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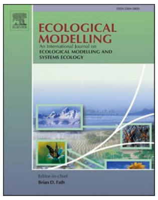

Evaluating biological realism in ecological modelling: application of a novel framework to compare mechanistic and process-based earthworm and wild pollinator population models

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ABSTRACT

Ecological models can support land management decisions and optimisation schemes that need to account for invertebrate population responses at the field to landscape level. However, models that incorporate greater biological detail (e.g. individual-level physiological and behavioural responses) often become computationally intractable at larger spatial extents. Such trade-offs in model development lead to ad hoc model design for different species and management questions, hindering generalisable insights needed to advance predictive ecological models for decision support. To facilitate model comparison, we developed and applied a novel approach to quantify the biological realism of models for two functionally important invertebrate groups commonly targeted by management interventions. Mechanistic and process-based population models for earthworms ($n = 23$) and wild pollinators ($n = 24$) were identified through a structured review. We find that earthworm models are predominantly non-spatial or micro-scale (<10 m extent) and often incorporate detailed physiological mechanisms. Pollinator models frequently simulate landscape-scale scenarios (≥1 km extent) and typically rely on aggregated processes to predict population dynamics or crop visitation rates, although some include detailed individual-level movement behaviours. Species- and scale-specific model structures highlight the need for greater integration of physiological and behavioural mechanisms across broader spatial extents. We recommend systematic strategies to build on the progress made by existing models, aiming to resolve the trade-off between realism and tractability for more informed population predictions at management-relevant spatial scales. Our framework complements existing efforts towards greater transparency in model development, communication, and application for robust environmental decision support.

1. Introduction

Ecological models are important tools for supporting evidence-based land management, as they enable the investigation of alternative policies, management scenarios, and changing environmental conditions, which are difficult to test experimentally (McLane et al., 2011; Schmolke et al., 2010b; Schuwirth et al., 2019; Stevens et al., 2007). All models are simplified representations of real systems, and so model development necessarily involves decisions and assumptions about the features that are included and how they are represented (i.e. the model structure) (Accolla et al., 2021; Gregr and Chan, 2015). A clear understanding of how model structure influences predictive power and scope of applicability to environmental and management scenarios is critical for robust and transparent decision support (Gregr and Chan, 2015; Grimm et al., 2020b; Schmolke et al., 2010b; Schuwirth et al., 2019). However, model comprehension and evaluation can be hindered by inconsistent model communication and infrequent model comparisons (Grimm, 2023; Schmolke et al., 2010b; Schuwirth et al., 2019).

Model structure is fundamentally constrained by a trade-off between realism and tractability (Wang et al., 2024). Models that include more

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detail of the organisation of a real system can generate more informed predictions, but increased model complexity amplifies output uncertainty and computational demand (process time and memory use) (Grimm and Berger, 2016a; Singer et al., 2016; Wang et al., 2024). Grimm and Berger (2016a) identified structural realism as an essential element of next-generation ecological modelling, highlighting the central importance of the interactions between biotic model components with one another and the abiotic model environment. These interactions can be represented statistically (i.e. correlative models) or causally (process-based or mechanistic models), representing different degrees of the realism-tractability trade-off (see Supplementary Table 1 for terminology and definitions used throughout) (Dormann et al., 2012; Gregr and Chan, 2015; Johnston, 2024).

Correlative, process-based and mechanistic predictive models differ in key aspects relating to accuracy, uncertainty, transferability, input data requirements, and computational demand (Dormann et al., 2012; Mouquet et al., 2015; Singer et al., 2016; Urban et al., 2016). Correlative species distribution models (SDMs), for instance, use statistical relationships between species occurrence and environmental predictors that are assumed to indirectly capture the biological processes driving observed distributions (Dormann et al., 2012; Guisan and Thuiller, 2005). Correlative SDMs are typically implemented over relatively large spatial extents, such as an entire species range, but are unable to account for nonstationarity and so have limited transferability beyond the original environmental domain (Rollinson et al., 2021; Yates et al., 2018). Process-based models can provide more informed predictions by accounting for the underlying dynamics (e.g. population growth, dispersal) that shape population patterns (abundance, distribution) (Briscoe et al., 2019; Guisan and Thuiller, 2005; Johnston, 2024; Schurr et al., 2012). Process-based models are a common choice for environmental decision support, as the use of aggregated functions and empirical parameters constrains uncertainty and reduces computational demand (Evans et al., 2013; Gardner et al., 2024; Johnston, 2024; Singer et al., 2016). This structure, however, restricts modelled population responses to the range of environmental and demographic variation present in the input data (Dormann et al., 2012; Johnston et al., 2019; Radchuk et al., 2019).

Mechanistic models are distinguished by their explicit representation of the physiological and/or behavioural responses from which population processes and patterns emerge (Johnston, 2024). These individual-level mechanisms are based on fundamental principles of life history theory that are expected to support model transferability (Grimm and Berger, 2016a; Kearney and Porter, 2009; Radchuk et al., 2019; van der Vaart et al., 2016). Physiological and/or behavioural mechanisms can be incorporated in several modelling frameworks, including SDMs (Evans et al., 2015; Kearney and Porter, 2009), demographic models (Jager et al., 2014), and individual-based models (IBMs) (Johnston et al., 2019). An IBM structure is ideally suited for representing the physiological and behavioural variation and interactions of autonomous individuals within heterogeneous environments, thereby capturing nonlinear responses, feedbacks, and interactive effects of multiple stressors to predict context-dependent population dynamics (Catford et al., 2022; DeAngelis and Grimm, 2014; Galic et al., 2018; Jager et al., 2014; Johnston et al., 2019). However, the computational demands of simulations involving detailed submodels for many individuals across fine-resolution heterogeneous environments can be substantial, typically limiting applications to small spatial scales (Gardner et al., 2024; Johnston, 2024). Furthermore, mechanistic IBM outputs may have high uncertainty due to their complex structure and requirement for detailed individual-level data, which can lead to the accumulation of stochastic effects and propagation of parameter and structural uncertainties (Evans, 2012; Johnston et al., 2019; Singer et al., 2016).

Here, we conduct a structured review and analysis of mechanistic and process-based population models for earthworms and wild pollinators, with the aim of evaluating a specific aspect of structural realism, which we term biological realism. We define biological realism as the level of detail in the representation of biological mechanisms and processes operating at the individual to population level (e.g. physiology, vital rates, population growth, dispersal), while excluding the representation of the model environment (e.g. resource dynamics, abiotic factors). Earthworms and wild pollinators (wild bees and hoverflies) exemplify the diverse invertebrate taxa that underpin key ecosystem functions commonly targeted by management interventions in agricultural landscapes (Bommarco et al., 2013). Wild bees (bumblebees and solitary bees) are efficient pollinators of widely grown and economically important crops, while hoverflies are abundant pollinators, with some species having aphidophagous larvae that also serve as important pest regulators (Breeze et al., 2011; Doyle et al., 2020; Garratt et al., 2014; Pekas et al., 2020). Earthworms play a central role in soil functioning (i.e. soil formation and structure, nutrient cycling, pest and disease control), both through their own activities and indirectly by modulating the wider soil environment and community, and are commonly seen as indicators of soil quality (Barrios, 2007; Blouin et al., 2013; Brown et al., 2000; Römbke et al., 2005).

Agri-environment schemes (AES), which incentivise environmentally sustainable land management, are the primary framework for implementing interventions to support invertebrate populations in agricultural landscapes (Batáry et al., 2020, 2015; Ekroos et al., 2014). AES actions can include a range of agricultural management practices and interventions, such as reduced tillage, beetle banks, and hedgerows, implemented at the field, farm, or landscape level (DEFRA, 2023; Garibaldi et al., 2014; Pe'er et al., 2017). While we understand the effects of certain individual actions, such as wildflower strips increasing pollinator visits to crops, the effects of implementing different combinations of management practices and interventions within the same field or across a larger area are more difficult to determine (Garibaldi et al., 2014; Kleijn et al., 2019; Pufal et al., 2017). Mixed findings regarding the effectiveness of AES for biodiversity outcomes have been attributed to taxon-specific and nonlinear responses to the interacting factors of landscape complexity and land-use intensity (Batáry et al., 2010; Díaz and Concepción, 2016; Diekötter et al., 2010; Gabriel et al., 2010; Kleijn et al., 2006). Optimising AES for diverse invertebrate taxa and different regional contexts will therefore require a better understanding of the interplay between in-field management practices, landscape composition and configuration, and species population responses (Batáry et al., 2020; Díaz and Concepción, 2016; Fahrig et al., 2011; Martin et al., 2019).

Biologically realistic models are essential for understanding and predicting emergent population responses under novel management scenarios and changing environmental conditions (Johnston et al., 2019; McLane et al., 2011; Stillman et al., 2015). However, land management decisions such as AES implementation also require reliable predictions at relevant spatial scales (DeAngelis and Yurek, 2017; Lindborg et al., 2017; Schuwirth et al., 2019; Stevens et al., 2007; Wang et al., 2024). Tractability at larger modelled extents is typically achieved through aggregation, which inherently involves a loss of biological detail (Fritsch et al., 2020). Decisions regarding model structure also depend on factors such as species traits, model purpose (i.e. management question), modeller preferences, and data availability (Gregr and Chan, 2015; Grimm, 2023; Johnston et al., 2019). Together, these constraints contribute to a culture of siloed modelling in ecology, where models are often developed in isolation, following the assumptions of different modelling paradigms, without systematic evaluation of the strengths and limitations of alternative model structures for supporting real-world management decisions (Grimm, 2023; Johnston, 2024).

While predictive ecological models can address critical evidence gaps for effective land management, those that incorporate greater biological detail often become computationally intractable at larger spatial extents. In practice, models tend to be developed on an ad hoc basis, with structures optimised for specific species, scenarios, and spatial scales. This strategy avoids directly addressing the trade-off between realism and tractability. Nevertheless, integrating insights and advances from a range of models offers a promising way forward to improve predictive ecological models for decision support. As a first step towards evaluating the relationship between structural realism, predictive performance, and computational tractability across diverse models, we developed and applied a novel approach to quantify biological realism. We demonstrate how this approach can be used to compare structural trade-offs across taxa and spatial scales. Finally, we identify how future modelling efforts can build on the progress made by existing models to resolve the realism-tractability trade-off, thereby enabling more informed population predictions at management-relevant spatial scales.

2. Methodology

Wild pollinators and earthworms were selected as the focus of this structured review and conceptual synthesis based on a literature review of functionally important invertebrates in agricultural systems and the authors' expert knowledge of taxa for which multiple population models exist. Our review is limited in scope to models in which population-level outputs result from biological mechanisms or processes relating to demographics and/or movement behaviour (e.g. physiology, vital rates, population growth, foraging, dispersal), elements that jointly determine emergent population responses at the spatiotemporal scales relevant to land management decisions (Cooke et al., 2014; Johnston et al., 2019). To synthesise the information extracted from the models identified in our structured review and facilitate their comparison, we developed a scoring scheme to quantify the representation of demographics and movement behaviour. The following sections detail the methodology of the structured review and biological realism scores.

2.1. *Structured review*

The structured review was conducted between December 2023 and February 2024 using the SciVerse Scopus database (www.scopus.com) to search for relevant models published at any time up to the end of February 2024. The general search strategy for both groups was: (“taxonomic/common name”) AND (“model type”). For example, the final search terms for pollinators included "wild bee*", bumblebee*, bombus, "solitary bee*", syrphid*, hoverfl*, pollinator*, and "population model*", "individual-based model*", "mechanistic model*", "process-based model*". The full list of search terms is provided in Supplementary Table 2. We are aware that the limitations of using a single database, alongside the large variation in modelling terminology, mean that a number of models may not have been captured in these searches. The systematic search was therefore supplemented with additional unique models identified from citations (Supplementary Figure 1).

