

A conceptual framework for scaling up emergent predictions from mechanistic individual-based models

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Abstract

Environmental decision-makers need robust, landscape-level predictions of population responses to inform management decisions before implementation. Mechanistic individual-based models (IBMs) can capture how individual behaviour and interactions in heterogeneous environments generate emergent population dynamics, but high computational costs typically restrict applications to small spatial extents. To address this limitation, we synthesise spatial modelling strategies across subfields of ecology and introduce the Spatial Threshold of Emergent Behaviour Stabilisation (STEBS) framework. STEBS capitalises on the biological realism of mechanistic IBMs through an *in silico* modelling experiment to quantify the Critical Emergence Threshold (CET) – the smallest spatial extent at which emergent system behaviour stabilises. The CET provides a biologically meaningful and computationally efficient scale for developing meta-models that relate environmental variables to emergent population patterns, which can then be extrapolated across unsimulated regions to predict landscape-level dynamics. This approach enables tractable scaling up of mechanistic IBMs, while retaining their biological realism. STEBS therefore offers a systematic pathway for applying IBMs to real-world environmental challenges, enhancing the evidence base for policy and management under accelerating global change. Future development of STEBS into an operational and transferable tool will require empirical validation across diverse species, landscapes and IBM structures, alongside evaluation of whether the upfront investment required to estimate CETs improves predictive efficiency compared to brute-force scaling approaches.

Key words: Agent-based modelling, behaviour, decision support, landscape, meta-modelling, physiology, population dynamics, scale dependency, spatial threshold



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Introduction

Environmental decision-making increasingly requires robust predictions of how populations respond to management interventions at the landscape level. Individual-based models (IBMs) have demonstrated predictive power across ecological systems, for example, through forecasting the effects of habitat loss on coastal shorebirds (Stillman and Goss-Custard 2010), simulating fish population responses to altered river flow regimes (Hajiesmaeili et al. 2024) and assessing the impacts of offshore wind farms on harbour porpoise populations (Nabe-Nielsen et

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al. 2018) to provide information for management actions. However, many IBMs remain reliant on imposed behaviour, so that population responses are constrained by empirical relationships between species life history traits and environmental conditions (Railsback 2001; Grimm and Berger 2016). In contrast, mechanistic IBMs explicitly represent the causative mechanisms (e.g. physiology) driving complex emergent dynamics (i.e. system-level behaviour originating from local interactions) (Johnston et al. 2019; Newman et al. 2019). Unlike purely statistical, demographic or trait-based modelling approaches, mechanistic IBMs, therefore, offer a powerful tool for prediction under novel environmental scenarios (Grimm et al. 2017; Pilowsky et al. 2022). Despite these advantages, the computational demand of applying mechanistic IBMs at large spatial extents remains a key constraint.

Scaling up mechanistic IBMs to entire landscapes or regions quickly becomes computationally intractable due to the magnitude of individuals and interactions being simulated (Purves et al. 2013). This limits the practical application of mechanistic IBMs for evidence-based policy and management, particularly as land-use strategies and regulatory frameworks increasingly emphasise landscape-level management of ecological processes. Ecological risk assessments of plant protection products, for instance, have typically focused on individual fields and margins, but the European Food Safety Agency now acknowledges that this approach underestimates cumulative effects, with new guidance supporting landscape-level approaches that account for broader population dynamics, habitat types and management practices (Tarazona et al. 2024). Land management optimisation schemes such as England's Environmental Land Management Scheme and Biodiversity Net Gain policy also require an understanding of how localised effects of management strategies extend to the landscape level (Stevens et al. 2007; Lindborg et al. 2017).

Several factors contribute to the computational challenge of scaling up mechanistic IBMs to entire landscapes. First, simulating each modelled individual's life cycle, movements, decisions and interactions means that a hundredfold increase in model environment area with a tenfold increase in linear spatial extent (e.g. from 5×5 km area to 50×50 km) can lead to exponential growth in memory use (Purves et al. 2013). Second, larger landscapes introduce greater environmental heterogeneity, requiring the simulation of diverse habitat types and management practices. Maintaining fine spatial resolution is critical for accurate predictions, but increases computational load, while coarse resolutions risk losing key spatial processes (Bocedi et al. 2012). Third, scenario-based simulations designed to address environmental management questions before implementation require enough replicates to account for stochastic uncertainty (Drake et al. 2024). When several scenarios with multiple replicates are needed to provide information for decisions, overall computational demand is amplified. This limitation poses a challenge: how can we harness the rich predictive power of mechanistic IBMs at the spatial scales relevant to environmental policy and management?

