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REVIEW

Predicting emergent animal biodiversity patterns across multiple scales

Alice S. A. Johnston

Cranfield Environment Centre, Cranfield University, Bedfordshire, UK

Correspondence
Alice S. A. Johnston, Cranfield Environment Centre, Cranfield University, Bedfordshire, UK.
Email: a.s.johnston@cranfield.ac.uk

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Abstract

Restoring biodiversity-based resilience and ecosystem multi-functionality needs to be informed by more accurate predictions of animal biodiversity responses to environmental change. Ecological models make a substantial contribution to this understanding, especially when they encode the biological mechanisms and processes that give rise to emergent patterns (population, community, ecosystem properties and dynamics). Here, a distinction between 'mechanistic' and 'process-based' ecological models is established to review existing approaches. Mechanistic and process-based ecological models have made key advances to understanding the structure, function and dynamics of animal biodiversity, but are typically designed to account for specific levels of biological organisation and spatiotemporal scales. Cross-scale ecological models, which predict emergent co-occurring biodiversity patterns at interacting scales of space, time and biological organisation, is a critical next step in predictive ecology. A way forward is to first capitalise on existing models to systematically evaluate the ability of scale-explicit mechanisms and processes to predict emergent patterns at alternative scales. Such model intercomparisons will reveal mechanism to process transitions across fine to broad scales, overcome approach-specific barriers to model realism or tractability and identify gaps which necessitate the development of new fundamental principles. Key challenges surrounding model complexity and uncertainty would need to be addressed, and while opportunities from big data can streamline the integration of multiple scale-explicit biodiversity patterns, ambitious cross-scale field studies are also needed. Crucially, overcoming cross-scale ecological modelling challenges would unite disparate fields of ecology with the common goal of improving the evidence-base to safeguard biodiversity and ecosystems under novel environmental change.

KEYWORDS
communities, ecological modelling, ecosystems, individuals, mechanisms, populations, processes, scale, space, time

1 | INTRODUCTION

Biodiversity conservation and ecosystem restoration are central international environmental goals that are inextricably linked (IPBES, 2019; Moreno-Mateos et al., 2020; UNEP, 2023). All biological species are connected to their ecosystems through networks of interactions which confer ecosystem functioning (Gonzalez et al., 2020; Montoya & Raffaelli, 2010). This complex relationship is often characterized as

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a unidirectional positive linear relationship between biodiversity (e.g. taxonomic richness) and ecosystem multifunctionality at local scales (Balvanera et al., 2006; Hooper et al., 2005; Manning et al., 2019). Biotic interactions, however, can be lost much quicker than species under environmental perturbations, with cascading effects on the ecosystem functions these interactions support (e.g. pollination, decomposition, pest regulation) (Albrecht et al., 2007; Harvey et al., 2017; Moreno-Mateos et al., 2020; Tylianakis et al., 2007). Reconstructing biodiversity-based resilience under ongoing anthropogenic change thus requires an understanding of the structure, function and dynamics of ecosystems, between multi-species communities with one another and their changing environment.

Ecosystems and their biodiversity are characterised by emergent properties: patterns that arise from interactions between components of the system at lower organisational levels. These 'patterns' cannot be linearly deduced from the properties of the component parts in dynamic environments (Grimm et al., 2005; van den Berg et al., 2022). For instance, species richness under novel environmental conditions cannot be predicted according to the current distribution of the constituent species alone. Rather, multi-species community dynamics emerge from mechanisms and processes (e.g. biotic interactions, adaptation) operating at multiple levels (e.g. individuals, meta-populations) and spatiotemporal scales (Holling, 1992). That is, species richness in novel environments will depend on how the constituent species populations respond to changing abiotic and biotic conditions across space and time. The complex interplay between these mechanisms, processes and their drivers (e.g. climate, land management, trophic feedbacks) often leads to the conclusion that ecological patterns can only be understood in the specific environmental context in which they are observed (Catford et al., 2022). Environmental management decisions such as those associated with ecosystem restoration, however, would ideally be supported by informed predictions of the likely ecological consequences of interventions before their implementation (Grimm et al., 2020).

Ecological models are developed for specific purposes, to address certain questions or problems relevant to distinct levels of biological organisation (populations, communities) and scales (field, landscape; years, decades) (Grimm et al., 2020). A model's purpose has classically been reflected in different model types that focus on the pattern of interest (e.g. Lotka-Volterra models of pairwise species interactions, May, 2019; Leslie matrix models of population stage structure, Leslie, 1945). By focusing on different patterns and scales of interest, distinct fields of ecology (e.g. ecosystem, community, population ecology) have developed different fundamental principles. For instance, generalisations are necessary to derive statistically predictable patterns at broad scales (e.g. ecological niches) from fine-scale details (e.g. individual variation) (Levin, 1992). Even when models address the same purpose and scales, the underlying assumptions of such generalisations can lead to disparate predictions for the same scenarios. Bahlburg et al. (2023), for instance, compare eight krill growth models and find contrasting model predictions are strongly determined by model structure and the scale-explicit patterns used during model calibration and validation. When models are needed to address real-world environmental problems in uncertain future conditions such model intercomparisons raise several questions about the structural realism of existing ecological models (Grimm, 2023).

Mechanistic and process-based ecological models, which encode biological mechanisms and processes, hold promise for predicting ecological patterns in novel environments (Grimm et al., 2017). Most ecological modelling approaches are increasingly mechanistic or process-based (Box 1) for the purpose of providing more informed predictions (Johnston et al., 2019; Pilowsky et al., 2022) but tend to focus on representing scale-explicit processes linking one hierarchical level of biological organisation to another (e.g. individuals to populations, communities to meta-communities). Much progress has been made in our mechanistic understanding of how individual species variation leads to differential shifts in population abundances and distributions (Huston et al., 1988; Johnston et al., 2019; Sibly et al., 2013), for instance, and how spatially separated communities are shaped by both biotic interactions and dispersal dynamics (Leibold et al., 2004, 2017; Thompson et al., 2020). Mechanistically linking individuals to ecosystems, however, presents a much greater challenge due to complex multi-species interactions and feedback between scale-explicit mechanisms and processes.