A total of 998 article abstracts (204 for earthworms, 794 for wild pollinators) were screened for relevance and read in full where necessary. We excluded those that did not present an original model, or implementation of a model, that met all the review criteria (Supplementary Figure 1). The full review criteria are provided in Supplementary Table 3, with an overview of the exclusion criteria provided here: (1) models that were not parameterised with realistic values for taxa included in this review, therefore excluding models of other taxa, and theoretical models which are typically unable to make specific predictions to support land management decisions; (2) models that did not include mechanisms and/or processes relating to demographics and/or movement behaviour, therefore excluding purely statistical models, and those which only included mechanisms and/or processes outside the scope of this review (e.g. evolutionary adaptation, community-level biotic interactions); (3) models that did not provide population-level outputs, therefore excluding models which did not use mechanisms and/or processes to provide predictions that could support land management decisions, and those focused on higher ecological levels which were not within the scope of this review.

Articles presenting the same model were grouped, and multiple models from the same article were considered separately. The lead article for each unique model was read in full and key information was collated in Supplementary Table 4. Models were classified according to group (pollinator/earthworm), species, and model type; the representation of demographics and movement behaviour was summarised and scored using our biological realism scores (detailed below); and the main model outputs, spatial and temporal scales, and methods of validation were recorded. Our analysis focuses on the relationship between biological realism and spatial representation due to the relevance for land management decisions and the challenges involved with upscaling detailed models, outlined above. The spatial resolution and extent of spatially explicit models were categorised in relation to a land management context rather than from a species-specific perspective: for example, we define a landscape as greater than or equal to 1 km^2 based on average farm sizes (see landscape definition, Supplementary Table 1). Count data extracted from Supplementary Table 4 was visualised in RStudio 4.3.0 (R Core Team, 2023) using the ggplot2 package (Wickham, 2016).

2.2. *Biological realism scoring scheme*

We established a scoring scheme (summarised in Fig. 1) to quantify the level of detail with which key biological mechanisms and processes are represented in the models reviewed here (full details are provided in Supplementary Table 5). The scoring scheme does not evaluate model performance, but instead provides a common framework for comparing and communicating biological realism across a range of models designed for different taxa and management questions. The scores are intended to align with the definitions of mechanistic and process-based given in Supplementary Table 1, so that high scores correspond to individual-level representations based on fundamental principles, whereas lower scores reflect aggregated representations and those with reduced biological detail.

Demographics refers to physiological processes, traits, or rates relating to growth, reproduction, and survival (for example: energy budgets, thermal performance curves, vital rates, life history traits, population growth rate). Movement behaviour incorporates the movement process, the representation of motion or the movement path, and behavioural decision-making, the way in which internal and/or external factors (e.g. energy level, memory, habitat quality) influence the movement direction and distance (DeAngelis and Diaz, 2019; Nathan et al., 2008). Movement process and behavioural decision-making are scored separately and summed to produce an overall score for movement behaviour that has a 1:1 relationship with the demographics score. This does not imply that the numerical scores are directly comparable, but ensures that demographics and movement behaviour are equally emphasised when presenting biological realism across models.

Although the scoring scheme does not explicitly consider the representation of the model environment or management practices, the biological mechanisms and processes categorised under demographics and movement behaviour are inherently shaped by external factors. Biological realism is also intrinsically related to model spatiotemporal resolution, as higher biological detail typically requires finer temporal and/or spatial resolution (e.g. daily allocation of energy to reproduction by individuals) compared with representations that aggregate over individuals, space, and time (e.g. annual reproduction rate of an entire population) (Fritsch et al., 2020; Radchuk et al., 2014). Thus, biological realism is directly linked to overall model complexity and associated tractability challenges.

3. Results

3.1. *Model summary*

Our structured review identified 87 articles, containing a total of 47

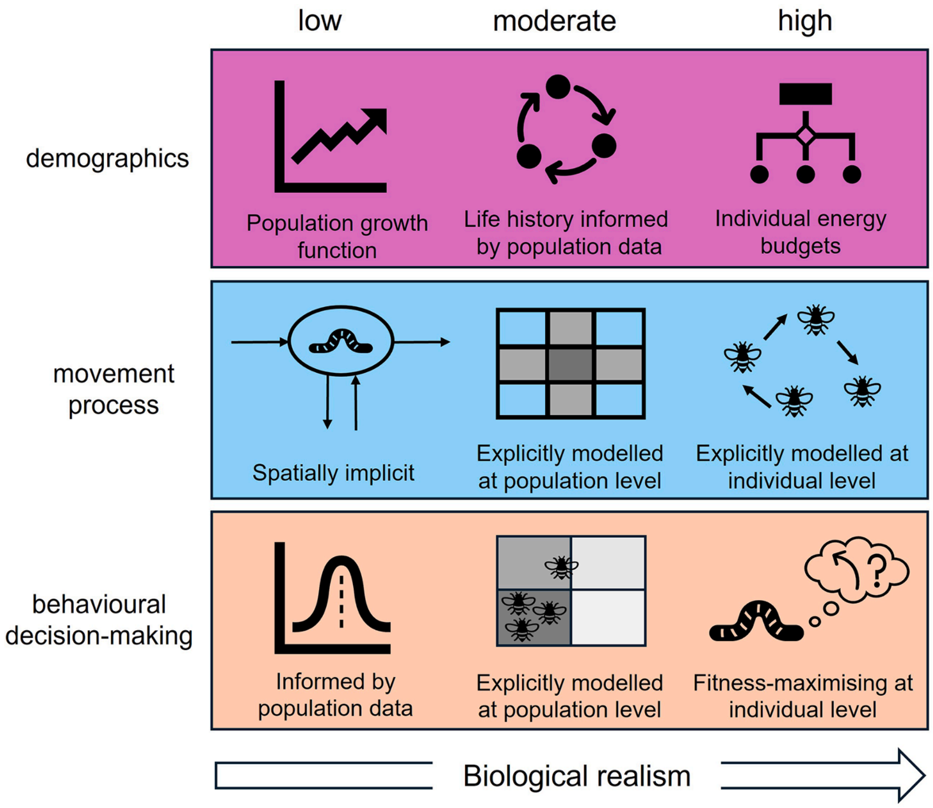

Fig. 1. Schematic representation of the biological realism scores used to compare earthworm and wild pollinator population models included in our review, depicting examples of mechanisms and processes relating to demographics and movement behaviour (separated into movement process and behavioural decision-making) with low, moderate, and high scores. Full details are available in Supplementary Table 5.

unique models comprising 24 wild pollinator and 23 earthworm models. We find that comparatively few models have been developed for hoverflies, which are represented by only 1 model in the pollinator group. The publication of articles presenting or implementing mechanistic or process-based pollinator models has increased in recent years, whereas model development for earthworms has not followed the same trend

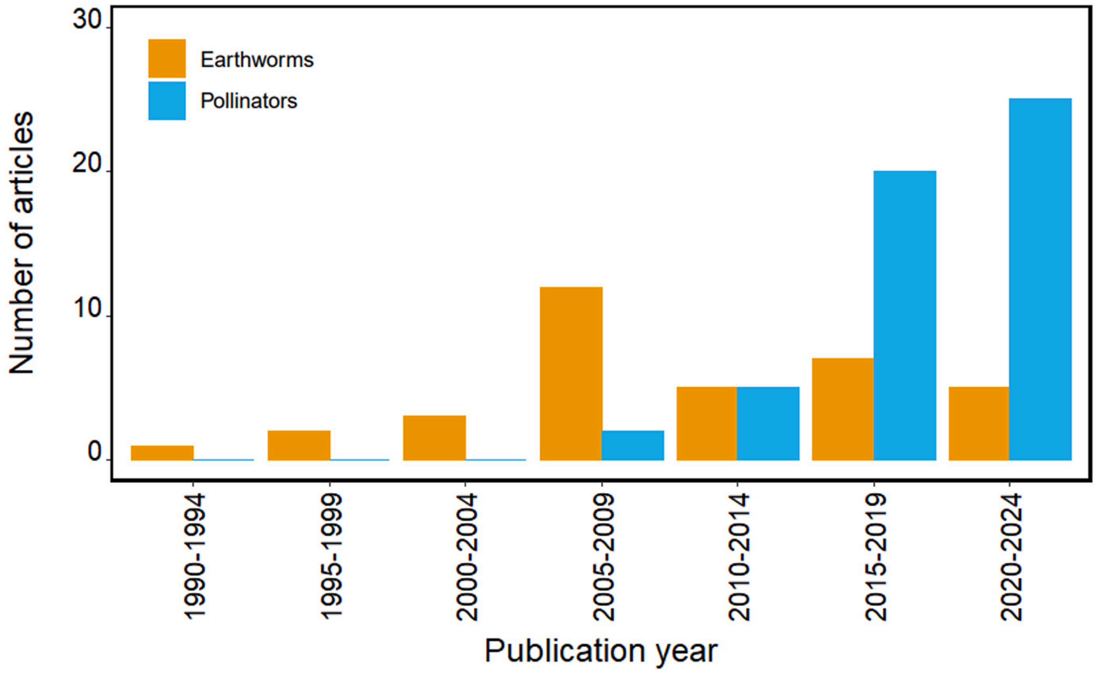

Fig. 2. Number of articles for earthworms (orange bars) and wild pollinators (blue bars) identified in the structured review. The number of articles (87 in total) is different to the number of reviewed models (47 in total) as some articles contained multiple models, and some models were presented in multiple articles. The figure includes articles published up to the end of February 2024.

(Fig. 2).

Table 1 provides a summary of the reviewed models, demonstrating the different population modelling approaches applied to earthworms and wild pollinators.

Earthworm models are predominantly non-spatial (56.5 % of models, compared to 4 % spatially implicit and 39 % spatially explicit), whereas spatially explicit models comprise the majority of wild pollinator models (62.5 %, compared to 12.5 % spatially implicit and 25 % non-spatial) (Fig. 3a). Spatially explicit earthworm models are typically at micro scale (<10 m spatial extent) (Fig. 3b), whilst spatially explicit pollinator models are largely at landscape (≥1 km spatial extent) or regional scales (Fig. 3c). The global earthworm model is a mechanistic SDM (Ruiz et al., 2021).

The inclusion of demographics and movement behaviour changes according to spatial representation, with non-spatial models focused on demographics and spatially implicit or explicit models more likely to include movement behaviour (Fig. 3a). Models that represent both elements are in the minority overall (25.5 %), as well as within spatially explicit models (42 %) (Fig. 3a). Across all spatial representations, 61 % of earthworm models represent demographics alone, followed by both elements (30 %) and movement behaviour alone (9 %); wild pollinator models are split across those which represent movement behaviour alone (42 %), demographics alone (37.5 %), and both elements (21 %) (Fig. 3a). For spatially explicit pollinator models, those representing movement alone rises to 67 % (Fig. 3c).

3.2. *Biological realism scores*

The distribution of biological realism scores, which quantify model representations of demographics and movement behaviour, shows that most of the reviewed models consider either demographics or movement behaviour alone (74.5 %), with very few models including detailed representations of both elements (Fig. 4). Models that score highly for movement behaviour or demographics alone tend to be IBMs for wild pollinators and DEB-based models for earthworms, respectively (Fig. 4).