Conventional strategies to address the trade-off between realism and tractability in ecological modelling often involve aggregating individuals, behaviour or environmental variables to reduce model complexity (Fritsch et al. 2020). While aggregation can facilitate prediction at larger spatial extents, it often comes at the cost of losing the mechanistic detail that drives emergent population dynamics. For instance, the ability of mechanistic IBMs to represent behavioural heterogeneity has proved essential for capturing the non-linear and indirect effects of

resource limitation, chronic stressor exposure and density-dependent feedbacks that characterise real-world population responses to land management interventions and environmental change (Johnston et al. 2015; Mintram et al. 2020; Watson et al. 2022; Archer et al. 2025). There is, thus, a pressing need for approaches that can retain the rich predictive power of mechanistic IBMs, while enabling tractable simulation at the landscape level. Achieving this aim requires a clear understanding of what constitutes a 'landscape' from the perspective of different species, a concept that is inherently trait- and context-dependent (see Box 1).

Box 1. What is a landscape? A species- and context-specific perspective.

It is important to recognise that the concept of a 'landscape' is not fixed, but inherently species- and context-dependent. In landscape ecology, spatial scale (extent and resolution) and heterogeneity are central to understanding ecological patterns and processes (Turner et al. 1989; Wiens 1989). However, these spatial properties must be interpreted relative to the functional and ecological traits of the focal species, such as body size, dispersal ability and habitat preference (Olden et al. 2004; Fahrig et al. 2011). Movement ecology further refines this view by considering how an individual's interactions with its environment are shaped by its internal state and motion and navigation capacities (Nathan 2008). Larger-bodied, mobile species, such as elephants, may perceive landscapes over tens of kilometres, for instance, while smaller or less mobile species respond to spatial heterogeneity at much finer resolution (Fig. 1). Hence, what constitutes a 'landscape' varies across species. It follows that 'landscape-level' management strategies cannot be defined by a single spatial scale. For example, conservation planning for elephants may focus on broad spatial extents to account for protected area networks, while a landscape approach to enhancing pollinator habitat could involve small-scale interventions across multiple farms. Mechanistic IBMs explicitly represent individual movement and behaviour across heterogeneous environments and so are ideally suited for predicting how population responses emerge from the interplay of species traits and changing abiotic and biotic conditions in different landscape contexts (Johnston et al. 2019).

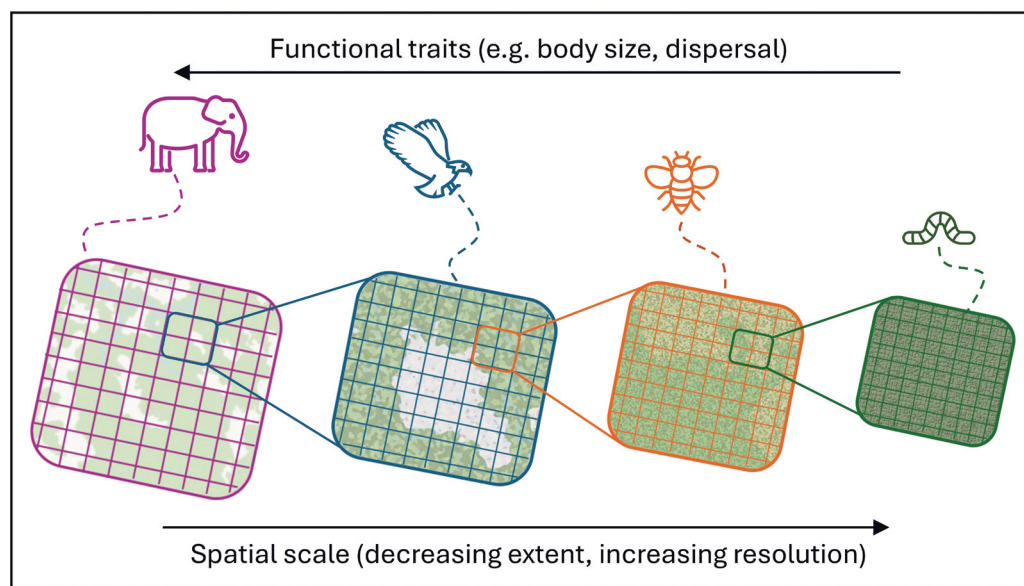


Figure 1. Schematic showing how different species perceive landscapes at different spatial scales (extent and resolution). Four taxa (elephant, bird, bee, earthworm) are illustrated with their associated landscape as gridded representations of habitat heterogeneity aligned with their movement ecology and resolution of perception. As functional traits like body size decrease, the experienced landscape becomes smaller in extent, but finer in resolution.