Biodiversity projection models, and ecosystem models that describe ecosystem components (e.g. species functional groups) and processes (e.g. dispersal), are increasingly utilised to address biodiversity conservation issues at large spatial scales (Geary et al., 2020; Urban et al., 2022). Yet, a recent review of 50 biodiversity projection models found that existing approaches typically lack the biological realism, by not accounting for key mechanisms (physiology) and processes (species interactions), needed to make dynamic predictions under environmental change scenarios (Urban et al., 2022). Similarly, macroecological theories have established a better understanding of biodiversity patterns at biogeographic scales according to general scaling laws based on area and energy (McGill, 2019), but cannot yet make dynamic predictions in novel environments (Newman et al., 2019). Such large-scale ecological models need to make simplifications to maintain model tractability, constrain the uncertainty of their predictions and allow extrapolation to different scenarios compared to complex empirical models (Geary et al., 2020). Simplification, however, can lead to the omission of key processes and the introduction of unrealistic biological assumptions that amplify model uncertainty (Evans et al., 2013).

Ecological models that cross multiple levels and scales via mechanisms and processes could address two key challenges in animal ecology. First, they would provide more accurate predictions of biodiversity responses to novel environmental changes, by informing system-level predictions at scales of interest to environmental decisions with realistic biological mechanisms and processes. Second, such tools would be invaluable in gaining a higher resolution understanding of biodiversity's organising principles, by using simulation experiments to develop and test eco-evolutionary theory across ecosystems and spatiotemporal scales that would be infeasible to conduct experimentally. A wealth of information is already encoded in existing ecological models about scale-explicit mechanisms and

BOX 1 The distinction between mechanisms and processes in ecological models

Mechanisms and processes are commonly used interchangeably in ecology to recognize explicit functions that alter system (ecosystem, community, population) dynamics. However, an important distinction between mechanisms and processes exists in ecological modelling, although not often recognised, with consequences for a model's scope of applicability to ecological questions (Grimm et al., 2014). Here, the definition of Connolly et al. (2017) is adapted for relevance across the biological hierarchy when modelling from individuals to ecosystems, the focus of this review:

Mechanisms describe how component parts shape the overall system. Modelling examples include the use of energy budget models to describe individual physiological responses to changing resource and temperature conditions (Johnston et al., 2019), or species ecological niches (not based on static functional responses) to predict species distributions (Diniz-Filho et al., 2019; Kearney & Porter, 2009).

Processes describe how the overall system is shaped by changes in its component parts. Modelling examples include the logistic model of population growth, predicted from birth and death rates (Wiegert, 1998), or pairwise density dependent species interaction strengths (Thompson et al., 2020).

Although mechanisms and processes seem indistinguishable on first glance, the fundamental difference is whether they consider the component part explicitly (e.g. modelling individual behaviour to capture population dynamics) or implicitly (e.g. modelling population dispersal kernels to capture population dynamics). Thus, a mechanism can be used to predict a process under dynamic environments, but a process cannot predict changes in the underpinning mechanisms and therefore how the process responds to novel conditions.

Importantly, models that include mechanisms or processes include them to better predict emergent patterns (system properties and dynamics) compared to correlative statistical models (Connolly et al., 2017; Johnston et al., 2019; Pilowsky et al., 2022). That is, they represent the underlying ecological components (individuals, species populations) that shape system (species population, multi-species community) responses to environmental perturbations.

Figure 1 illustrates a simplified example of mechanistic, process-based and correlative model structures where the models' purpose is to predict the population abundance of two species over time according to measured changes in temperature (Figure 1a). In this example, the statistical model replicates the observed population pattern (abundance over time) via regression models (Figure 1b), the process-based model predicts the pattern from species population growth rates across temperature gradients (Figure 1c) and the mechanistic model predicts patterns from the temperature dependence of species-specific metabolic rates (Figure 1d). Additional processes and/or mechanisms are needed alongside these functions: for instance, the mechanistic model would simulate how energy is acquired and expended on life history processes and emergent competition for resources, and the process model may include imposed density dependent species interaction coefficients. The key distinction here is that the mechanism is explicitly modelled, whereas the process is implicit (Figure 1e). Not shown here is the expectation that the mechanistic and process models would better capture independent population patterns for the modelled species in different environmental contexts (e.g. geographic locations) compared to the statistical approach, as their structure is not restricted by the availability of detailed system-level empirical data (Kearney & Porter, 2009).

processes that are important in capturing emergent biodiversity responses to environmental change. However, most ecological models do not deal with scale explicitly (Fritsch et al., 2020). Here, scale-explicit mechanisms and processes are synthesised from a review of existing mechanistic and process-based ecological models.