3.3. *Spatially explicit models*

Spatially explicit models plotted in Fig. 5 show that there is very little overlap in the spatial extent and resolution of earthworm and wild pollinator models. Except for a mechanistic SDM (E26), spatially explicit earthworm models are limited to micro or local extents and very fine to fine resolutions (Fig. 5). Spatially explicit pollinator IBMs tend to be at landscape extent and medium resolution, while process-based and distance decay models also extend to regional extent with coarse resolution (Fig. 5).

4. Discussion

Our structured review and conceptual synthesis reveal how population models for earthworms and wild pollinators employ distinct structures to address scale-specific environmental and management questions (Table 1, Fig. 3). Biological realism scores highlight structural trade-offs in model representations of demographics and movement behaviour, reflecting differing priorities in model development for these taxa (Fig. 4). Combined with a trade-off between spatial resolution and extent (Fig. 5), this leads to a notable distinction: earthworm models are predominantly non-spatial or micro-scale and often incorporate physiological mechanisms, whereas pollinator models are typically implemented across landscape to regional extents and focus on individual-level or aggregated movement behaviours. Greater integration of physiological and behavioural mechanisms across broader spatial extents would enable more informed predictions at management-relevant scales. The models reviewed here have made important advances in predictive ecology, and our review serves to catalogue these alternative modelling approaches as a starting point for future adaptation and testing.

4.1. *Modelling approaches and structural trade-offs across taxa and spatial scales*

Earthworm models reviewed here are largely demographic frameworks, applied primarily to predict population responses to non-spatial stressors, reflecting the common role of earthworms as environmental

Table 1

Summary model table categorising the reviewed earthworm and wild pollinator population models according to key features of model structure. Full details for individual models are available in Supplementary Table 4 along with references for model IDs.

Model type	Focus level	Output	Demographics	Movement behaviour	Spatial representation	Dynamic/ static	Earthworm IDs	Pollinator IDs
Energy budget IBM (1)	Individual	PD, STRUC, DIST	Yes, EB	Yes, IL	SE	Dynamic	E4M2, E10, E11, E13	
IBM (2)	Individual	PD, BR	Yes, LHP. No (E3, P7, P39, P47)	Yes, IL	SE	Dynamic	E3	P2, P7, P8, P20, P39, P40, P47, P49
DEB-based demographic	Individual + population	PG, STRUC	Yes, EB	No	NS	Dynamic	E4M1, E9M1, E9M3, E17, E31	
Demographic (3)	Population	PD, PG, STRUC	Yes, DR, GF	No	NS	Dynamic	E1, E5, E7, E8, E9M2, E14, E23, E27, E29	P5, P6, P10, P13, P15, P16, P30
Spatially explicit process-based	Population	PD, VISIT, DIST	Yes, DR, GF. No (P11, P33, P48)	Yes, DK	SE	Dynamic	E2, E22, E35	P11, P29, P33, P48
Distance decay	Population	VISIT	No	Yes, DDF	SE	Static		P22, P36, P42, P44
Mechanistic SDM	Individual	DIST	TPF (P52)	BP (E26)	SE	Static	E26	P52

(1) Includes E4M2 (IBM parameterised with DEB model) which does not represent movement

(2) Includes P40 which is non-spatial and P49 which is spatially implicit; these models do not explicitly represent movement behaviour

(3) Includes E23, P13 and P30, which are spatially implicit; E23 and P30 include spatially implicit movement behaviour

Abbreviations key.

Model type: DEB Dynamic Energy Budget; IBM Individual-Based Model; SDM Species Distribution Model.

Output: BR behavioural response; DIST distribution; PD population dynamics; PG population growth; STRUC population structure; VISIT visitation rates.

Demographics: EB energy budget; DR demographic rates; GF growth function; LHP life history parameters; TPF thermal performance function.

Movement: BP biophysical model; IL individual level; DDF distance decay function; DK dispersal kernel.

Spatial representation: NS non-spatial; SE spatially explicit; SI spatially implicit.

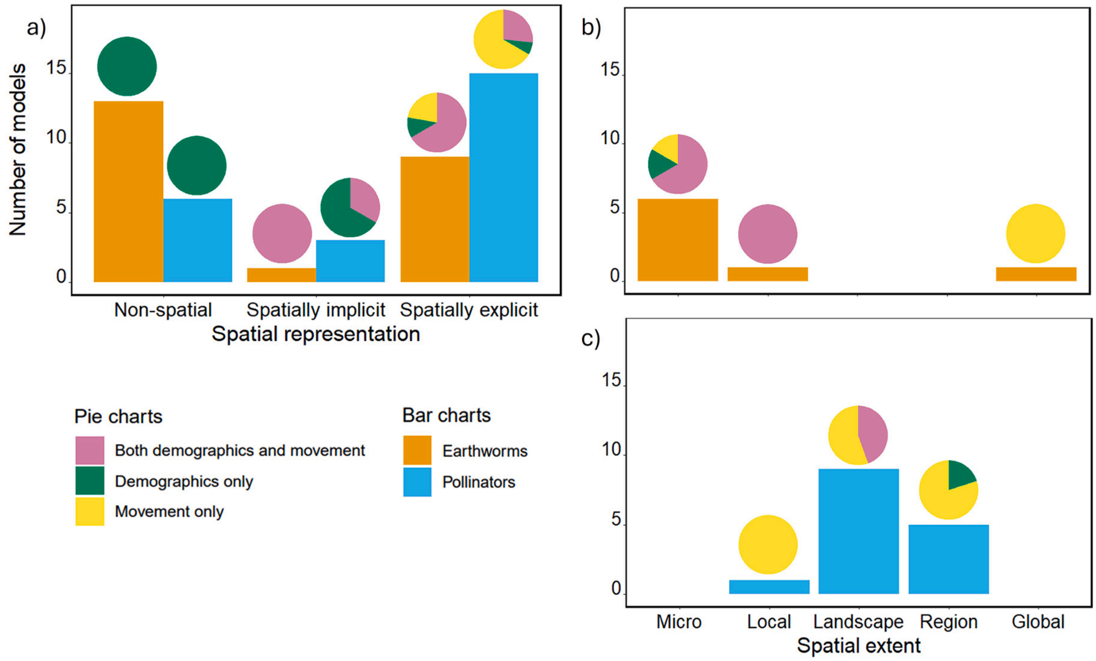

Fig. 3. Number of earthworm and wild pollinator models that include demographics, movement behaviour or both elements, across non-spatial, spatially implicit and spatially explicit models (panel a), and at different spatial extents for spatially explicit models of earthworms (panel b) and pollinators (panel c). Bars represent the number of models and accompanying pie charts represent the proportion of models for that bar which include demographics, movement behaviour or both elements. Movement behaviour refers to summed scores for movement process and behavioural decision-making. One spatially explicit earthworm model is excluded from panel b due to missing information (E22: spatial extent not reported). Spatial extent is standardised as the length of 1D models, square root of area of 2D models, and cube root of volume of 3D models; categories are as follows: micro: <10 m; local: <1 km; landscape: ≥1 km; regional: named region, country, supranational union or continent; global: whole world. Non-spatial models do not represent or specify locations, and spatially implicit models account for the effects of space without explicit representation.

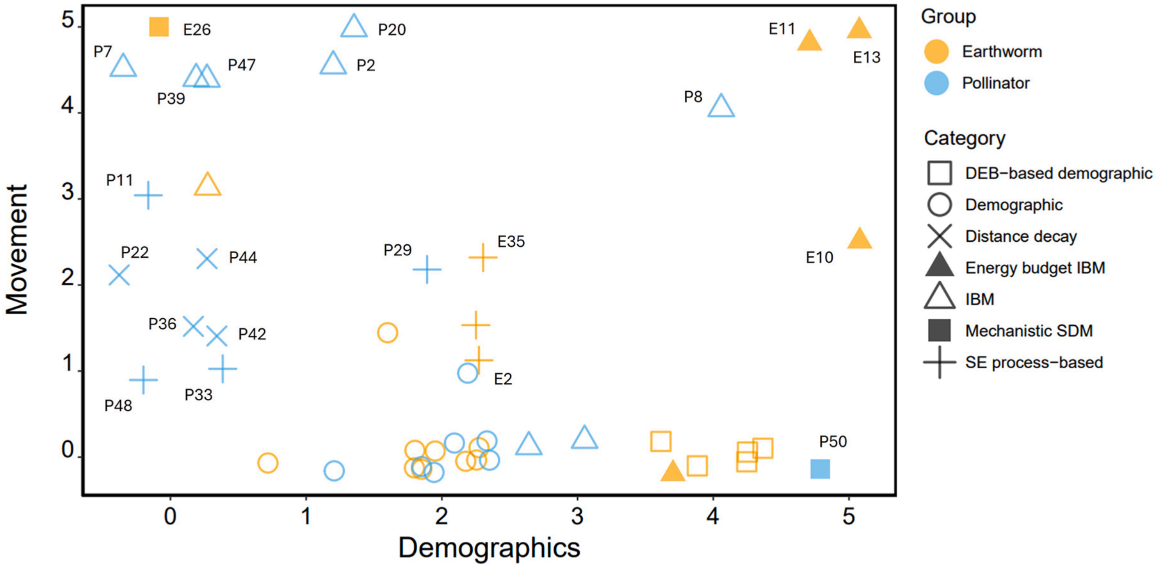

Fig. 4. Biological realism scores for demographics and movement behaviour (summed scores for movement process and behavioural decision-making). Shapes correspond to the model categories in Table 1 (also shown in the inset legend) and references for model IDs are available in Supplementary Table 4. Model IDs are given for spatially explicit models included in Fig. 5. Orange and blue shapes represent models for earthworms and pollinators, respectively, and have been jittered for visibility.

indicators (Table 1). In several cases, non-spatial demographic models have been linked with DEB models, which provide increased physiological detail and enable extrapolation of population responses to untested conditions (Jager et al., 2014). Johnston et al. (2018, 2014a, 2014b) employed an alternative energy budget modelling approach in a series of spatially explicit earthworm IBMs (E10, E11, E13). In addition to the detailed representation of physiology in these models, the inclusion of directional movement behaviour has proven critical for predicting population responses to multiple, often interacting, stressors such as tillage, herbicide applications, and climate change (Johnston et al., 2018; 2015). Although earthworms have relatively low mobility, experimental data indicates maximum annual dispersal rates that