In this paper, we propose the conceptual Spatial Threshold of Emergent Behaviour Stabilisation (STEBS) framework for systematically scaling up mechanistic IBMs. STEBS is grounded in the principle that emergent ecological patterns, such as habitat structure, species distributions and population dynamics, frequently exhibit scale-dependent behaviour (Levin 1992). Crucially, these types of behaviour are often marked by critical thresholds, beyond which significant shifts in dominant system properties occur (Wiens 1989). Landscape metrics,

such as diversity and contagion, for example, respond non-linearly to increasing spatial extent before stabilising at larger extents (Turner et al. 1989; Wiens 1989). Demographic thresholds reinforce the same principle. For instance, variance in animal population fluctuations increases sub-linearly with mean abundance (Ferguson and Ponciano 2015), extinction risk declines disproportionately as carrying capacity increases (White et al. 2017) and vole population cycles dampen at higher densities (Millon et al. 2014). Together, these findings demonstrate that stability frequently emerges beyond critical thresholds of spatial extent, abundance or connectivity. Recognising these thresholds is essential for accurately interpreting ecological processes at the landscape level (Groffman et al. 2006).

Here, STEBS aims to couple insights from landscape ecology with the predictive power of mechanistic IBMs through systematic *in silico* experiments to identify the spatial threshold at which multiple emergent dynamics stabilise, termed the Critical Emergence Threshold (CET). We first synthesise spatial strategies employed across subfields of ecology to introduce the conceptual foundations of the STEBS framework. Then, we demonstrate a conceptual three-step STEBS approach that involves quantifying the CET, conducting modular simulations and developing a meta-model for efficient, landscape-level predictions that retain the biological realism of mechanistic IBMs. Finally, we identify key research needs to address outstanding questions for the implementation of STEBS as a practical tool for environmental decision support.

Conceptual foundations: spatial strategies in ecological modelling

Ecologists have long recognised that spatial scale fundamentally shapes ecological patterns and processes, with interactions at one scale often driving emergent dynamics at another scale (Levin 1992; Dunning et al. 1995; Grimm et al. 2005). Classical multi-scale empirical studies from landscape ecology have demonstrated a non-linear response of habitat diversity, dominance and contagion metrics with changes in the spatial extent and resolution of study landscapes (Turner et al. 1989). More recently, Wu (2004) found that, while some landscape metrics show predictable scaling functions with spatial extent or resolution, others display unpredictable patterns indicative of system-level shifts at specific spatial scales. The Hierarchical Patch Dynamics (HPD) paradigm provides another valuable framework for interpreting system behaviour across scales. HPD views ecosystems as nested patch mosaics, where each scale consists of assemblages of smaller-scale patches, forming a discontinuous hierarchy (Wu and Loucks 1995). Crucially, processes at one scale can give rise to emergent properties at another. For example, local disturbances and interactions within patches generate variability, but when integrated over a broader landscape, may produce relatively stable macro-patterns (Wu and Loucks 1995).

Cross-scale interactions pose a challenge for ecological modelling, as models must balance the representation of fine-resolution, lower-level mechanisms with the need to generate predictions at broader spatial scales. Nevertheless, the importance of capturing spatial processes has resulted in progressive embedding of spatially explicit environments into models that were traditionally non-spatial or spatially implicit (DeAngelis and Yurek 2017). Early models in population ecology represented population growth through non-spatial frameworks, such as exponential and logistic growth equations (Leslie 1945; MacArthur 1958; May

1958). Reaction-diffusion models advanced the field by representing population density as a continuous variable across space, incorporating random movement via diffusion terms to capture large-scale phenomena such as range expansions or travelling wave fronts (El-Hachem et al. 2021; Calvez et al. 2022). Patch-based models introduced a discrete view of space, using migration matrices or transition probabilities to represent dispersal across habitat patches, thus allowing for explicit treatment of spatial connectivity (Karnatak and Wollrab 2020). Similarly, community ecology traditionally used non-spatial models assuming well-mixed species pools (e.g. Lotka-Volterra, food webs), while more recent spatial extensions incorporate dispersal across grids or patches (Thompson et al. 2020).

IBMs are increasingly used to simulate population dynamics, while accounting for the effects of individual variation, local interactions and adaptive behaviour (DeAngelis and Grimm 2014). However, an important distinction exists between demographic and mechanistic IBMs. Demographic IBMs represent individual life events (e.g. birth, dispersal) using statistical rules to reproduce population patterns for forecasting purposes, but are often spatially implicit or use simplified representations of environmental heterogeneity (Stillman et al. 2000; Grimm and Berger 2016). Mechanistic IBMs explicitly represent the underlying mechanisms (e.g. physiology) that drive individual decisions and life cycles and are typically spatially explicit to enable simulation of individual movement and behaviour across detailed, heterogeneous environments (Evans et al. 2019; Johnston 2024).