2 | ECOLOGICAL MODELS AT DIFFERENT LEVELS OF BIOLOGICAL ORGANIZATION

Ecological models have been developed to address questions at different levels of biological organisation. For instance, how species richness is affected by habitat fragmentation (Thompson et al., 2020); or how single species populations respond to multiple stressors at local to landscape scales (Horn et al., 2016; Johnston et al., 2018; Schmolke et al., 2023). Reviews of models developed at each organisational level (e.g. populations, Ehrlén & Morris, 2015; Grimm et al., 2017; Johnston et al., 2019), meta-populations (Barton & Olusanya, 2022; Hanski, 1998), multi-species communities (Boit et al., 2012; Pontarp et al., 2019; Thompson et al., 2012; van den Berg et al., 2022) and ecosystems (Geary et al., 2020; Urban et al., 2022) show a common progression from classical phenomenological approaches to more mechanistic and process-based models that predict emergent animal biodiversity patterns. This review focuses on advances in mechanistic and process-based modelling at distinct levels of biological organisation, as these models encode mechanisms and processes to capture emergent (implicit or explicit, see Box 1) animal biodiversity patterns at specific scales. In doing so, mechanistic and process-based ecological models have attempted to optimize the trade-off between model complexity and the biological

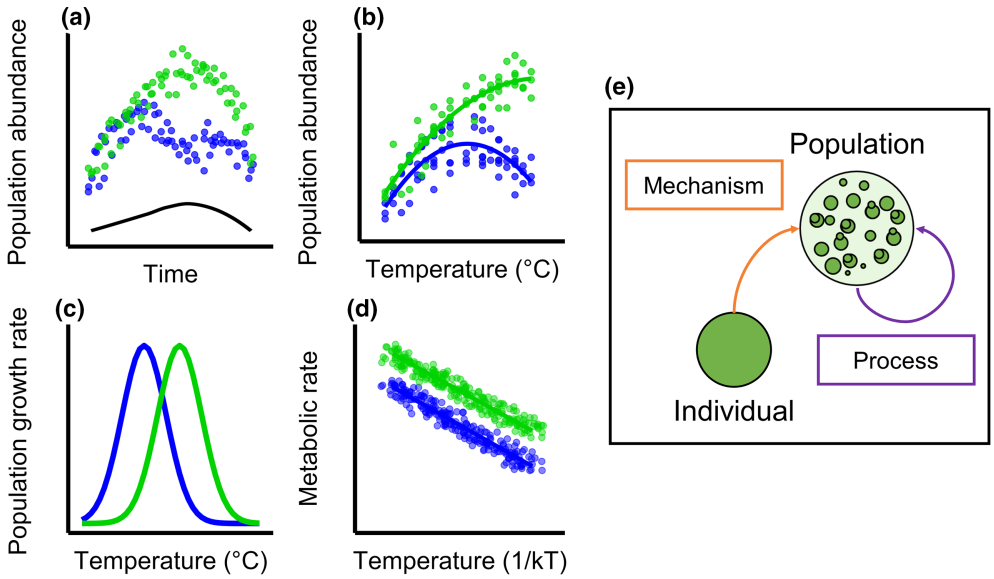

FIGURE 1 Illustration of different modelling approach structures for predicting ecological patterns. Each model aims to predict (a) the population abundance of two species (blue and green symbols) over time, with known variations in environmental temperature (black line). In this simple example (b), the correlative model uses the population abundance and temperature data in (a) to fit regression models for both species (colored lines); (c) the process-based model predicts (a) from population growth rates over temperature gradients; and (d) the mechanistic model predicts population growth from known temperature and body size dependence of individual metabolic rates (note the plot shows body mass corrected metabolic rates plotted against the Arrhenius temperature). This example is intended to illustrate (e) the distinction between an explicit mechanism (orange arrow) and implicit process (purple arrow) at the population level.

realism of model predictions at the ecological scales of interest (Evans et al., 2013; Grimm et al., 2005).

The following sections provide a general overview of classical approaches applied to different levels of biological organisation before identifying the mechanisms and processes incorporated in more recent models, alongside the identification of underlying assumptions and challenges. This review does not aim to provide an exhaustive review of modelling approaches at different levels and scales, which have been addressed in the reviews mentioned above. Rather, the focus is on providing a general cross-scale understanding of the quantifiable mechanisms and processes at each level of biological organisation, as ecologists and modellers tend to focus only on those that are directly applicable to their questions. Progress in predictive ecology could, however, be achieved by testing the further integration of these mechanisms and processes across scales. Although the models reviewed here are in principle general across all biological species and ecosystems, the focus of this review is on animal communities in terrestrial ecosystems as mechanisms, processes, hierarchical levels of interest and system-level structure can be very different for microbial, plant and aquatic ecological modelling.

2.1 | Ecosystems to communities

Ecosystem models include interactions between biological species or community groups (e.g. functional groups, trophic levels) that confer ecosystem processes (e.g. predation, energy flow, decomposition) (Geary et al., 2020). Multi-species interactions, such as mutualisms and food webs, are represented in diverse ways depending on the scale of interest (Urban et al., 2022). The Madingley model, for example, which can be applied at a global scale and across terrestrial and marine ecosystems, allows ecosystem functions to emerge from interactions between trophic functional groups and species traits such as body mass, alongside mass-specific metabolic, growth and dispersal rates (Harfoot et al., 2014). More commonly, ecosystem models represent multi-species communities as networks of ecological interactions at finer (regional to landscape) spatial scales. Ecological interactions can be modelled in myriad ways, depending on the interaction type (e.g. uni-, bi- or k-partite network) and the likely scale-explicit processes shaping network structure (e.g. trophic niche, phylogenetic distance, functional trait matching) (Elmasri et al., 2020; Morales-Castilla et al., 2015; Petchey et al., 2008; Pomeranz et al., 2019).

Interaction networks have been classically characterised as non-spatial networks comprising nodes (biological entities) and links (ecological interactions) and understood according to conventional regression models (Pichler et al., 2020). Graph theory has also been extensively applied to interaction networks to provide a mathematical framework for measuring and understanding how network structure and dynamics (e.g. stability, resilience) are linked to ecosystem service provision (Harvey et al., 2017; Keyes et al., 2021). Network structure is often abstracted at the ecosystem level irrespective of network composition and variation in species traits. This simplification has been justified by the identification of a structural backbone for food webs (Bramon Mora et al., 2018; Dalla Riva & Stouffer, 2016) and the persistence of network structure

despite strong compositional turnover at large spatial scales (Poisot et al., 2021), and is necessary given the lack of empirical data for complete species networks and the biotic interactions linking them (Montoya & Raffaelli, 2010).