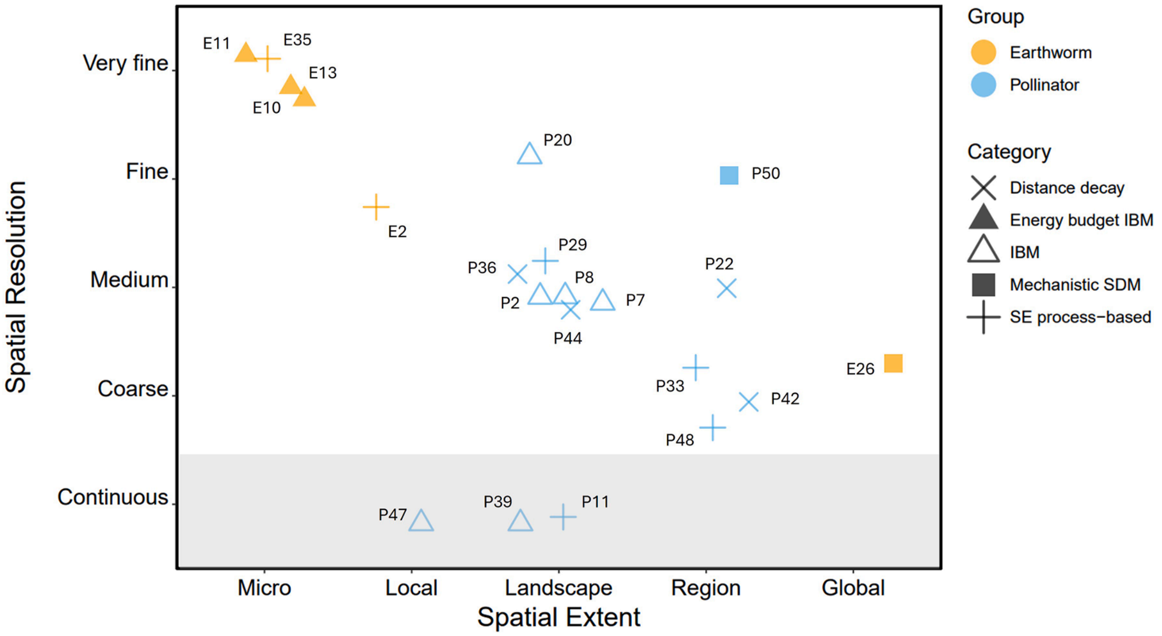

Fig. 5. Spatially explicit earthworm and wild pollinator models plotted against modelled spatial extent and resolution (excluding spatially implicit and non-spatial models). Shapes correspond to the model categories in Table 1 (also shown in the inset legend) and references for model IDs are available in Supplementary Table 4. Orange and blue shapes represent models for earthworms and pollinators, respectively, and have been jittered for visibility. Biological realism scores for these models can be identified from Fig. 4. Three spatially explicit earthworm models are excluded from this figure due to missing information (E3: micro extent, resolution not reported; E4M2: micro extent, resolution not reported; E22: continuous resolution, extent not reported). For spatial extent categories see Fig. 3 caption. Spatial resolution categories are as follows: very fine: <1 m^2; fine: <100 m^2; medium: <1000 m^2; coarse: ≥ 1000 m^2. Models that represent space continuously do not have a specified resolution.

exceed the spatial extent of existing mechanistic IBMs (e.g. 4.6 m per year for *Lumbricus terrestris* in an arable field; Nuutinen et al., 2011). However, uncertainty propagation, the accumulation of stochastic effects, and the computational demands of biologically detailed, fine-resolution simulations present tractability challenges for extending mechanistic IBMs to larger spatial extents (Evans, 2012; Johnston, 2024).

Wild pollinator models have often been developed to predict crop visitation rates (as a proxy for pollination services) and so characteristically represent movement behaviour within spatially explicit model environments (Table 1). Spatially explicit pollinator IBMs relate individual-level movement behaviour to landscape composition and configuration through decision-making processes informed by assessment of habitat quality or memory of rewarding locations. For example, Arrignon et al. (2007, P7) and Everaars and Dormann (2014, P20) implement patch departure rules based on the Marginal Value Theorem (Charnov, 1976) to describe fitness-maximising foraging behaviour and its influence on survival or reproductive outcomes, respectively. However, the integration of movement behaviour with a complete life cycle is rare within pollinator IBMs (Becher et al., 2018, P8 is a notable exception; Fig. 4). At the population level, wild pollinator models often employ functional responses between colony or population growth and floral resources in demographic models, or use aggregated representations of movement, such as diffusion equations or dispersal kernels, in spatially explicit models (Table 1). Model capacity to predict population abundance or visitation rates will, however, be limited when feedback between these dynamics is not accounted for (Häussler et al., 2017).

The trade-off between biological realism and spatial extent is well demonstrated by distance decay models, which achieve tractability at the landscape level through simplifying assumptions that derive pollinator abundance from habitat suitability and equate foraging behaviour with diffusion (Lonsdorf et al., 2009, P36) (Fig. 5). Subsequent adaptations have incorporated principles of optimal foraging, enhancing model capacity to predict spatial variation in visitation rates in response to small-scale interventions such as flower strips (Fernandes et al., 2020, P22; Nicholson et al., 2019; Olsson et al., 2015, P44). Nevertheless, models of this type produce static predictions that cannot account for the effects of intra- and inter-seasonal population dynamics on visitation rates. Of the process-based pollinator models reviewed here, only Häussler et al. (2017, P29) combine demographics and movement behaviour in a spatially explicit model, enabling predictions of contrasting short- and long-term effects of land management interventions on visitation rates, driven by increasing population abundance over time. Gardner et al. (2021) note that the explicit representation of dispersal paths could improve predictions for fragmented agricultural landscapes by accounting for adaptive movement behaviour. However, the continued refinement of landscape-level pollinator population models is constrained by computational demand (Gardner et al., 2020).

Mechanistic SDMs are based on fundamental constraints to species distribution (here, thermal performance functions in Tomlinson et al., 2018, P50; and biomechanical limits to burrowing in Ruiz et al., 2021, E26), which enable extrapolation of individual-level responses over large spatial extents. In this way, mechanistic SDMs subvert the overall trend for decreasing biological realism with increasing spatial scale. However, similar to correlative SDMs, mechanistic SDMs are designed to provide static, equilibrium predictions rather than to simulate the demographic and dispersal processes that determine population dynamics in spatiotemporally heterogeneous environments (Briscoe et al., 2019; Evans et al., 2015; Guisan and Zimmermann, 2000; Kearney and Porter, 2009; Peterson et al., 2015). Mechanistic SDMs therefore have limited capacity to address critical evidence gaps regarding land management interventions, such as the occurrence of time lags in population responses, which require predictions of transient dynamics (Guisan and Zimmermann, 2000; Iles et al., 2018; Kleijn et al., 2019; Zurell et al., 2022).

4.2. *Evaluating biological realism: strengths and limitations of our approach*

The variation in earthworm and wild pollinator population model structures was addressed, for the purpose of this review, by developing a novel scoring scheme. The biological realism scores were critical in enabling us to quantify trade-offs in model structure across taxa and spatial scales (Figs. 4 and 5), which has rarely been attempted in ecological modelling. Model intercomparisons which involve the re-implementation of models under a standardised environmental scenario, such as that of Bahlburg et al. (2023), enable a comprehensive assessment of model structures, computational demands, predictive performance, and transferability. However, this type of comparison will not necessarily be possible or informative across models developed for different taxa, management questions, and spatiotemporal scales. Our approach therefore relies on model documentation, which does not consistently include measures of computational tractability (e.g. CPU time) or predictive performance (validation).

Our scoring scheme holds promise for reproducible and transparent model comparisons by providing a common framework to evaluate diverse models. The biological realism scores can also be used to guide model development and communicate design choices in a similar manner to how the categories of general, realistic, and precise are used within the Pop-GUIDE framework to link model purpose and data availability to the appropriate representation of model characteristics (Raimondo et al., 2021). However, our approach is not without limitations and could be refined in future applications. Developing standardised scores for a wide range of models inevitably involved a loss of nuance regarding some aspects of the representation of demographics and movement behaviour. For example, the distinct ecology of eusocial pollinators presented a complication: colonies function as reproductive units and could arguably be considered individuals for demographic purposes, but were treated here as sub-populations for consistency. More generally, the scheme allocates a single score to each of demographics, movement process, and behavioural decision-making, and therefore does not fully account for the number or variety of mechanisms and/or processes included in a model.

Our approach is restricted to demographics and movement behaviour because our aim was to evaluate biological realism in relation to population-level outputs at the spatiotemporal scales relevant to land management decisions. However, these are not the only elements that contribute to biological or structural realism. Future applications could extend the framework to include additional biological mechanisms and processes (e.g. evolutionary adaptation, community-level biotic interactions) and/or incorporate other dimensions of structural realism (e.g. resource dynamics, landscape heterogeneity, weather, climate) (Evans et al., 2019; Grimm and Berger, 2016a; Johnston, 2024; Rouabah et al., 2024). A comprehensive evaluation of structural realism, including the representation of biotic and abiotic model components and their relevance to the system in question, would enable assessment of model suitability for specific land management or environmental scenarios (Schuwirth et al., 2019).

Although our analysis focuses on biological realism in relation to spatial scale, we recognise that different temporal representations (e.g. continuous time or discrete time steps, varying temporal extents) may strongly influence predictions, and warrant further investigation (Radchuk et al., 2014). For example, pollinator population dynamics in the Poll4pop model are closely tied to the definition of seasons (floral periods), which can be varied for different applications (Gardner et al., 2021; Häussler et al., 2017; Image et al., 2022).

4.3. *Future directions for earthworm and wild pollinator population modelling*

Grimm and Berger (2016a) argue that ecological models achieve greater structural realism when population dynamics emerge from lower-level interactions described by first principles of physiological and behavioural ecology. Such approaches allow for phenotypic plasticity in spatiotemporally heterogenous environments, which is particularly important for small ectotherms such as bees and earthworms, whose demographic and behavioural responses are strongly shaped by physiological processes (e.g. thermal performance, moisture sensitivity) (Abram et al., 2017; Deutsch et al., 2008; Kenna et al., 2021; Singh et al., 2019; Woods et al., 2015). Our findings indicate, however, that integrating physiological and behavioural mechanisms remains a key challenge for predicting invertebrate population responses at management-relevant spatial scales. Despite the divergent trajectories of earthworm and wild pollinator population models (Figs. 4 and 5), our framework therefore points to complementary directions for future work, for instance by scaling up dispersal processes for earthworms and incorporating greater physiological detail in landscape-level pollinator models.

In a recent review, Rouabah et al. (2024) identified weather and climate, floral resource dynamics, and agricultural management practices such as pesticide applications as future avenues for improving pollination models. However, concurrent advances in the representation of physiological detail will be required to capture the interactive effects of these factors on emergent population dynamics (Leroy et al., 2023). Since the completion of our literature review, several models have made progress in this direction through distinct approaches. Schmolke at al. (2024) extended an existing trait-based solitary bee model by incorporating a toxicokinetic–toxicodynamic module to capture individual-level effects of pesticide exposure. Capera-Aragones et al. (2025) linked a colony-level DEB model for bumblebees with spatially explicit predictions of forager distributions, using a system of differential equations and MaxEnt methods to manage computational demand. Addressing the limited availability of hoverfly models, App et al. (2025) developed an IBM that simulates in detail the life cycle and movement behaviour of *Episyrphus balteatus*. App et al. (2025) follow a similar approach to BumbleBEEHAVE (Becher et al., 2018, P8) (for example in terms of the landscape representation, use of cohort-based life stages, and tracking of energy gain and expenditure) to predict population responses to resource availability at the landscape level. These publications reflect sustained momentum in pollinator model development (Fig. 2) and are not matched by recent progress in earthworm population modelling.

Small-bodied yet highly mobile invertebrates such as bees and hoverflies present particular difficulties regarding the realism-tractability trade-off due to the need for large model spatial extents relative to resolution. However, future directions in earthworm modelling also pose significant tractability challenges, with calls for further integration of the complex feedbacks between earthworms and soil properties alongside extension of models to larger spatial scales (Johnston et al., 2018; Reed et al., 2016). More informed predictions of spatiotemporal earthworm population dynamics at the field level could address key evidence gaps in agricultural management and ecological risk assessment (Bartlett et al., 2010; Schneider and Schröder, 2012). Cross-taxon approaches that support the application of mechanistic models across broad spatial extents will therefore be highly valuable and contribute to reduced siloing in ecological modelling.