Landscape ecology frequently employs spatially explicit simulations or modelling tools to examine fragmentation, connectivity and habitat mosaics at large spatial extents (Turner 2005; Synes et al. 2016). Graph theory (Mancini et al. 2022) and circuit theory (McRae et al. 2008) approaches, for instance, can efficiently identify corridors and barriers for dispersal across entire landscapes and regions. Ecosystem models, on the other hand, have traditionally employed compartment-based flows of matter and energy amongst aggregated pools or functional groups. Spatial extensions of traditional ecosystem models couple local fluxes across coarse-gridded landscapes, enabling more detailed predictions of large-scale biogeochemical and ecological dynamics (Harfoot et al. 2014).

Different subfields of ecology have developed modelling approaches that emphasise different positions along the spectrum of spatial resolution and spatial extent (Fig. 2 illustrates this conceptual space). For instance, population ecology often adopts local-scale models, such as IBMs or population dynamics models; community and metapopulation ecology integrate species interactions or subpopulation connectivity across moderate spatial scales; and landscape and ecosystem ecology utilise models that operate at coarser resolution and broader extents (e.g. graph models, mass-balance ecosystem models) to capture large-scale patterns and processes (Fig. 2).

Building on the conceptual overview in Fig. 2, we provide a summary of spatial strategies employed in ecological modelling, with examples applied to terrestrial animal species (Table 1). These strategies reflect ongoing efforts to balance biological realism with computational tractability at specific spatial scales of interest and, where possible, to bridge across multiple scales. Table 1 does not aim to be exhaustive, but rather illustrates representative approaches for addressing spatial scale, ranging from cohort averaging and patch-based simplification to empirical parameterisation and the application of scale transition theory. To ensure broad relevance, we surveyed models that are widely

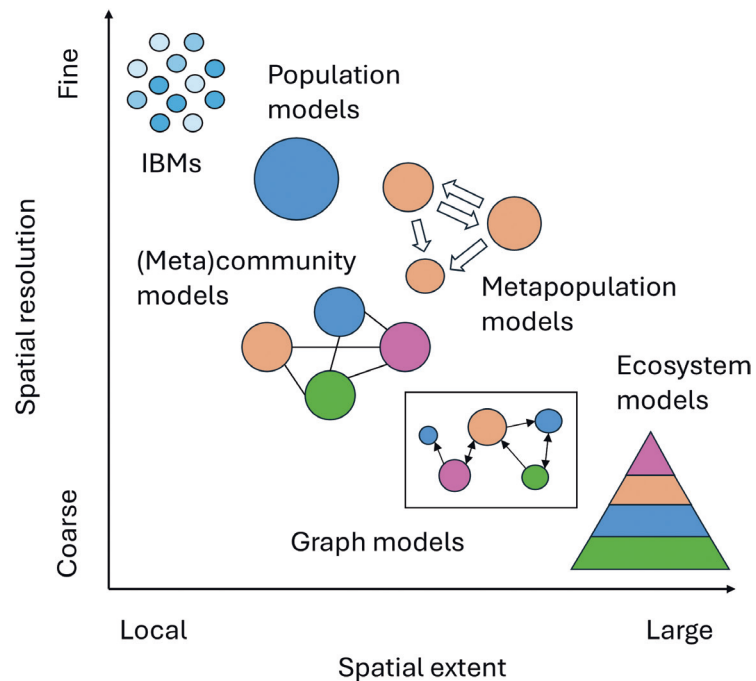


Figure 2. Relationship between spatial resolution and spatial extent across different subfields of ecology and their associated modelling approaches. Spatial resolution ranges from fine (detailed, small-scale observations or models) to coarse (aggregated, large-scale observations) and spatial extent ranges from local to large (e.g. geographic region, entire ecosystem) scales. Various modelling approaches are positioned according to general spatial resolution and extent ranges, with colours representing different species, trophic groups or habitat patches. Individual-based models (IBMs) represent individual variation and local interactions; population models average across individuals (sometimes differentiated by age/stage/size) in a population; metapopulation models represent networks of local subpopulations linked by dispersal; (meta)community models focus on species interactions within a local habitat or across a network of habitat patches; graph models describe habitat connectivity across landscape mosaics; and ecosystem models estimate biomass structure and flows across trophic or functional groups.

cited and recognised as influential within their subfields, selecting examples that illustrate distinct spatial strategies while remaining comparable across taxa. Examples in Table 1 are largely restricted to terrestrial animal species to provide a consistent basis for comparison, but the identified strategies are broadly applicable to models developed for other organisms and ecosystems.