Dynamical systems theory approaches, based on Lotka-Volterra equations of pairwise species interactions, can predict how ecological networks change over time (Geary et al., 2020). The ecosystem network model adapted by Baker et al. (2019), for instance, combined 20 ecosystem elements (species and functional groups, using an ensemble modelling approach to include relevant biological processes and reduce unknown parameter uncertainty) to simulate the effect of species reintroductions at Booderee National Park in Australia over a 6 year period. Such process-based ecosystem models can capture the ecological interactions that shape ecological network structure but have large data requirements that can result in high structural uncertainty in novel environments. Similar to the Madingley model, dynamic food web models (DFWMs) can resolve this issue by considering the flow of energy and nutrients through different trophic levels (Cohen et al., 2003), while accounting for population dynamics (e.g. species biomass) at various trophic levels via allometric scaling relationships (Boit et al., 2012; Cohen et al., 2003; Curtsdotter et al., 2019; Jonsson et al., 2018).

DFWMs have integrated biotic interactions beyond those directly related to trophic transfer, such as competition for resources, mutualistic relationships, and facilitation (Corcket et al., 2017), population growth rates along abiotic gradients (Gotelli & Ellison, 2006; Sentis et al., 2021), species distributions (Hamm & Drossel, 2021; Mougi, 2019; Pellissier et al., 2013), and evolutionary processes such as adaptation and mutation (Allhoff et al., 2015; Cattin et al., 2004), all of which influence species population dynamics at different trophic levels. By incorporating these various processes, DFWMs provide a quantitative framework for understanding complex ecological networks according to fundamental principles (e.g. energy conservation, ecological stoichiometry) and can predict the potential cascading effects of environmental changes on ecosystem processes linked to food web dynamics (Thompson et al., 2012). Depending on their structural complexity, however, most DFWMs are restricted to small spatial scales and/or few species and may not account for space and time explicitly.

2.2 | Metacommunities to metapopulations

Metacommunities, networks of communities across local habitat patches connected by dispersal, incorporate species which interact with each other and the landscape (Leibold et al., 2017). Metacommunity models (MCMs) are largely based on the extension of classical theoretical models that cross concepts of competitive exclusion, ecological niche, population demography and stochasticity in to four main paradigms: patch-dynamic, species-sorting, mass-effect and neutral (Leibold et al., 2004). These paradigms are based on different assumptions about how co-variation in species traits and patch conditions interact to shape community composition at local to regional scales (Brown et al., 2017). MCMs thus typically make inferences based on species relatedness rather than biological mechanisms, but also identify several processes that underpin community assembly across scales. Thompson et al. (2020) establish three key processes: (1) density-independent responses to abiotic conditions (e.g. Figure 1c); (2) density-dependent biotic interactions and (3) dispersal, alongside stochasticity in how these processes impact species demographic rates. Inclusion of these processes in MCMs enables simulation of community dynamics in virtual novel environments. The reliability of such predictions is difficult to infer, however, as model validation tends to be restricted by the need to use available system-level patterns for model development (parameterisation, calibration).

Process-based MCMs focus on the population level and require a-priori parameterisation of species-specific dispersal rates, population growth rates across abiotic gradients and interaction coefficients for species pair strengths (Thompson et al., 2020). These parameters, however, are difficult to disentangle from empirical observations of naturally occurring populations and communities in dynamic environments. Traditional community ecology approaches that underpin metacommunity theory (e.g. the Lotka–Volterra model and recent extensions) (May, 2019) and functional trait approaches (McGill et al., 2006) take a similar approach to understanding community assembly through a process of ecological filtering via dispersal, abiotic and biotic traits (Violle et al., 2012). However, such filters are almost impossible to separate into distinct functional traits as they often act in unison. Such approaches are thus better suited to demonstrating, rather than understanding or predicting (Grimm et al., 2020), how community composition relates to ecosystem functioning in specific biotic and abiotic scenarios (van den Berg et al., 2022).

2.3 | Metapopulations to populations

Metapopulations are composed of single species populations across suitable habitat patches, typically characterised by the presence or absence of subpopulations across patch matrices (Mackey & Lindenmayer, 2001). In MCMs, described in the previous section, subpopulations of multiple species can co-exist and interact within patches. At both population and community levels, subpopulations are spatially structured according to the availability of suitable patches, separated by barriers such as impervious surfaces, and connected by dispersal behaviour (Opdam, 1991). The processes discussed in this section are thus also relevant to the above section on metacommunities: in particular, local populations within patches can become extinct and re-established due to the interactive effects of dispersal behaviour and habitat attributes, resulting in dynamic species distribution patterns across space and time.

The metapopulation concept was originally developed to better understand small metapopulations, consisting of extinction-prone subpopulations which persist at the regional scale when extinction and colonization are balanced (Levins, 1969). Classical theoretical

metapopulation models (MPMs) were not spatially explicit (Hanski & Simberloff, 1997), but space was soon integrated to fully address questions about the ecological interactions and processes that are key to describing metapopulation dynamics (Hanski, 1998). In particular, MPMs represent the effects of patch area and isolation on individual movement via dispersal kernels, population extinction and colonization of new patches (Dallas et al., 2020). The aggregated metapopulation growth rate therefore depends on a combination of local species properties and processes (subpopulation growth rates, and demographic, environmental and genetic stochasticity) and regional metapopulation processes (the spatial configuration of habitat patches and their connectivity, dispersal behaviour).