4.4. *Strategies to advance ecological models for evidence-based land management*

Optimising model structure for a specific species, management question, and spatial scale allows model development to fall within the Medawar zone of effort versus payoff, leading to models that appear suitable for, and may perform well in, a certain context (Grimm, 2023; Wang et al., 2024). Nevertheless, the potential for enhanced predictive power and transferability across management scenarios, environmental conditions, and geographic regions provides a strong rationale for focusing modelling efforts towards approaches that enable greater biological realism over broader spatial extents (Grimm and Berger, 2016a; Radchuk et al., 2019; Schuwirth et al., 2019; Topping et al., 2015). Systematic model testing is a crucial next step for quantifying the relationship between biological realism, spatial extent, computational demand, and predictive performance (Grimm and Berger, 2016b; Johnston, 2024). Where possible, building on the progress made by existing models (for example, adapting an energy budget for a new species or using established theories of behavioural decision-making) will allow for more effort to be put towards model implementation, modification, and testing (Grimm, 2023; Grimm et al., 2017; Thiele and Grimm, 2015).

Several strategies are available to streamline this process. Deep-shallow model comparison can be used to systematically simplify a complex model to identify a minimum realistic model at a new spatial scale (Fulton et al., 2003; Raick et al., 2006). Pattern-oriented modelling (POM) evaluates the ability of alternative submodels to reproduce multiple empirical patterns across different spatial scales and ecological levels (Gallagher et al., 2021; Grimm et al., 2005; Grimm and Railsback, 2012; Wang et al., 2024). Complementing POM, robustness analysis (RA) involves making modifications to model structure and parameterisation to identify robust explanations of system behaviour (Grimm and Berger, 2016b). Rejection-Approximate Bayesian Computation (ABC) further provides a quantitative method for comparing submodels with different structures while accounting for variations in complexity and uncertainty (Grimm and Berger, 2016a; van der Vaart et al., 2016). These strategies can help reveal relationships between mechanisms, processes, and system behaviour across spatial scales, providing evidence for where higher biological realism is important and where efficiencies can be gained. It may not always be possible to initiate these strategies with highly detailed (sub)models, depending on existing models of the intended species or the availability of suitable individual-level data for model development. However, identifying knowledge gaps that cause parameter and structural uncertainty through model development and testing can guide empirical research, thereby enabling greater biological realism and improved predictions in future model iterations (Railsback et al., 2025; Urban et al., 2016).

Systematic model testing will underpin the development of more predictive models at management-relevant spatial scales. In turn, adaptive management practices provide the opportunity to test models in a real-world setting, where the implementation and monitoring of land management interventions generates empirical data to inform iterative model refinement and validation (Lahoz-Monfort et al., 2014; Perry and Bond, 2013; Schuwirth et al., 2019). Validation is essential for assessing model predictive performance and should ideally encompass transferability, requiring independent data sets that also represent distinct conditions (Schuwirth et al., 2019; Wenger and Olden, 2012). New monitoring requirements associated with national AES schemes and the European Union’s Nature Restoration Law are set to improve future data availability for earthworms and pollinators (European Commission, 2024; Rural Payments Agency, 2023). Models that can incorporate greater biological detail at broad spatial extents will be best able to make use of both large-scale data sets for model validation and individual-level data for parameterisation, to improve the reliability of predictions supporting management decisions (Railsback et al., 2025; Rouabah et al., 2024; Singer et al., 2016; Urban et al., 2016).

Transparency in model development must be accompanied by consistent model communication to overcome the culture of siloed modelling in ecology and increase the accessibility of biologically realistic models for decision support (Gregr and Chan, 2015; Grimm, 2023; Grimm and Berger, 2016a; Schuwirth et al., 2019). Model reviews and comparisons provide a synthesis of existing approaches that is crucial for guiding future modelling efforts but can be hindered by unclear terminology and incomplete model documentation (Grimm, 2023; Thiele and Grimm, 2015). Consistent and precise use of key terms aids the identification and categorisation of relevant models (Schmolke et al., 2010a). However, the terms ‘mechanistic’ and ‘process-based’ are often used interchangeably, obscuring a critical distinction between ecological modelling approaches (Johnston, 2024). Discrepancies in model reporting make it difficult to locate information about model structure, whereas articles that adopt the Overview, Design concepts and Details (ODD) protocol (Grimm et al., 2020a) or the TRAnsparent and Comprehensive Ecological modelling documentation (TRACE) framework (Grimm et al., 2014) facilitate clearer model comprehension and here enabled more direct evaluation using our biological realism scores.

5. Conclusion

Biologically realistic models are essential for predicting emergent population responses under alternative land management scenarios and changing environmental conditions. Yet, model development faces a fundamental trade-off between realism and tractability, which is magnified with increasing spatial extent. Our novel biological realism scores reveal how existing earthworm and wild pollinator population models address this trade-off through species- and scale-specific approaches. Consequently, there remains a need for greater integration of physiological and behavioural mechanisms across broader spatial extents and alongside other essential elements for representing detailed land management and environmental scenarios (e.g. resource dynamics, landscape heterogeneity, weather, climate). We propose systematic model testing across spatial scales as a crucial next step to advance predictive ecological models. This process would: (1) enable further quantification of the relationship between biological realism, computational demand, predictive performance, and spatial extent; (2) facilitate the identification of new approaches to resolve the trade-off between realism and tractability; and (3) ensure decisions about model structure are explicit, supporting transparent model communication. Our biological realism scoring scheme complements this process by providing a framework to categorise, communicate, and compare key model elements. The scoring scheme will benefit from further testing and refinement to ensure its applicability across diverse taxa and model types and establish its use across model development, reporting, and comparisons. Lastly, integrating model development with empirical research and adaptive management practices will be essential for accessing data to support reliable predictions. Together, these developments will be critical to strengthening the role of ecological models in evidence-based land management.

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CRediT authorship contribution statement

Harriet M. Gold: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Conceptualization. **Jacqueline A. Hannam:** Writing – review & editing, Methodology. **Simon G. Potts:** Writing – review & editing, Methodology. **Claire Brittain:** Writing – review & editing. **Nika Galic:** Writing – review & editing. **Alice S.A. Johnston:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Harriet Gold reports financial support was provided by Syngenta UK Ltd. Harriet Gold reports financial support was provided by Biotechnology and Biological Sciences Research Council. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2025.111399.

Data availability

No data was used for the research described in the article.

References

Abram, P.K., Boivin, G., Moiroux, J., Brodeur, J., 2017. Behavioural effects of temperature on ectothermic animals: unifying thermal physiology and behavioural plasticity. Biol. Rev. 92, 1859–1876. https://doi.org/10.1111/brv.12312.

Accolla, C., Vaugeois, M., Grimm, V., Moore, A.P., Rueda-Cediel, P., Schmolke, A., Forbes, V.E., 2021. A review of key features and their implementation in unstructured, structured, and agent-based population models for ecological risk assessment. Integr Env. Assess Manag. 17, 521–540. https://doi.org/10.1002/ieam.4362.

App, M., Hellwig, N., Schneider-Hohenbrink, A.-K., Burmeister, J., Schröder, B., Thiele, J., 2025. SyrFitSources: an agent-based model to investigate the effects of land use on the population dynamics of aphidophagous hoverflies. Ecol. Modell. 507, 111098. https://doi.org/10.1016/j.ecolmodel.2025.111098.

Arrignon, F., Deconchat, M., Sarthou, J.-P., Balent, G., Monteil, C., 2007. Modelling the overwintering strategy of a beneficial insect in a heterogeneous landscape using a multi-agent system. Ecol. Modell. 205, 423–436. https://doi.org/10.1016/j.ecolmodel.2007.03.006.

Bahlburg, D., Thorpe, S.E., Meyer, B., Berger, U., Murphy, E.J., 2023. An intercomparison of models predicting growth of Antarctic krill (Euphausia superba): the importance of recognizing model specificity. PLOS ONE 18, e0286036. https://doi.org/10.1371/journal.pone.0286036.

Barrios, E., 2007. Soil biota, ecosystem services and land productivity. Ecol. Econ. Spec. Sect. - Ecosyst. Serv. Agric. 64, 269–285. https://doi.org/10.1016/j.ecolecon.2007.03.004.

Bartlett, M.D., Briones, M.J.I., Neilson, R., Schmidt, O., Spurgeon, D., Creamer, R.E., 2010. A critical review of current methods in earthworm ecology: from individuals to populations. Eur. J. Soil Biol. 46, 67–73. https://doi.org/10.1016/j.ejsobi.2009.11.006.

Batáry, P., Báldi, A., Ekroos, J., Gallé, R., Grass, I., Tscharntke, T., 2020. Biologia Futura: landscape perspectives on farmland biodiversity conservation. Biol. Futura 71, 9–18. https://doi.org/10.1007/s42977-020-00015-7.

Batáry, P., Báldi, A., Kleijn, D., Tscharntke, T., 2010. Landscape-moderated biodiversity effects of agri-environmental management: a meta-analysis. Proc. R. Soc. B: Biol. Sci. 278, 1894–1902. https://doi.org/10.1098/rspb.2010.1923.

Batáry, P., Dicks, L.V., Kleijn, D., Sutherland, W.J., 2015. The role of agri-environment schemes in conservation and environmental management. Conserv. Biol. 29, 1006–1016. https://doi.org/10.1111/cobi.12536.

Becher, M.A., Twiston-Davies, G., Penny, T.D., Goulson, D., Rotheray, E.L., Osborne, J.L., 2018. Bumble-BEEHAVE: a systems model for exploring multifactorial causes of bumblebee decline at individual, colony, population and community level. J. Appl. Ecol. 55, 2790–2801. https://doi.org/10.1111/1365-2664.13165.

Blouin, M., Hodson, M.E., Delgado, E.A., Baker, G., Brussaard, L., Butt, K.R., Dai, J., Dendooven, L., Peres, G., Tondoh, J.E., Cluzeau, D., Brun, J.-J., 2013. A review of earthworm impact on soil function and ecosystem services. Eur. J. Soil Sci. 64, 161–182. https://doi.org/10.1111/ejss.12025.

Bommarco, R., Kleijn, D., Potts, S.G., 2013. Ecological intensification: harnessing ecosystem services for food security. Trends Ecol. Evol. 28, 230–238. https://doi.org/10.1016/j.tree.2012.10.012.

Breeze, T.D., Bailey, A.P., Balcombe, K.G., Potts, S.G., 2011. Pollination services in the UK: how important are honeybees? Agric. Ecosyst. Env. 142, 137–143. https://doi.org/10.1016/j.agee.2011.03.020.

Briscoe, N.J., Elith, J., Salguero-Gómez, R., Lahoz-Monfort, J.J., Camac, J.S., Giljohann, K.M., Holden, M.H., Hradsky, B.A., Kearney, M.R., McMahon, S.M., Phillips, B.L., Regan, T.J., Rhodes, J.R., Vesk, P.A., Wintle, B.A., Yen, J.D.L., Guillera-Arroita, G., 2019. Forecasting species range dynamics with process-explicit models: matching methods to applications. Ecol. Lett. 22, 1940–1956. https://doi.org/10.1111/ele.13348.

Brown, G.G., Barois, I., Lavelle, P., 2000. Regulation of soil organic matter dynamics and microbial activityin the drilosphere and the role of interactionswith other edaphic functional domains. Eur. J. Soil Biol. 36, 177–198. https://doi.org/10.1016/S1164-5563(00)01062-1.

Capera-Aragones, P., Mariño, J., Hurford, A., Tyson, R.C., Foxall, E., 2025. Whole-colony dynamic energy budget model for bumble bees: assessing the impact of wildflower patches on crop pollination. Bull. Math. Biol. 87, 83. https://doi.org/10.1007/s11538-025-01448-8.

Catford, J.A., Wilson, J.R.U., Pyšek, P., Hulme, P.E., Duncan, R.P., 2022. Addressing context dependence in ecology. Trends Ecol. Evol. 37, 158–170. https://doi.org/10.1016/j.tree.2021.09.007.