A common feature of models at the population to ecosystem level is the aggregation of individuals, behaviour or environmental variables (Fritsch et al. 2020). The Madingley general ecosystem model (Harfoot et al. 2014), for example, groups organisms into broad functional types, applying simplified traits and metabolic scaling rules across coarse spatial grids (Table 1). At intermediate spatial scales, metapopulation and metacommunity models emulate processes such as dispersal, turnover and colonisation by aggregating populations or species across patches or networks (Hanski et al. 2017; Thompson et al. 2020; Table 1). These approaches simplify internal patch dynamics (population growth, species interactions) and rely on parameterised dispersal kernels or occupancy functions.

Poll4pop (Häussler et al. 2017) exemplifies the more recent integration of GIS-based raster landscapes in population modelling, allowing for detailed

representation of spatial heterogeneity (Table 1). Häussler et al. (2017) balance realism and tractability by simulating wild bee populations over 25 m cells using colony-level growth, foraging and dispersal functions to generate predictions at the landscape and national level. Capera-Aragones et al. (2021) demonstrate an alternative strategy, using diffusion terms to model the movements of a foraging bee population as a continuous process (Table 1). Circuit theory models, such as that of Grafius et al. (2017), similarly abstract animal movement as a flow across a resistance surface, without explicitly simulating individuals or collectives (Table 1).

Aggregation can improve computational tractability at larger spatial extents by reducing model complexity, but often obscures the lower-level mechanisms that underpin emergent system dynamics (Parry and Evans 2008; Bolnick et al. 2011). For instance, patch simplification may mask behavioural responses to small-scale habitat features, while abstracted movement processes cannot accommodate behavioural nuance (Bocedi et al. 2012; Gardner et al. 2021). On the other hand, fine-resolution IBMs, such as ALMaSS (Topping et al. 2003) and EEEworm (Johnston et al. 2018), simulate individual behaviour and energetics across detailed spatial domains to capture fine-resolution interactions (Table 1). The trade-off between biological realism and tractability in IBMs requires modellers to select model environments that are large enough to capture the key environmental variables, management practices and individual behaviour driving species population dynamics, but small enough for feasible simulation run-times. The ALMaSS IBM system, for example, can theoretically simulate 50×50 km landscapes, but, in practice, applications are limited to $\sim 10 \times 10$ km areas at 1 m resolution to retain the necessary detail without overwhelming computational demand (Topping et al. 2019).

Brute-force scaling, running an original detailed model in each cell of a larger landscape grid, enables retention of mechanistic detail across broader spatial extents, but typically demands high-performance computing (Cipriotti et al. 2016; Fritsch et al. 2020). Similarly, hybrid strategies aim to combine fine-resolution biological realism with broader spatial prediction. For example, mechanistic niche models couple individual physiology, behaviour and microclimatic conditions with coarse regional or continental grids (Kearney and Porter 2009; Table 1). Their large-scale outputs are usually static projections of fitness or suitability from which persistence is inferred, rather than explicit, dynamic population trajectories (Kearney and Porter 2009).

Meta-modelling provides additional scaling routes through either the propagation of outputs from detailed simulations into simpler models at broader spatial extents (Urban 2005; Fritsch et al. 2020) or training of statistical or machine-learning emulators (surrogates) to approximate a mechanistic model's input-output mapping (Marie and Simioni 2014). While meta-modelling has mainly been applied to sensitivity analysis and calibration of detailed simulation models (Coutts and Yokomizo 2014; Prowse et al. 2016; Fer et al. 2018), the ability to preserve fine-resolution responses at far lower computational cost shows promise for scaling applications (Marie and Simioni 2014). The performance of any meta-model, however, hinges on the credibility of the source model, representativeness of the training data and sensitivities to input variation and non-linear interactions (Urban 2005; Marie and Simioni 2014).

Table 1. Representative models from different subfields of ecology and their spatial strategies. Spatial strategies refer to different approaches taken by models to reconcile the trade-off between capturing fine-resolution processes and extending models across broad spatial extents. See text for further explanation of each strategy.