Local processes within MPMs (subpopulation dynamics) are typically described according to demographic rates (e.g. birth and death rates), which depend on patch size and habitat quality, and both influence and are influenced by dispersal behaviour (Huang et al., 2020). Environmental heterogeneity of habitat patches (and between patches) can also lead to the adaptation of species within local populations (Howell et al., 2018), while metapopulation dynamics maintain genetic variation at the landscape level (Hanski & Ovaskainen, 2000). The ability of MPM's to describe gene flow via dispersal and subpopulation turnover and the subsequent genetic structure of metapopulations makes MPMs ideal for integrating eco-evolutionary processes (Bocedi et al., 2021; Szép et al., 2021). For instance, Hanski et al. (2017) used a genetic MPM to identify a closely coupled relationship between allelic variation in a gene associated with dispersal and metapopulation size in viable networks. Such findings have promoted the need to extend MPMs to the individual level, to better describe the mechanisms that give rise to the genetic structure of covarying traits, which cannot be resolved at the population level (Baguette et al., 2017).

2.4 | Populations to individuals

Population ecology has classically understood how population dynamics (e.g. abundance, stage-structure, distribution) are determined by demographic rates and their functional relationships with abiotic (e.g. temperature) and/or biotic (e.g. density) constraints. Classical population models thus typically describe how changing birth and death rates determine population growth rates over time (Leslie, 1945; MacArthur, 1958). Demographic processes are central to process-based models at the metapopulation level and beyond (Hanski, 1998; Thompson et al., 2020), and are crucial for integrating genetic data to understand species eco-evolutionary dynamics at broad spatial scales (Diniz-Filho et al., 2019; Smallegange & Coulson, 2013). Genetic data for naturally occurring species is often constrained to the population level and expression of genotype–phenotype relationships modelled according to reaction norm regressions (Oomen & Hutchings, 2022). Individual heterogeneity, however, plays a key role in genetic architecture (Vindenes & Langangen, 2015) but complex genotype–phenotype interactions are difficult to disentangle as they act in unison (Smallegange, 2022). Nevertheless, recent development of a genetic inheritance function in Integral Projection Models shows promise for teasing apart phenotypic plasticity and micro-evolution to better predict adaptive species responses to environmental change (Simmonds et al., 2020).

Mechanistic population models have been more widely developed to predict population dynamics from individual-level physiological and behavioural mechanisms (Johnston et al., 2019). For instance, demographic rates are increasingly replaced by energy budget models to predict emergent population responses to changing resource and temperature conditions from individual energy acquisition and expenditure on life cycle processes (e.g. growth, reproduction) (Kearney et al., 2009; Kooijman, 2009; Sibly et al., 2013). Behavioral mechanisms such as foraging are central to understanding species distributions at local scales but are far more variable across species than biochemically governed physiological mechanisms. Maladaptive behavioural responses to environmental change also suggest that classical approaches to understanding animal movement (e.g. ideal free distribution) do not always hold true (Wong & Candolin, 2015).

The movement ecology framework establishes four key mechanisms to predict emergent movement patterns across heterogeneous and spatially-explicit landscapes: internal state, motion, navigation and external factors (Nathan et al., 2008). Yet, advances in theoretical movement ecology (that is, testing quantitative frameworks that integrate these mechanisms for diverse species and environments) have not kept pace with technological improvements in the monitoring and recording of animal movement (e.g. GPS tracking), and typical models currently used in the field (e.g. state-space models, Auger-Méthé et al., 2021) are largely statistical (Joo et al., 2022). The computational structure of statistical approaches, however, have a limited ability to capture adaptive behaviour in response to changing environmental conditions and population dynamics. Individual-based models (IBMs), also known as agent-based models, address this gap by simulating the behaviour and interactions of unique individuals across heterogeneous environments (Grimm et al., 2017).

IBMs are distinctive in their ability to predict how population dynamics emerge from stochastic physiological, behavioural and biotic mechanisms, and how these mechanisms are influenced by dynamic feedbacks between individuals with one another and their environment (Johnston et al., 2019). Complexity is a central issue in bottom-up simulation models, with IBMs of populations often becoming complex when many unique and autonomous individuals are simulated across heterogeneous and changing environments (Grimm et al., 2005, 2017). Mechanistic representations of individual variation according to bioenergetic submodels have resolved some of this complexity (Kooijman, 2009; Sibly et al., 2013), enabling the representation of multiple species according to the same standardised submodels with species-specific parameters (Grimm et al., 2017). Mechanistic IBMs for multi-species communities and large spatial scales, however, are restricted by the computational cost of detailed submodels for many autonomous individuals interacting with one another and their environment.

3 | TOWARDS CROSS-SCALE MECHANISTIC ECOLOGICAL MODELS

Mechanistic and process-based ecological models encode several mechanisms and processes that operate together across the biological hierarchy. Existing models reviewed here, however, generally focus on mechanisms and/or processes related to coupled levels of biological organisation. Figure 2 synthesises scale-explicit mechanisms and processes quantified in existing ecological models from the individual to ecosystem level. The mechanisms and processes shown in Figure 2 are not necessarily the 'correct' drivers of emergent animal biodiversity patterns across scales, but the most tested across a range of existing mechanistic or process-based ecological models. Specifically, physiology provides a critical link between intraspecific trait variation at the individual level by determining the capacity of species populations to grow and/or move in response to varying food, nutrient and temperature conditions. As spatial scale increases, dispersal behaviour is key to understanding how metapopulations are distributed across fragmented habitats. Intraspecific competition for resources and space at the population and metapopulation levels can feed-back to individual fitness by constraining resource availability. At the community and metacommunity levels, multi-species dynamics emerge form interspecific biotic interactions alongside their feedbacks to individual fitness. Finally, how multi-species communities interact with their abiotic environment is central to understanding how biodiversity relates to a wide range of ecosystem functions (e.g. decomposition, pollination) and how these shifts in the abiotic and biotic environment feed-back to adaptive responses at the individual level. Crucially, both bottom-up mechanisms and top-down processes give rise to animal biodiversity patterns at any one level and scale, but existing ecological models do not typically address these complex interactions.