Charnov, E.L., 1976. Optimal foraging, the marginal value theorem. Theor. Popul. Biol. 9, 129–136. https://doi.org/10.1016/0040-5809(76)90040-X.

Cooke, S.J., Blumstein, D.T., Buchholz, R., Caro, T., Fernández-Juricic, E., Franklin, C.E., Metcalfe, J., O'Connor, C.M., St. Clair, C.C., Sutherland, W.J., Wikelski, M., 2014. Physiology, behavior, and conservation. Physiol. Biochem. Zool. 87, 1–14. https://doi.org/10.1086/671165.

DeAngelis, D.L., Diaz, S.G., 2019. Decision-making in agent-based modeling: a current review and future prospectus. Front. Ecol. Evol. 6. https://doi.org/10.3389/fevo.2018.00237.

DeAngelis, D.L., Grimm, V., 2014. Individual-based models in ecology after four decades. F1000Prime Rep. 6, 39. https://doi.org/10.12703/P6-39.

DeAngelis, D.L., Yurek, S., 2017. Spatially explicit Modeling in Ecology: a review. Ecosystems 20, 284–300. https://doi.org/10.1007/s10021-016-0066-z.

DEFRA, 2023. Environmental Land Management update: How Government Will Pay For Land-Based Environment and Climate Goods and Services. Department for Environment, Food and Rural Affairs e.

Deutsch, C.A., Tewksbury, J.J., Huey, R.B., Sheldon, K.S., Ghalambor, C.K., Haak, D.C., Martin, P.R., 2008. Impacts of climate warming on terrestrial ectotherms across latitude. Proc. Natl. Acad. Sci. 105, 6668–6672. https://doi.org/10.1073/pnas.0709472105.

Díaz, M., Concepción, E.D., 2016. Enhancing the effectiveness of CAP greening as a conservation tool: a plea for regional targeting considering landscape constraints. Curr. Landsc. Ecol. Rep. 1, 168–177. https://doi.org/10.1007/s40823-016-0017-6.

Diekötter, T., Wamser, S., Wolters, V., Birkhofer, K., 2010. Landscape and management effects on structure and function of soil arthropod communities in winter wheat. .. Agric. Ecosyst. Environ. Spec. Sect. Harvest. Perenn. Grassl.: Ecol. Models Farming's Perenn. Future 137, 108–112. https://doi.org/10.1016/j.agee.2010.01.008.

Dormann, C.F., Schymanski, S.J., Cabral, J., Chuine, I., Graham, C., Hartig, F., Kearney, M., Morin, X., Römermann, C., Schröder, B., Singer, A., 2012. Correlation and process in species distribution models: bridging a dichotomy. J. Biogeogr. 39, 2119–2131. https://doi.org/10.1111/j.1365-2699.2011.02659.x.

Doyle, T., Hawkes, W.L.S., Massy, R., Powney, G.D., Menz, M.H.M., Wotton, K.R., 2020. Pollination by hoverflies in the Anthropocene. Proc. R. Soc. B: Biol. Sci. 287, 20200508. https://doi.org/10.1098/rspb.2020.0508.

Ekroos, J., Olsson, O., Rundlöf, M., Wätzold, F., Smith, H.G., 2014. Optimizing agri-environment schemes for biodiversity, ecosystem services or both? Biol. Conserv. 172, 65–71. https://doi.org/10.1016/j.biocon.2014.02.013.

European Commission, 2024. The EU #NatureRestoration Law [WWW Document]. URL. https://environment.ec.europa.eu/topics/nature-and-biodiversity/nature-restoration-law_en. accessed 9.3.24.

Evans, L.C., Sibly, R.M., Thorbek, P., Sims, I., Oliver, T.H., Walters, R.J., 2019. Integrating the influence of weather into mechanistic models of butterfly movement. Mov. Ecol. 7, 24. https://doi.org/10.1186/s40462-019-0171-7.

Evans, M.R., 2012. Modelling ecological systems in a changing world. Philos. Trans. R. Soc. B: Biol. Sci. 367, 181–190. https://doi.org/10.1098/rstb.2011.0172.

Evans, M.R., Grimm, V., Johst, K., Knuuttila, T., De Langhe, R., Lessells, C.M., Merz, M., O'Malley, M.A., Orzack, S.H., Weisberg, M., Wilkinson, D.J., Wolkenhauer, O., Benton, T.G., 2013. Do simple models lead to generality in ecology? Trends Ecol. Evol. 28, 578–583. https://doi.org/10.1016/j.tree.2013.05.022.

Evans, T.G., Diamond, S.E., Kelly, M.W., 2015. Mechanistic species distribution modelling as a link between physiology and conservation. Conserv. Physiol. 3, cov056. https://doi.org/10.1093/conphys/cov056.

Everaars, J., Dormann, C.F., 2014. Simulation of solitary (Non-Apis) bees competing for pollen. Silico Bees. CRC Press.

Fahrig, L., Baudry, J., Brotons, L., Burel, F.G., Crist, T.O., Fuller, R.J., Sirami, C., Siriwardena, G.M., Martin, J.-L., 2011. Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. Ecol. Lett. 14, 101–112. https://doi.org/10.1111/j.1461-0248.2010.01559.x.

Fernandes, J., Antunes, P., Santos, R., Zulian, G., Clemente, P., Ferraz, D., 2020. Coupling spatial pollination supply models with local demand mapping to support collaborative management of ecosystem services. Ecosyst. People 16, 212–229. https://doi.org/10.1080/26395916.2020.1800821.

Fritsch, M., Lischke, H., Meyer, K.M., 2020. Scaling methods in ecological modelling. Methods Ecol. Evol. 11, 1368–1378. https://doi.org/10.1111/2041-210X.13466.

Fulton, E.A., Smith, A.D.M., Johnson, C.R., 2003. Effect of complexity on marine ecosystem models. Mar. Ecol. Prog. Ser. 253, 1–16. https://doi.org/10.3354/meps253001.

Gabriel, D., Sait, S.M., Hodgson, J.A., Schmutz, U., Kunin, W.E., Benton, T.G., 2010. Scale matters: the impact of organic farming on biodiversity at different spatial scales. Ecol. Lett. 13, 858–869. https://doi.org/10.1111/j.1461-0248.2010.01481.x.

Galic, N., Sullivan, L.L., Grimm, V., Forbes, V.E., 2018. When things don't add up: quantifying impacts of multiple stressors from individual metabolism to ecosystem processing. Ecol. Lett. 21, 568–577. https://doi.org/10.1111/ele.12923.

Gallagher, C.A., Chudzinska, M., Larsen-Gray, A., Pollock, C.J., Sells, S.N., White, P.J.C., Berger, U., 2021. From theory to practice in pattern-oriented modelling: identifying and using empirical patterns in predictive models. Biol. Rev. 96, 1868–1888. https://doi.org/10.1111/brv.12729.

Gardner, E., Breeze, T.D., Clough, Y., Smith, H.G., Baldock, K.C.R., Campbell, A., Garratt, M.P.D., Gillespie, M.A.K., Kunin, W.E., McKerchar, M., Memmott, J., Potts, S.G., Senapathi, D., Stone, G.N., Wäckers, F., Westbury, D.B., Wilby, A., Oliver, T.H., 2020. Reliably predicting pollinator abundance: challenges of calibrating process-based ecological models. Methods Ecol. Evol. 11, 1673–1689. https://doi.org/10.1111/2041-210X.13483.

Gardner, E., Breeze, T.D., Clough, Y., Smith, H.G., Baldock, K.C.R., Campbell, A., Garratt, M.P.D., Gillespie, M.A.K., Kunin, W.E., McKerchar, M., Potts, S.G., Senapathi, D., Stone, G.N., Wäckers, F., Westbury, D.B., Wilby, A., Oliver, T.H., 2021. Field boundary features can stabilise bee populations and the pollination of mass-flowering crops in rotational systems. J. Appl. Ecol. 58, 2287–2304. https://doi.org/10.1111/1365-2664.13948.

Gardner, E., Robinson, R.A., Julian, A., Boughey, K., Langham, S., Tse-Leon, J., Petrovskii, S., Baker, D.J., Bellamy, C., Buxton, A., Franks, S., Monk, C., Morris, N., Park, K.J., Petrovan, S., Pitt, K., Taylor, R., Turner, R.K., Allain, S.J.R., Bradley, V., Broughton, R.K., Cartwright, M., Clarke, K., Cranfield, J., Fuentes-Montemayor, E., Gandola, R., Gent, T., Hinsley, S.A., Madsen, T., Reading, C., Redhead, J.W., Reveley, S., Wilkinson, J., Williams, C., Woodward, I., Baker, J., Briggs, P., Dyason, S., Langton, S., Mawby, A., Pywell, R.F., Bullock, J.M., 2024. A family of process-based models to simulate landscape use by multiple taxa. Landsc. Ecol. 39, 102. https://doi.org/10.1007/s10980-024-01866-4.

Garibaldi, L.A., Carvalheiro, L.G., Leonhardt, S.D., Aizen, M.A., Blaauw, B.R., Isaacs, R., Kuhlmann, M., Kleijn, D., Klein, A.M., Kremen, C., Morandin, L., Scheper, J., Winfree, R., 2014. From research to action: enhancing crop yield through wild pollinators. Front. Ecol. Env. 12, 439–447. https://doi.org/10.1890/130330.

Garratt, M.P.D., Coston, D.J., Truslove, C.L., Lappage, M.G., Polce, C., Dean, R., Biesmeijer, J.C., Potts, S.G., 2014. The identity of crop pollinators helps target conservation for improved ecosystem services. Biol. Conserv. 169, 128–135. https://doi.org/10.1016/j.biocon.2013.11.001.

Gregr, E.J., Chan, K.M.A., 2015. Leaps of faith: how implicit assumptions compromise the utility of ecosystem models for decision-making. BioScience 65, 43–54. https://doi.org/10.1093/biosci/biu185.

Grimm, V., 2023. Ecology needs to overcome siloed modelling. Trends Ecol. Evol. 38, 1122–1124. https://doi.org/10.1016/j.tree.2023.09.011.

Grimm, V., Augusiak, J., Focks, A., Frank, B.M., Gabsi, F., Johnston, A.S.A., Liu, C., Martin, B.T., Meli, M., Radchuk, V., Thorbek, P., Railsback, S.F., 2014. Towards better modelling and decision support: documenting model development, testing, and analysis using TRACE. .Ecol. Model. Popul. Models Ecol. Risk Assess. Chem. 280, 129–139. https://doi.org/10.1016/j.ecolmodel.2014.01.018.

Grimm, V., Ayllón, D., Railsback, S.F., 2017. Next-generation individual-based models integrate biodiversity and ecosystems: yes we can, and yes we must. Ecosystems 20, 229–236. https://doi.org/10.1007/s10021-016-0071-2.

Grimm, V., Berger, U., 2016a. Structural realism, emergence, and predictions in next-generation ecological modelling: synthesis from a special issue. .....Ecol. Model. Next Gener. Ecol. Model. Concepts Theory: Struct. Realism Emerg. Predict. 326, 177–187. https://doi.org/10.1016/j.ecolmodel.2016.01.001.

Grimm, V., Berger, U., 2016b. Robustness analysis: deconstructing computational models for ecological theory and applications. Ecol. Model. Next Gener. Ecol. Model. Concepts Theory: Struct. Realism Emerg. Predict. 326, 162–167. https://doi.org/10.1016/j.ecolmodel.2015.07.018.