Model type	Model/key reference	Taxa	Spatial extent and resolution	Mechanisms and/or processes	Spatial strategy
Ecosystem model	Madingley model (Harfoot et al. 2014)	Broad functional groups (e.g. herbivores)	Regional to global, $1^\circ \times 1^\circ$ cells ($\sim 100 \text{ km}^2$)	Metabolism, life cycle, dispersal drive ecosystem trophic dynamics	Aggregation (cohorts with identical traits)
Process-based metacommunity model	Thompson et al. (2020)	Multiple species (theoretical)	Regional (e.g. 100 patches), continuous spatial domain	Community dynamics (growth, interaction, turnover), with dispersal	Aggregation (species abundance), patch simplification
Metapopulation model	Hanski et al. (2017)	Butterfly	Regional ($50 \times 70 \text{ km}$), network of habitat patches of specified size	Patch occupancy dynamics (extinction, colonisation, connectivity)	Parameterisation (patch occupancy data), patch simplification
Mechanistic niche model	Kearney and Porter (2009)	Various terrestrial species	Regional to continental, microclimate scale (cm–m) integrated in coarse grid (km)	Physiology-driven niche, based on microclimate (energy/water/mass balance)	Hybrid multi-scale (fine microclimate + coarse climate data)
Process-based population model	Poll4pop (Häussler et al. 2017)	Wild bees (bumblebees, solitary bees)	Landscape (e.g. 10 km^2) to national (Image et al. 2022), $25 \times 25 \text{ m}$ cells	Central-place foraging and colony-level population growth, based on floral and nesting resources	Aggregation (population growth and dispersal functions)
IBM/ABM	ALMaSS (Topping et al. 2003)	Multiple (vertebrates, invertebrates)	Landscape (e.g. 100 km^2), $1 \times 1 \text{ m}$	Behavioural states, life cycle events, species-specific detail (e.g. energetics)	Species-specific aggregation (e.g. super-individuals)
Partial integro-differential equation	Capera-Aragones et al. (2021)	Bumblebees	Landscape (4 km), continuous one-dimensional spatial domain	Forager density via diffusion/advection, resource memory and depletion	Aggregation (population density, diffusion)
IBM/ABM	EEEWorm (Johnston et al. 2018)	Earthworm	Plot to field ($3\text{--}8 \times 1 \text{ m}$ vertical soil profile), $1 \times 1 \text{ cm}$	Energy budgets and movement in response to micro-soil conditions	Individual-based simulation: no aggregation
Connectivity model	Circuitscape (Grafius et al. 2017)	Birds (great tits, blue tits)	Landscape (urban areas), $5 \times 5 \text{ m}$ cells	None: landscape connectivity derived using circuit theory from resistance maps, based on habitat suitability	Reduced biological realism: different types of movement behaviour implicit in current flows
Process-based population model	Melbourne and Chesson (2005)	Caddisfly	Local (riffle) scaled up to regional (stream) level	Population dynamics scaled via non-linear interactions and spatial heterogeneity	Scale transition theory (non-linear averaging)

Scale transition theory provides a conceptual and analytical approach for understanding how ecological patterns and processes observed at local scales can aggregate or transition into broader-scale dynamics (Chesson et al. 2005; Melbourne and Chesson 2006; Chesson 2012). Application of scale transition theory to a caddisfly population model (Melbourne and Chesson 2005), for instance, identified scale transition terms that quantify how non-linearities and spatial variation drive changing dynamics when scaling from riffle to stream level (Table 1). Crucially, scale transition theory acknowledges that emergent properties do not change linearly with an increase in spatial extent, but that new dynamics can emerge suddenly, and population patterns eventually become scale invariant. However, scale transition terms do not provide a mechanistic understanding of the individual behaviour shaping population dynamics. While conceptually powerful, scale transition models have, thus, been largely applied to relatively simple systems, though extensions to more complex, individual-based simulations do exist (Vance et al. 2010).

There remains a pressing need for formalised frameworks that can preserve the mechanistic detail underpinning complex emergent dynamics, while enabling tractable predictions at the spatial extents relevant for environmental decision-making. Foundational insights from landscape ecology highlight the importance of capturing the non-linear scaling of processes with spatial extent (Levin 1992) and recognising the characteristic thresholds of emergent system properties (Wiens 1989; Holling 1992). Scale transition theory seeks to scale up local dynamics, while preserving the effects of scale-dependent processes using non-linear averaging, but remains limited through its reliance on statistical relationships (Chesson 2012). Meanwhile, mechanistic IBMs allow explicit representation of individual interactions, environmental variability and emergent dynamics, but at present, their application at larger spatial extents is constrained by computational demand. Combining the conceptual contributions of landscape ecology and scale transition theory with the predictive power of mechanistic IBMs suggests a pathway for scaling up population predictions, based on the identification of species- and context-specific spatial thresholds of emergent system behaviour stabilisation (Fig. 1). Here, we use scaling up to mean an increase in the spatial extent to which modelled population patterns are representative.