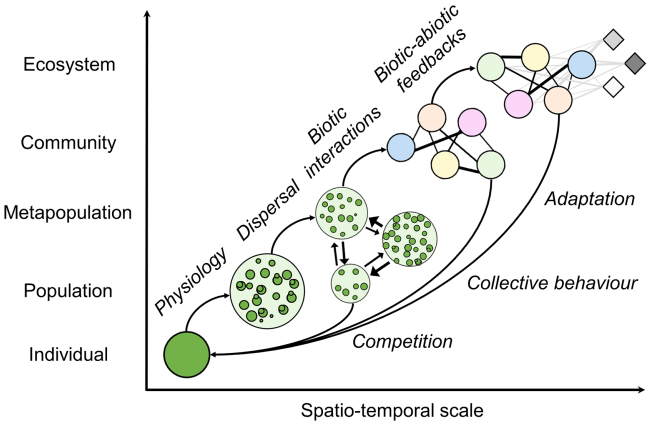

FIGURE 2 Scale-explicit mechanisms and processes commonly represented in existing mechanistic and process-based ecological models at different levels of biological organisation. This figure is not intended to capture the extensive range of mechanisms and processes described across all ecological models but identifies the most common when modelling across the levels of biological organization reviewed here. Spatiotemporal units are not specified, as these will differ vastly between the species, communities and ecosystems of interest.

3.1 | Individuals to ecosystems: Is it possible?

Individuals represent the fundamental building blocks of ecosystems (Figure 2), but as reviewed here are often not considered in models designed to predict species dynamics beyond the population level. Not including individuals explicitly, however, could restrict the ability of larger scale ecological models to capture realistic animal biodiversity responses to novel environmental change (Youngflesh et al., 2023). At present no ecological modelling approach could feasibly model from unique, autonomous individuals with their own adaptive behaviour to multi-species communities in dynamic ecosystems at the resolution needed. Purves et al. (2013), for instance, estimate that it would take a standard laptop around 47 billion years to simulate every multicellular animal in one 1-degree grid-cell for 100 years. Yet, IBMs provide an ideal framework for cross-scale ecological modelling because they can directly predict the emergence of broad ecological patterns from fine biological mechanisms and processes (Fritsch et al., 2020).

Ecosystem and community models often account for individual variation as traits across aggregated species, size classes, functional groups or trophic levels (Boit et al., 2012; Curtsdotter et al., 2019; Geary et al., 2020; Schneider et al., 2012; Urban et al., 2022). In doing so, fine-scale individual details which are obscured in broad-scale biodiversity patterns are abstracted to deal with model complexity (Newman et al., 2019; Thompson et al., 2012). When a model aims to predict biodiversity responses to novel environmental changes this individual detail and the spatial heterogeneity of landscapes at species-relevant scales can be crucial. For instance, adaptive foraging by consumers has a key role in stabilising complex food webs (Kondoh, 2003) and habitat diversity has been linked to higher prey production and stabilising trophic interactions (Scholl et al., 2023).

An alternative approach to abstracted functional traits is to identify fundamental principles across the biological hierarchy that together constrain model complexity while retaining cross-scale ecological realism (Franklin et al., 2020; Grimm et al., 2017; Johnston et al., 2019). First, however, we need to understand the ability of existing ecological models, reviewed above, to predict biodiversity patterns across spatiotemporal scales.

3.2 | Systematic model intercomparisons across multiple scales

Mechanistic and process-based model intercomparisons can act as a platform for systematically testing the performance of different encoded mechanisms and processes across scales not considered during model development. For instance, intercomparisons could determine whether existing mechanistic IBMs designed at the field scale can predict meta-population dynamics across isolated

habitat patches at the landscape scale, or whether process-based MCMs can predict local species population dynamics (Figure 3). Intercomparison frameworks with foundations in pattern-oriented modelling (POM) would evaluate the need for diverse models to capture multiple biodiversity patterns at different scales and hierarchical levels (Grimm et al., 2005), that together demonstrate the model encodes the necessary detail to capture adaptive system dynamics (Gallagher et al., 2021; Pontarp et al., 2019). Model testing across scales would also enable evaluation of the often implied but rarely quantified trade-off between a models structural realism and model tractability. That is, alongside quantification of each models predictive power via standardised POM evaluation procedures, intercomparisons can also quantify the computational cost of a models encoded information (for instance through computer processing unit [CPU] times for simulation runs) across scales (Figure 3).

Scale-explicit mechanistic and process-based ecological models are rarely designed to consider mechanisms, processes and