Grimm, V., Railsback, S.F., 2012. Pattern-oriented modelling: a 'multi-scope' for predictive systems ecology. Philos. Trans. R. Soc. B: Biol. Sci. 367, 298–310. https://doi.org/10.1098/rstb.2011.0180.

Grimm, V., Railsback, S.F., Vincenot, C.E., Berger, U., Gallagher, C., Deangelis, D.L., Edmonds, B., Ge, J., Giske, J., Groeneveld, J., Johnston, A.S.A., Milles, A., Nabe-Nielsen, J., Polhill, J.G., Radchuk, V., Rohwäder, M.S., Stillman, R.A., Thiele, J.C., Ayllón, D., 2020a. The ODD protocol for describing agent-based and other simulation models: a second update to improve clarity, replication, and structural realism. J. Artif. Soc. Soc. Simul. 23.

Grimm, V., Revilla, E., Berger, U., Jeltsch, F., Mooij, W.M., Railsback, S.F., Thulke, H.-H., Weiner, J., Wiegand, T., DeAngelis, D.L., 2005. Pattern-oriented modeling of agent-based Complex systems: lessons from ecology. Science 310, 987–991. https://doi.org/10.1126/science.1116681.

Grimm, V., Johnston, A.S.A., Thulke, H.-H., Forbes, V.E., Thorbek, P., 2020b. Three questions to ask before using model outputs for decision support. Nat. Commun. 11, 4959. https://doi.org/10.1038/s41467-020-17785-2.

Guisan, A., Thuiller, W., 2005. Predicting species distribution: offering more than simple habitat models. Ecol. Lett. 8, 993–1009. https://doi.org/10.1111/j.1461-0248.2005.00792.x.

Guisan, A., Zimmermann, N.E., 2000. Predictive habitat distribution models in ecology. Ecol. Modell. 135, 147–186. https://doi.org/10.1016/S0304-3800(00)00354-9.

Häussler, J., Sahlin, U., Baey, C., Smith, H.G., Clough, Y., 2017. Pollinator population size and pollination ecosystem service responses to enhancing floral and nesting resources. Ecol. Evol. 7, 1898–1908. https://doi.org/10.1002/ece3.2765.

Iles, D.T., Williams, N.M., Crone, E.E., 2018. Source-sink dynamics of bumblebees in rapidly changing landscapes. J. Appl. Ecol. 55, 2802–2811. https://doi.org/10.1111/1365-2664.13175.

Image, M., Gardner, E., Clough, Y., Smith, H.G., Baldock, K.C.R., Campbell, A., Garratt, M., Gillespie, M.A.K., Kunin, W.E., McKerchar, M., Memmott, J., Potts, S.G., Senapathi, D., Stone, G.N., Wackers, F., Westbury, D.B., Wilby, A., Oliver, T.H., Breeze, T.D., 2022. Does agri-environment scheme participation in England increase pollinator populations and crop pollination services? .Agric. Ecosyst. Env. 325, 107755. https://doi.org/10.1016/j.agee.2021.107755.

Jager, T., Barsi, A., Hamda, N.T., Martin, B.T., Zimmer, E.I., Ducrot, V., 2014. Dynamic energy budgets in population ecotoxicology: applications and outlook. Ecol. Modell. Popul. Models Ecol. Risk Assess. Chem. 280, 140–147. https://doi.org/10.1016/j.ecolmodel.2013.06.024.

Johnston, A.S.A., 2024. Predicting emergent animal biodiversity patterns across multiple scales. Glob. Chang. Biol. 30, e17397. https://doi.org/10.1111/gcb.17397.

Johnston, A.S.A., Boyd, R.J., Watson, J.W., Paul, A., Evans, L.C., Gardner, E.L., Boult, V. L., 2019. Predicting population responses to environmental change from individual-level mechanisms: towards a standardized mechanistic approach. Proc. R. Soc. B: Biol. Sci. 286, 20191916. https://doi.org/10.1098/rspb.2019.1916.

Johnston, A.S.A., Hodson, M.E., Thorbek, P., Alvarez, T., Sibly, R.M., 2014a. An energy budget agent-based model of earthworm populations and its application to study the effects of pesticides. Ecol. Modell. Popul. Models Ecol. Risk Assess. Chem. 280, 5–17. https://doi.org/10.1016/j.ecolmodel.2013.09.012.

Johnston, A.S.A., Holmstrup, M., Hodson, M.E., Thorbek, P., Alvarez, T., Sibly, R.M., 2014b. Earthworm distribution and abundance predicted by a process-based model. Appl. Soil Ecol. 84, 112–123. https://doi.org/10.1016/j.apsoil.2014.06.001.

Johnston, A.S.A., Sibly, R.M., Hodson, M.E., Alvarez, T., Thorbek, P., 2015. Effects of agricultural management practices on earthworm populations and crop yield: validation and application of a mechanistic modelling approach. J. Appl. Ecol. 52, 1334–1342. https://doi.org/10.1111/1365-2664.12501.

Johnston, A.S.A., Sibly, R.M., Thorbek, P., 2018. Forecasting tillage and soil warming effects on earthworm populations. J. Appl. Ecol. 55, 1498–1509. https://doi.org/10.1111/1365-2664.13096.

Kearney, M., Porter, W., 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. Ecol. Lett. 12, 334–350. https://doi.org/10.1111/j.1461-0248.2008.01277.x.

Kenna, D., Pawar, S., Gill, R.J., 2021. Thermal flight performance reveals impact of warming on bumblebee foraging potential. Funct. Ecol. 35, 2508–2522. https://doi.org/10.1111/1365-2435.13887.

Kleijn, D., Baquero, R.A., Clough, Y., Díaz, M., De Esteban, J., Fernández, F., Gabriel, D., Herzog, F., Holzschuh, A., Jöhl, R., Knop, E., Kruess, A., Marshall, E.J.P., Steffan-Dewenter, I., Tscharntke, T., Verhulst, J., West, T.M., Yela, J.L., 2006. Mixed biodiversity benefits of agri-environment schemes in five European countries. Ecol. Lett. 9, 243–254. https://doi.org/10.1111/j.1461-0248.2005.00869.x.

Kleijn, D., Bommarco, R., Fijen, T.P.M., Garibaldi, L.A., Potts, S.G., W.H. van der, P., 2019. Ecological intensification: bridging the gap between science and practice. Trends Ecol. Evol. 34, 154–166. https://doi.org/10.1016/j.tree.2018.11.002.

Lahoz-Monfort, J.J., Guillera-Arroita, G., Hauser, C.E., 2014. From planning to implementation: explaining connections between adaptive management and population models. Front. Ecol. Evol. 2. https://doi.org/10.3389/fevo.2014.00060.

Leroy, C., Brunet, J.-L., Henry, M., Alaux, C., 2023. Using physiology to better support wild bee conservation. Conserv. Physiol. 11, coac076. https://doi.org/10.1093/conphys/coac076.

Lindborg, R., Gordon, L.J., Malinga, R., Bengtsson, J., Peterson, G., Bommarco, R., Deutsch, L., Gren, Å., Rundlöf, M., Smith, H.G., 2017. How spatial scale shapes the generation and management of multiple ecosystem services. Ecosphere 8, e01741. https://doi.org/10.1002/ecs2.1741.

Lonsdorf, E., Kremen, C., Ricketts, T., Winfree, R., Williams, N., Greenleaf, S., 2009. Modelling pollination services across agricultural landscapes. Ann. Bot. 103, 1589–1600. https://doi.org/10.1093/aob/mcp069.

Martin, E.A., Dainese, M., Clough, Y., Báldi, A., Bommarco, R., Gagic, V., Garratt, M.P.D., Holzschuh, A., Kleijn, D., Kovács-Hostyánszki, A., Marini, L., Potts, S.G., Smith, H.G., Al Hassan, D., Albrecht, M., Andersson, G.K.S., Asís, J.D., Aviron, S., Balzan, M.V., Baños-Picón, L., Bartomeus, I., Batáry, P., Burel, F., Caballero-López, B., Concepción, E.D., Coudrain, V., Dänhardt, J., Diaz, M., Diekötter, T., Dormann, C.F., Duflot, R., Entling, M.H., Farwig, N., Fischer, C., Frank, T., Garibaldi, L.A., Hermann, J., Herzog, F., Inclán, D., Jacot, K., Jauker, F., Jeanneret, P., Kaiser, M., Krauss, J., Le Féon, V., Marshall, J., Moonen, A.-C., Moreno, G., Riedinger, V., Rundlöf, M., Rusch, A., Scheper, J., Schneider, G., Schüepp, C., Stutz, S., Sutter, L., Tamburini, G., Thies, C., Tormos, J., Tscharntke, T., Tschumi, M., Uzman, D., Wagner, C., Zubair-Anjum, M., Steffan-Dewenter, I., 2019. The interplay of landscape composition and configuration: new pathways to manage functional biodiversity and agroecosystem services across Europe. Ecol. Lett. 22, 1083–1094. https://doi.org/10.1111/ele.13265.

McLane, A.J., Semeniuk, C., McDermid, G.J., Marceau, D.J., 2011. The role of agent-based models in wildlife ecology and management. Ecol. Modell. 222, 1544–1556. https://doi.org/10.1016/j.ecolmodel.2011.01.020.

Mouquet, N., Lagadeuc, Y., Devictor, V., Doyen, L., Duputié, A., Eveillard, D., Faure, D., Garnier, E., Gimenez, O., Huneman, P., Jabot, F., Jarne, P., Joly, D., Julliard, R., Kéfi, S., Kergoat, G.J., Lavorel, S., Le Gall, L., Meslin, L., Morand, S., Morin, X., Morlon, H., Pinay, G., Pradel, R., Schurr, F.M., Thuiller, W., Loreau, M., 2015. REVIEW: predictive ecology in a changing world. J. Appl. Ecol. 52, 1293–1310. https://doi.org/10.1111/1365-2664.12482.

Nathan, R., Getz, W.M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., Smouse, P.E., 2008. A movement ecology paradigm for unifying organismal movement research. Proc. Natl. Acad. Sci. 105, 19052–19059. https://doi.org/10.1073/pnas.0800375105.

Nicholson, C.C., Ricketts, T.H., Koh, I., Smith, H.G., Lonsdorf, E.V., Olsson, O., 2019. Flowering resources distract pollinators from crops: model predictions from landscape simulations. J. Appl. Ecol. 56, 618–628. https://doi.org/10.1111/1365-2664.13333.

Nuutinen, V., Butt, K.R., Jauhiainen, L., 2011. Field margins and management affect settlement and spread of an introduced dew-worm (*Lumbricus terrestris* L.) population. In: Pedobiologia, 9th International Symposium on Earthworm EcologyXalapa. Veracruz, Mexico, 54, pp. S167–S172. https://doi.org/10.1016/j.pedobi.2011.07.010, 5th –10th September 2010.

Olsson, O., Bolin, A., Smith, H.G., Lonsdorf, E.V., 2015. Modeling pollinating bee visitation rates in heterogeneous landscapes from foraging theory. Ecol. Modell. 316, 133–143. https://doi.org/10.1016/j.ecolmodel.2015.08.009.

Pe'er, G., Zinngrebe, Y., Hauck, J., Schindler, S., Dittrich, A., Zingg, S., Tscharntke, T., Oppermann, R., Sutcliffe, L.M.E., Sirami, C., Schmidt, J., Hoyer, C., Schleyer, C., Lakner, S., 2017. Adding some green to the greening: improving the EU's ecological focus areas for. Biodivers. Farmers. Conserv. Lett. 10, 517–530. https://doi.org/10.1111/conl.12333.