The STEBS framework: leveraging mechanistic IBMs to identify spatial thresholds of emergence

The Spatial Threshold of Emergent Behaviour Stabilisation (STEBS) framework is based on the concept that, beyond a certain spatial threshold, here defined as the Critical Emergence Threshold (CET), simulation of mechanistic IBMs at larger spatial extents will yield minimal new population patterns due to the non-linear stabilisation of emergent system behaviour. The first iteration of the conceptual STEBS framework broadly consists of three steps: 1) identify the spatial extent at which multiple emergent dynamics become scale-invariant, i.e. the spatial extent beyond which no new population patterns emerge; 2) develop a meta-model between these scale-invariant patterns and environmental variables; and 3) extrapolate the meta-model to produce landscape-level predictions grounded in mechanistic detail.

Step 1) Identify the Critical Emergence Threshold (CET)

Central to the STEBS framework is determination of the CET for a given set of individuals (e.g. species, life stage), defined here as the smallest spatial extent beyond which further increases in modelled extent yield only marginal changes in emergent model outputs. Identification of the CET relies on running a series of mechanistic IBM simulations across progressively larger spatial extents (referred to here as modules). Together, these modules incorporate spatial heterogeneity representative of realistic environmental gradients and variability (Turner and Gardner 2015) (Fig. 3). At each modelled extent, a suite of emergent metrics, such as population size, biomass and spatial distribution is recorded and standardised (standardised population patterns, SPPs). In this context, we standardise the population pattern time series by the series' minimum and maximum, which scales the population pattern series to between 0 and 1.

For each individual SPP, at each in a series of modelled extents (e.g. $j = 1, 2, 3 \dots j_{max}$), the sum of the Euclidean distance between SPP_j and SPP_{j-1} is calculated to give a change in emergent patterns, ΔSPP , calculated for a particular spatial extent, j , according to:

$$\Delta SPP(j) = \sum_{t=1}^N |\bar{x}_{j,t} - \bar{x}_{j-1,t}| \quad \text{Eq. 1}$$

where $\bar{x}$ represents the modelled replicate-average SPP (e.g. biomass) from a given timestep t and a given spatial extent j , and N is the number of data points in each spatial extent time series. By plotting ΔSPP over spatial extent increments, an emergence-area curve is constructed to describe changes in emergent patterns with increasing area (Fig. 4). The CET is identified as the inflection point beyond which increasing the modelled area no longer generates new population patterns. Quantification of ΔSPP enables clearer identification of the CET, as the value for all ecological metrics approaches zero (Fig. 4). The CET can be identified visually in conjunction with an understanding of modelled system dynamics or mathematically by fitting a power-law relationship to ΔSPP points and taking a percentage of the asymptote value (e.g. 95%).

Mechanistic IBM predictions are expected to display high variability in response to early incremental increases in spatial extent as new population patterns emerge due to non-linear interactions and spatial heterogeneity (Melbourne and Chesson 2006). As spatial extent increases, the expectation is for different emergent patterns to stabilise at different rates, with some showing delayed and oscillating responses and all SPPs flattening beyond a particular spatial extent, indicating overall system behaviour stabilisation (Fig. 4). The CET, therefore, represents an optimal spatial extent for efficient