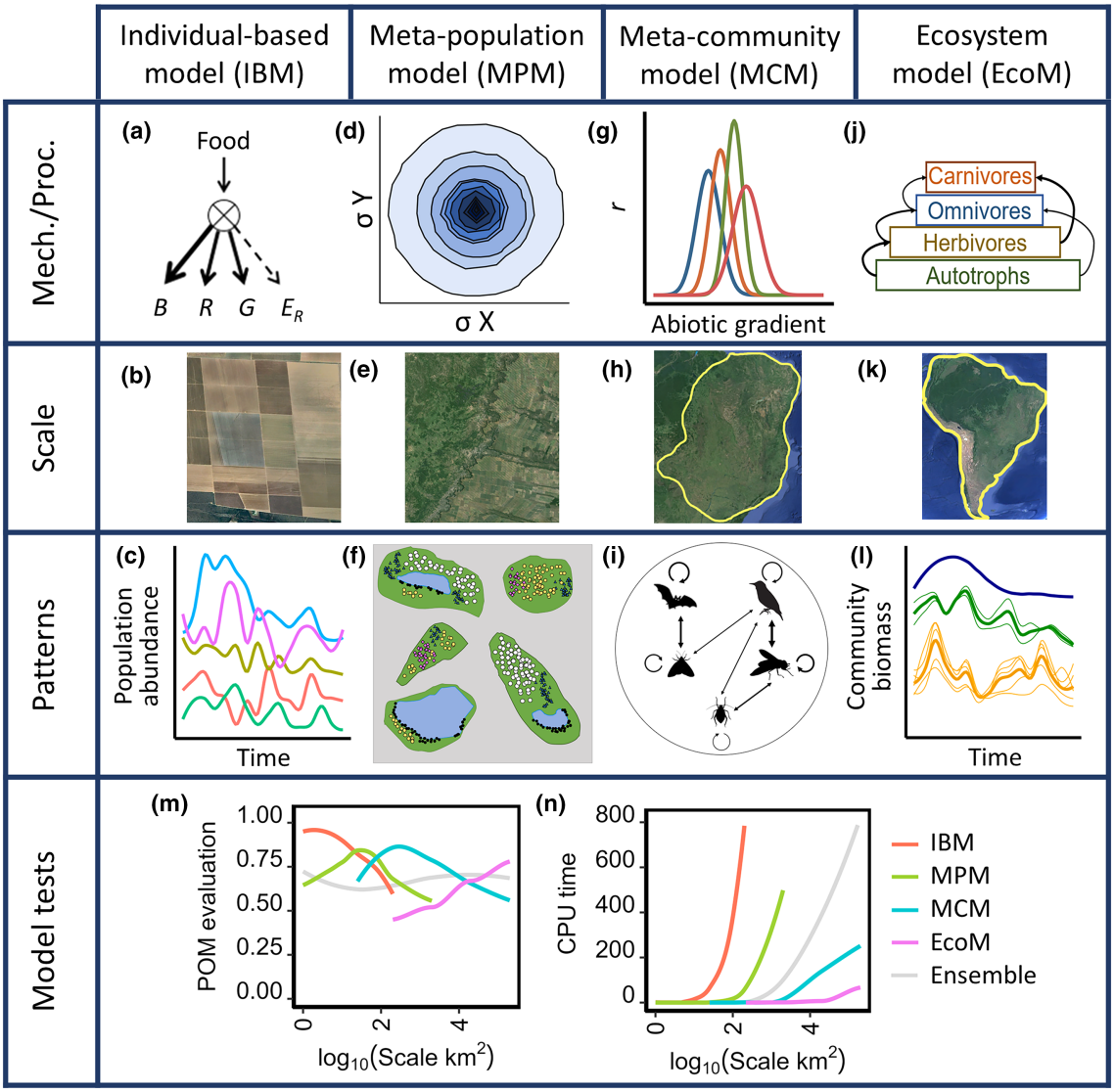

FIGURE 3 Example systematic model intercomparison framework for testing existing mechanistic and process-based ecological models (a, d, g, j) across multiple spatiotemporal scales (b, e, h, k) and levels of biological organization (c, f, i, l). This example illustrates a comparison between an energy budget IBM (a) developed at the field scale (b) to predict population dynamics (c), dispersal kernel metapopulation model (d) to predict landscape-scale (e) meta-population dynamics (f), metacommunity model with species-specific population growth rates (*r*) across abiotic gradients (g) and pairwise interaction strengths to predict regional-scale (h) species interaction networks (i) and trophic ecosystem model (j) to predict national to global (k) community dynamics (l). All existing models would be simulated at each scale and model predictions compared to multiple empirical patterns at different levels of biological organization according to a standardized pattern-oriented modelling (POM) evaluation procedure (m) and computational tractability monitored, for example according to computer processing unit (CPU) time across scales (n). Model comparisons (m, n) would provide valuable information about important mechanisms and processes at specific scales and act as a platform for cross-scale ecological modelling, for example by comparing alternative ensemble models (grey line in m, n) that address scale-explicit model constraints.

patterns at multiple scales. It is therefore unlikely that any of the existing models evaluated in intercomparison frameworks such as that suggested in Figure 3 will be clear forerunners in cross-scale ecological modelling. Yet, systematic intercomparisons can guide a better understanding of important mechanisms and processes when the scale of interest changes (Evans et al., 2013). Alternative model structures, or ensemble modelling with different model combinations (e.g. Geary et al., 2020), can then be tested following the same procedure to identify promising approaches for cross-scale ecological modelling. This systematic abstraction of ecologically relevant mechanisms and processes has already been conducted for scale-explicit ecological models, hence the existence of mechanistic and process-based models, but is rarely conducted with multiple scales in mind (Levin, 1992).

Model intercomparisons will be constrained to well-studied species, communities and ecosystems in the first instance, for which existing models have been developed and empirical observations collected at different levels of biological organisation and spatiotemporal scales. Systematic intercomparisons will also need to reconcile substantial differences in sampling protocols and analytical biases at different spatiotemporal scales (Gallagher et al., 2021; Grimm et al., 2020; Zipkin et al., 2023) by capitalising on advances in ensemble modelling approaches often adopted at the ecosystem scale (Geary et al., 2020). Fundamentally, however, the identification of new fundamental principles in cross-scale ecological modelling will depend on the generation of new empirical studies of naturally occurring communities designed to address research questions that bridge multiple levels and scales, from individuals to ecosystems.

