. 2018; Warren et al. 2020), suggesting that modelling these ecological processes and compromising on predictive power over current data may be acceptable if achieving greater predictive confidence in unfamiliar future scenarios is the aim. What is considered sufficient predictive power will likely vary according to the decision-maker and the situation (e.g. risk of negative consequences/irreversible effects), and it is unlikely (and generally inadvisable) for decisions to be made based on model predictions alone. Importantly, we have shown these models have the potential to make ecologically meaningful predictions, which could be used to inform discussions within a decision-making process that also integrates information from other sources.

Our explorations demonstrate there are multiple opportunities to test the realism of process-based models. We validated their species activity predictions at different spatial scales (1km, 750m and species presence at 1m resolution; Table 5; Fig. 6),

**Table 6** Results from regressing mean number of breeding yellowhammer pairs predicted by bird4pop in each 1km BBS square ($B_i$) against the arable area within the BBS square ($C_i$; units = 1000ha), allowing an interaction with the arable:grass ratio group ($G$) of the 33 × 33km tile within 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 distribution

| Parameterisation | $\beta_{1,G1}$ | $\beta_{1,G2}$ | $\beta_{1,G3}$ | $R^2$ |
|---|---|---|---|---|
| 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 |

Results are shown for the original yellowhammer model parameterisation and for a second parameterisation (Yellowhammer_n), where the yellowhammer nesting resource score is set to zero for all landcovers except for arable field margins and hedgerows. All $ß_{1,G1}$ are significantly different from zero ($P < 0.001$) and all $ß_{1,G2}$ and $ß_{1,G3}$ coefficients are significantly different from their corresponding $ß_{1,G1}$ coefficient ($P < 0.001$)

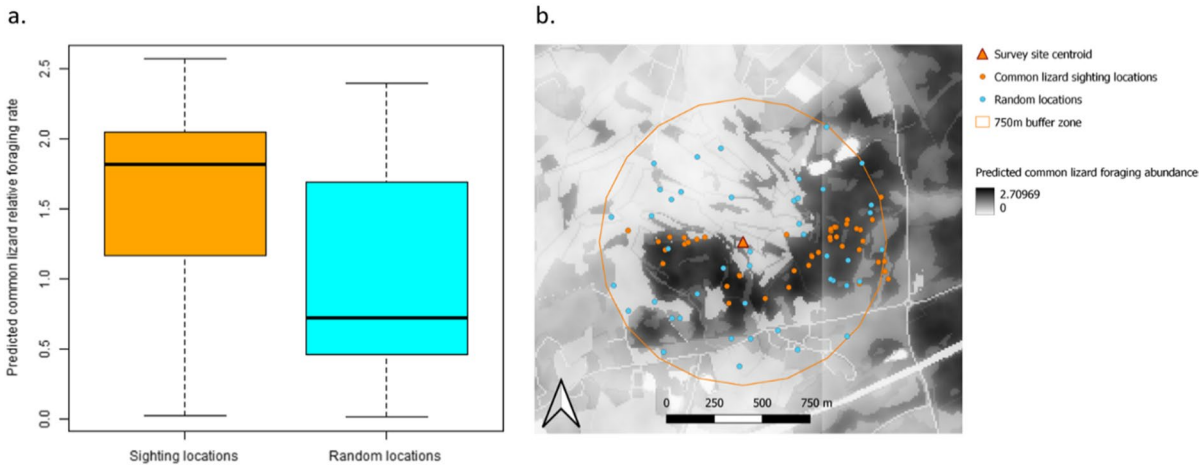



**Fig. 6** **a** Distribution of rept4pop's predicted common lizard foraging rates (arbitrary units) at common lizard sighting locations recorded by surveyors during visits to SARG's long-term reptile survey sites compared to its predicted common lizard foraging rates at a matched sample of random locations within 750m of the survey site centroids. **b** Map of one survey site (assumed bounds indicated by orange line) illustrating the sighting locations and randomly selected locations within it, superimposed over rept4pop's common lizard foraging rate predictions

**Table 7** Spearman's ρ values for correlations between observed habitat-use rankings derived from the Toad Patrols' questionnaire responses and habitat-use rankings predicted by amph4pop, as well as habitat rankings based on the mean percentage area of each habitat available within the 10 × 10km validation landscapes

| 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 |

Results are shown using data from all sites and for an analysis restricted to data from only those sites showing non-zero toad population predictions when road mortality effects are included. All correlations are statistically significant at $P < 0.01$

checked their ability to reproduce context-dependent interactions derived from statistical model fits to observational data (Table 6) and quantified their ability to reproduce observed habitat preferences of species (Table 7). We also ensured the models reproduced observed distributions of roost sizes and minimum area responses to habitat fragmentation (Fig. S1; Fig. S2). These additional checks help assess performance of the models' underlying processes and we suggest those developing process-based models could be imaginative in finding multiple approaches to validate their functionality.