Pekas, A., De Craecker, I., Boonen, S., Wäckers, F.L., Moerkens, R., 2020. One stone; two birds: concurrent pest control and pollination services provided by aphidophagous hoverflies. Biol. Control 149, 104328. https://doi.org/10.1016/j.biocontrol.2020.104328.

Perry, G.L.W., Bond, N.R., 2013. Spatial population models for animals. Environmental Modelling. John Wiley & Sons, Ltd, pp. 221–234. https://doi.org/10.1002/9781118351475.ch13.

Peterson, A.T., Papeş, M., Soberón, J., 2015. Mechanistic and correlative models of ecological niches. Eur. J. Ecol. 1, 28–38. https://doi.org/10.1515/eje-2015-0014.

Pufal, G., Steffan-Dewenter, I., Klein, A.-M., 2017. Crop pollination services at the landscape scale. Current opinion in Insect science, pests and resistance * behavioural ecology 21, 91–97. https://doi.org/10.1016/j.cois.2017.05.021.

R Core Team, 2023. R: a language and environment for statistical computing.

Radchuk, V., Johst, K., Groeneveld, J., Turlure, C., Grimm, V., Schtickzelle, N., 2014. Appropriate resolution in time and model structure for population viability analysis: insights from a butterfly metapopulation. Biol. Conserv 169, 345–354. https://doi.org/10.1016/j.biocon.2013.12.004.

Radchuk, V., Kramer-Schadt, S., Grimm, V., 2019. Transferability of mechanistic ecological models is about emergence. Trends Ecol. Evol. (Amst.) 34, 487–488. https://doi.org/10.1016/j.tree.2019.01.010.

Raick, C., Soetaert, K., Grégoire, M., 2006. Model complexity and performance: how far can we simplify? Prog. Ocean. 70, 27–57. https://doi.org/10.1016/j.pocean.2006.03.001.

Railsback, S.F., Gallagher, C.A., Grimm, V., McCary, M.A., Harvey, B.C., 2025. Empirical ecology to support mechanistic modelling: different objectives, better approaches and unique benefits. Methods Ecol. Evol. https://doi.org/10.1111/2041-210X.70083.

Raimondo, S., Schmolke, A., Pollesch, N., Accolla, C., Galic, N., Moore, A., Vaugeois, M., Rueda-Cediel, P., Kanarek, A., Awkerman, J., Forbes, V., 2021. Pop-guide: population modeling guidance, use, interpretation, and development for ecological risk assessment. Integr. Env. Assess. Manag. 17, 767–784. https://doi.org/10.1002/ieam.4377.

Reed, M., Alvarez, T., Chelinho, S., Forbes, V., Johnston, A., Meli, M., Voss, F., Pastorok, R., 2016. A risk assessment example for soil invertebrates using spatially explicit agent-based models. Integr. Env. Assess. Manag. 12, 58–66. https://doi.org/10.1002/ieam.1713.

Rollinson, C.R., Finley, A.O., Alexander, M.R., Banerjee, S., Dixon Hamil, K.-A., Koenig, L.E., Locke, D.H., DeMarche, M.L., Tingley, M.W., Wheeler, K., Youngflesh, C., Zipkin, E.F., 2021. Working across space and time: nonstationarity in ecological research and application. Front. Ecol. Env. 19, 66–72. https://doi.org/10.1002/fee.2298.

Römbke, J., Jänsch, S., Didden, W., 2005. The use of earthworms in ecological soil classification and assessment concepts. .Ecotoxicol. Environ. Saf. Incl. Spec. Issue: Ecol. Soil Qual. 62, 249–265. https://doi.org/10.1016/j.ecoenv.2005.03.027.

Rouabah, A., Rabolin-Meinrad, C., Gay, C., Therond, O., 2024. Models of bee responses to land use and land cover changes in agricultural landscapes – a review and research agenda. Biol. Rev. https://doi.org/10.1111/brv.13109.

Ruiz, S.A., Bickel, S., Or, D., 2021. Global earthworm distribution and activity windows based on soil hydromechanical constraints. Commun. Biol. 4, 1–9. https://doi.org/10.1038/s42003-021-02139-5.

Rural Payments Agency, 2023. How to do the SFI actions for soils [WWW Document]. GOV.UK. URL. https://www.gov.uk/guidance/how-to-do-the-sfi-actions-for-soils. accessed 9.3.24.

Schmolke, A., Galic, N., Roeben, V., Preuss, T.G., Miles, M., Hinarejos, S., 2024. SolBeePopecotox: a population model for pesticide risk assessments of solitary bees. Environ. Toxicol. Chem. 43, 2645–2661. https://doi.org/10.1002/etc.5990.

Schmolke, A., Thorbek, P., Chapman, P., Grimm, V., 2010a. Ecological models and pesticide risk assessment: current modeling practice. Environ. Toxicol. Chem. 29, 1006–1012. https://doi.org/10.1002/etc.120.

Schmolke, A., Thorbek, P., DeAngelis, D.L., Grimm, V., 2010b. Ecological models supporting environmental decision making: a strategy for the future. Trends Ecol. Evol. 25, 479–486. https://doi.org/10.1016/j.tree.2010.05.001.

Schneider, A.-K., Schröder, B., 2012. Perspectives in modelling earthworm dynamics and their feedbacks with abiotic soil properties. Appl. Soil Ecol. 58, 29–36. https://doi.org/10.1016/j.apsoil.2012.02.020.

Schurr, F.M., Pagel, J., Cabral, J.S., Groeneveld, J., Bykova, O., O'Hara, R.B., Hartig, F., Kissling, W.D., Linder, H.P., Midgley, G.F., Schröder, B., Singer, A., Zimmermann, N. E., 2012. How to understand species' niches and range dynamics: a demographic research agenda for biogeography. J. Biogeogr. 39, 2146–2162. https://doi.org/10.1111/j.1365-2699.2012.02737.x.

Schuwirth, N., Borgwardt, F., Domisch, S., Friedrichs, M., Kattwinkel, M., Kneis, D., Kuemmerlen, M., Langhans, S.D., Martínez-López, J., Vermeiren, P., 2019. How to make ecological models useful for environmental management. Ecol. Modell. 411, 108784. https://doi.org/10.1016/j.ecolmodel.2019.108784.

Singer, A., Johst, K., Banitz, T., Fowler, M.S., Groeneveld, J., Gutiérrez, A.G., Hartig, F., Krug, R.M., Liess, M., Matlack, G., Meyer, K.M., Pe'er, G., Radchuk, V., Voinopol-Sassu, A.-J., Travis, J.M.J., 2016. Community dynamics under environmental change: how can next generation mechanistic models improve projections of species distributions? .....Ecol. Model. Next Gener. Ecol. Model. Concepts Theory: Struct. Realism Emerg. Predict. 326, 63–74. https://doi.org/10.1016/j.ecolmodel.2015.11.007.

Singh, J., Schädler, M., Demetrio, W., Brown, G.G., Eisenhauer, N., 2019. Climate change effects on earthworms - a review. Soil Org. 91, 113–137. https://doi.org/10.25674/so91iss3pp114.

Stevens, C.J., Fraser, I., Mitchley, J., Thomas, M.B., 2007. Making ecological science policy-relevant: issues of scale and disciplinary integration. Landsc. Ecol. 22, 799–809. https://doi.org/10.1007/s10980-007-9092-8.

Stillman, R.A., Railsback, S.F., Giske, J., Berger, U., Grimm, V., 2015. Making predictions in a changing world: the benefits of individual-based ecology. BioScience 65, 140–150. https://doi.org/10.1093/biosci/biu192.

Thiele, J.C., Grimm, V., 2015. Replicating and breaking models: good for you and good for ecology. Oikos 124, 691–696. https://doi.org/10.1111/oik.02170.

Tomlinson, S., Webber, B.L., Bradshaw, S.D., Dixon, K.W., Renton, M., 2018. Incorporating biophysical ecology into high-resolution restoration targets: insect pollinator habitat suitability models. Restor. Ecol. 26, 338–347. https://doi.org/10.1111/rec.12561.

Topping, C., Alrøe, H., Farrell, K., Grimm, V., 2015. Per Aspera ad Astra: through complex population modeling to predictive theory. Am. Nat. 186. https://doi.org/10.1086/683181, 000–000.

Urban, M.C., Bocedi, G., Hendry, A.P., Mihoub, J.-B., Pe'er, G., Singer, A., Bridle, J.R., Crozier, L.G., De Meester, L., Godsoe, W., Gonzalez, A., Hellmann, J.J., Holt, R.D., Huth, A., Johst, K., Krug, C.B., Leadley, P.W., Palmer, S.C.F., Pantel, J.H., Schmitz, A., Zollner, P.A., Travis, J.M.J., 2016. Improving the forecast for biodiversity under climate change. Science 353, aad8466. https://doi.org/10.1126/science.aad8466.

van der Vaart, E., Johnston, A.S.A., Sibly, R.M., 2016. Predicting how many animals will be where: how to build, calibrate and evaluate individual-based models. Ecol. Modell. Next Gener. Ecol. Model. Concepts Theory: Struct. Realism Emerg. Predict. 326, 113–123. https://doi.org/10.1016/j.ecolmodel.2015.08.012.

Wang, M., Wang, H.-H., Koralewski, T.E., Grant, W.E., White, N., Hanan, J., Grimm, V., 2024. From known to unknown unknowns through pattern-oriented modelling: driving research towards the Medawar zone. Ecol. Modell. 497, 110853. https://doi.org/10.1016/j.ecolmodel.2024.110853.

Wenger, S.J., Olden, J.D., 2012. Assessing transferability of ecological models: an underappreciated aspect of statistical validation. Methods Ecol. Evol. 3, 260–267. https://doi.org/10.1111/j.2041-210X.2011.00170.x.

Wickham, H., 2016. ggplot2: Elegant Graphics For Data Analysis. Springer International Publishing.

Woods, H.A., Dillon, M.E., Pincebourde, S., 2015. The roles of microclimatic diversity and of behavior in mediating the responses of ectotherms to climate change. ..J. Therm. Biol. What sets limit? How Therm. Limits Perform. Prefer. Ectotherms Influ. Water Energy Balance 54, 86–97. https://doi.org/10.1016/j.jtherbio.2014.10.002.

Yates, K.L., Bouchet, P.J., Caley, M.J., Mengersen, K., Randin, C.F., Parnell, S., Fielding, A.H., Bamford, A.J., Ban, S., Barbosa, A.M., Dormann, C.F., Elith, J., Embling, C.B., Ervin, G.N., Fisher, R., Gould, S., Graf, R.F., Gregr, E.J., Halpin, P.N., Heikkinen, R.K., Heinänen, S., Jones, A.R., Krishnakumar, P.K., Lauria, V., Lozano-Montes, H., Mannocci, L., Mellin, C., Mesgaran, M.B., Moreno-Amat, E., Mormede, S., Novaczek, E., Oppel, S., Crespo, G.O., Peterson, A.T., Rapacciuolo, G., Roberts, J.J., Ross, R.E., Scales, K.L., Schoeman, D., Snelgrove, P., Sundblad, G., Thuiller, W., Torres, L.G., Verbruggen, H., Wang, L., Wenger, S., Whittingham, M.J., Zharikov, Y., Zurell, D., Sequeira, A.M.M., 2018. Outstanding challenges in the transferability of ecological models. Trends Ecol. Evol. 33, 790–802. https://doi.org/10.1016/j.tree.2018.08.001.

Zurell, D., König, C., Malchow, A.-K., Kapitza, S., Bocedi, G., Travis, J., Fandos, G., 2022. Spatially explicit models for decision-making in animal conservation and restoration. Ecography 2022. https://doi.org/10.1111/ecog.05787.