3.3 | New empirical and data tool needs for cross-scale ecological models

Over the last few decades, short term field trials have made key advances in our knowledge of ecological systems. Some examples include quantifying biodiversity and ecosystem functioning relationships (Balvanera et al., 2006; Gonzalez et al., 2020; Hooper et al., 2005), biotic process and landscape heterogeneity effects on community assembly (Albrecht et al., 2007, 2021; Bellmore et al., 2015; Leibold et al., 2017; Poisot et al., 2021), and single-species population responses to multiple stressors (Di Prisco et al., 2016; Goulson et al., 2015; Wagner et al., 2021). Yet empirical studies, like the models that aim to understand their measured patterns, tend to be limited to single spatiotemporal scales and/or system-level patterns rather than targeting multiple scale-explicit animal biodiversity patterns simultaneously. Ambitious cross-scale empirical studies would ideally address this gap by measuring multiple biodiversity patterns across scales. For instance, measuring individual, population, community and ecosystem dynamics across spatiotemporal gradients (from fine to broad) to better determine the thresholds at which mechanisms and processes are obscured by scale. Time and cost constraints, however, make such sampling designs infeasible for many species and ecosystems.

Big data approaches can deal with the issue of scale through the development of deep learning algorithms that detect patterns, for instance of trait-matching and species interactions, in large biodiversity datasets across diverse ecosystems, spatiotemporal scales, experimental designs and sampling biases (Pichler et al., 2020). Deep learning algorithms are data-intensive, however, and crossing levels of biological organisation with these techniques would require a global synthesis of controlled experimental observations that match current efforts for global syntheses of field-based biodiversity measurements (Gonzalez et al., 2023). Big data also entails computational costs equivalent to the most complex ecological models (Tuia et al., 2022), which need to be further operationalised for complex, dynamic ecosystems (de Koning et al., 2023). Big data algorithms are furthermore developed with the mechanisms, processes and patterns they detect in mind (Strydom et al., 2021), but our current understanding of ecological phenomena is scale-explicit and often ignores interactions between multiple scales and levels of biological organisation. Future efforts to develop and test both cross-scale ecological models and big data approaches could therefore hold much greater potential when pursued together. Still, new high-resolution observations are needed to validate the presence of novel cross-scale interactions in real ecosystems.

4 | DISCUSSION

Animal biodiversity patterns emerge from mechanisms and processes operating across extensive spatiotemporal scales (within-field to continental, days to centuries) and levels of biological organisation (individuals to ecosystems). Mechanistic and process-based ecological models have made substantial contributions to understanding the structure, function and dynamics of animal biodiversity, but are typically designed to account for specific levels of biological organisation and spatiotemporal scales. Progress in predictive ecology, however, needs to recognise the importance of co-occurring biodiversity changes at interacting scales of space, time and biological organisation (Figure 2).

Further advances in ecological modelling could be achieved through the systematic testing of existing models to evaluate the performance and tractability of scale-explicit mechanisms and processes at alternative scales. Such efforts would capitalize on the progress that has been made in mechanistic and process-based ecological modelling across disparate fields of ecology. This includes the micro-scale (individuals, within-field, days) at which biodiversity change originates, to the ecosystem-scale (multi-species communities, continental, decades) that impose constraints on ecosystem dynamics (Figure 3).

Systematic model intercomparisons through simulation experiments would reveal key mechanisms and processes that enable cross-scale predictions of emergent animal biodiversity patterns, approach-specific barriers to model tractability (e.g. computational cost with increasing scale) and identify gaps which necessitate the development of new approaches. Commendable efforts have

already been made to incorporate individual variation in ecosystem models (e.g. Harfoot et al., 2014) but this is achieved with species traits and macroecological theory that ignore important processes operating at intermediate levels and scales (Figure 2). It is unclear whether more biologically realistic ecosystem-level models are feasible, but efforts addressing the fundamental issue of scale could reap big rewards for predictive ecology. That is, by identifying scale-explicit mechanisms and processes that act as barriers or enablers in restoring biodiversity-based ecosystem resilience.

Greater integration of mechanisms and processes has been achieved in plant ecology, through the combination of plant ecophysiology, biogeochemistry, forest ecology and micrometeorology in dynamic vegetation models (DVMs) from local to global scales (Foley et al., 1998). Yet DVMs are confronted by a complexity trap, in which accumulating processes are introduced to increase model realism for specific scenarios at the cost of model tractability, predictive power across a range of scenarios and greater uncertainty (Franklin et al., 2020; Prentice et al., 2015). Franklin et al. (2020) suggest that overcoming this challenge will depend on the identification of fundamental principles that constrain system behaviour from the plant to ecosystem level. Cross-scale modelling in animal ecology can strive to identify these principles now by identifying the underlying mechanisms that give rise to several processes underpinning emergent animal biodiversity patterns.

Capitalising on existing mechanistic and process-based models is a logical first step to achieving cross-scale ecological modelling, using ensemble and big data approaches to streamline integration as we strive to scale from individuals to ecosystems. Yet, the overarching goal should be to unify disparate fields of ecology to enhance predictions of animal biodiversity responses to environmental change. More than one framework will be able to confront cross-scale ecological modelling, making diverse perspectives alongside standardised model intercomparison frameworks (Grimm, 2023) and open-access, collaborative platforms (Urban et al., 2022) an important starting point. This new approach to ecological modelling would support a next generation of versatile modellers, collectively developing a common evidence-base to safeguard biodiversity and ecosystems across interrelated environmental problems.

AUTHOR CONTRIBUTIONS

Alice S. A. Johnston: Conceptualization; resources; visualization; writing – original draft; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The author declares no conflict of interest.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

ORCID

Alice S. A. Johnston https://orcid.org/0000-0001-8781-4039

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