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

## Species-level versus guild-level approaches

We compared species-level versions of the bird models with guild-level versions, which collectively model a group of species with similar life histories, habitat usage and movement ranges. The guild-level parameterisation outperformed the species-level parameterisation for woodland specialists, but not for farmland passerines.

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

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

## Supporting biodiversity-inclusive landscape decision-making

Mobile species that require access to multiple habitat types are often not well catered for by decision-making approaches that fail to take into account habitat configurations and species' movement ranges (e.g. habitat accounting; Gardner et al. 2022). In contrast, our model adaptations show poll4pop's highly

flexible framework can represent multi-habitat use over a wide range of taxa, spatial and temporal scales. From originally simulating seasonally-resolved short-range foraging of bees around their nests and longer-range dispersal of their reproductives to new nest sites, we have adapted the model to simulate analogous behaviour by birds, with probabilistic yearly survival included for these longer lived species. Other adaptations simulate the home range behaviour of lizards, core activity zones of bats resulting from separation of roosting and foraging habitat and the seasonally distinct distributions of amphibians due to migration from aquatic to terrestrial habitats. This enables the models to identify situations where population sizes may be limited by availability of one particular resource despite ample supply of another. For example, they indicate the changing relationship between yellowhammer abundance and arable cover could be explained by populations being forage resource limited in pasture-dominated landscapes and nest site limited in arable-dominated landscapes. Their outputs could therefore help decision-makers take on board the requirements of multiple taxa and ensure proposed landscape changes do not cause imbalances that force landscapes into a resource-limited state for any particular species (Pöysä & Pöysä 2002; Desaegher et al. 2021).

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

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

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

A key challenge when building any biodiversity models is discrepancies between the habitat distinctions available in (usually remote-sensed) input landcover data and habitat distinctions of relevance to the modelled species. The *4pop models can account for small-scale habitat features (see Sect. "Landcover data") and be parameterised for a finely-graded habitat classification system (Sect. "Model parameterisation") to capture the needs of species and of decision-makers investigating future scenarios. However, their operationalisation in the present day (and the set of species to which they can be confidently applied) may be limited in practice by the coarser spatial and thematic resolution of current landcover datasets (Betts et al. 2014). This is particularly problematic if

poorly detected, small or ephemeral habitat features are essential resources for seeding populations in the digitised landscape but missing from input landcover data. Incorporating on-the-ground survey information, structural descriptors from LiDAR data and future advances in very high resolution remote-sensing may help to address this issue and increase predictive power (Bradter et al. 2020; Price et al. 2023).

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

## Conclusions

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

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**Author contributions** EG led the project, built and validated the models, and wrote the initial manuscript. The bird (bird-4pop), herptile (rept4pop & amph4pop) and bat (bat4pop) models were co-developed with RAR, AJ and KB, respectively. Authors RAR to JT-L contributed to model parameterisation and validation, and provided access to and guided interpretation of observational datasets. SP helped develop the traffic mortality function for amph4pop. Authors DB to BKT provided additional input, which influenced model development and

assisted with exploration of the real-world utility of the models. Authors SJRA to IW provided expert opinion for model parameterisation. Authors JB to AM assisted with provision, gathering and interpretation of observational datasets. RFP and JMB oversaw the project and provided advice throughout. All authors were involved in revising the manuscript.

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**Data availability** All *4pop models are being made freely available from the Environmental Information Data Centre. Observational datasets used for model validation are available on request from British Trust for Ornithology, Bat Conservation Trust, Amphibian and Reptile Groups of UK, Surrey Amphibian and Reptile Group, and Froglife.

**Declarations**

**Competing interests** The authors have no relevant financial or non-financial interests to disclose.



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