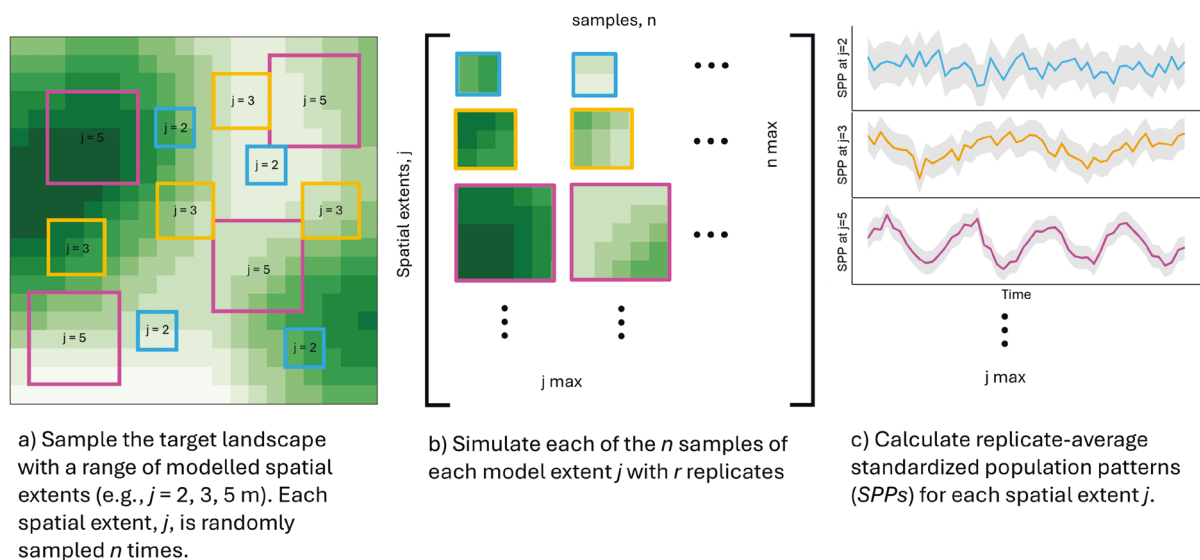


Figure 3. Conceptual workflow for quantifying standardised population patterns (SPPs) across spatial extents (j) using an *in-silico* modelling experiment. a. Sample the target landscape with different spatial extents j (represented by differently coloured boxes with side lengths of $j = 2, 3, 5$ m) to represent the model landscape. Each spatial extent j is sampled n times to capture environmental heterogeneity; b. Simulate the IBM for each sampled spatial extent (j) with r replicates to capture stochastic variability in population outputs. IBM outputs are used to construct a matrix of simulation outputs across spatial extents; c. Calculate replicate-average SPPs at each spatial extent j by averaging simulation outputs across n samples and r replicates.

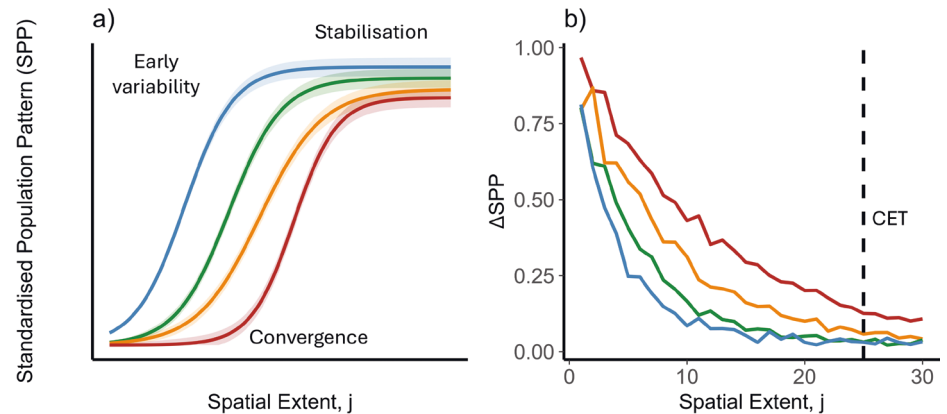


Figure 4. Conceptual illustration of the Critical Emergence Threshold (CET) for several emergent patterns. **a.** Several emergent population outputs from simulation of a mechanistic IBM shown as standardised population patterns (SPPs). As the mechanistic IBM is simulated at incremental spatial extents, panel a demonstrates expected early variability, mid-scale convergence and large-scale stabilisation of SPPs. **b.** As spatial extent increases, the sum Euclidean distance between replicate mean SPP (ΔSPP) approaches zero at the CET (marked by the dashed vertical line beyond which the curves in both panels plateau, which can be estimated visually or calculated). A global CET can be taken once all patterns have stabilised with scale or trait-dependant CETs can be estimated for each simulated population output (e.g. biomass).

IBM simulation, as extending model environments beyond this threshold incurs increased computational demands without capturing meaningful additional system dynamics.

Step 2) Meta-model development

The CET identifies the spatial extent beyond which emergent population patterns become scale invariant and, therefore, represents the optimal level at which to develop meta-models for extrapolation to broader spatial extents where mechanistic IBMs incur large computational demands. Meta-models are computationally efficient approximations, trained on input-output relationships, that can be used to scale up modelled emergent patterns (Marie and Simioni 2014). In this context, the sub-sampled environmental domain at the CET, taken from Step 1, can be used to build a relationship between environmental variables and population patterns. For example, a generalised additive model (GAM) could be trained on CET-derived outputs of bee colony size as a function of floral resource density, nesting habitat and temperature. Alternatively, machine-learning emulators, such as random forests or boosted regression trees, could be used to capture non-linear interactions when interpretability is less critical (Elith et al. 2008; Angione et al. 2022). The meta-model should capture the fundamental relationships derived from fine-resolution simulations and enable rapid generalisation across unsimulated regions (Fig. 5). Critical to this process is rigorous validation, which may include cross-validation with IBM outputs from modules withheld during meta-model training, direct comparisons against outputs from simulations at larger spatial extents or more heterogeneous landscapes (Araújo and Guisan 2006) and sensitivity testing to assess how well the meta-model generalises beyond the landscape used for model training.

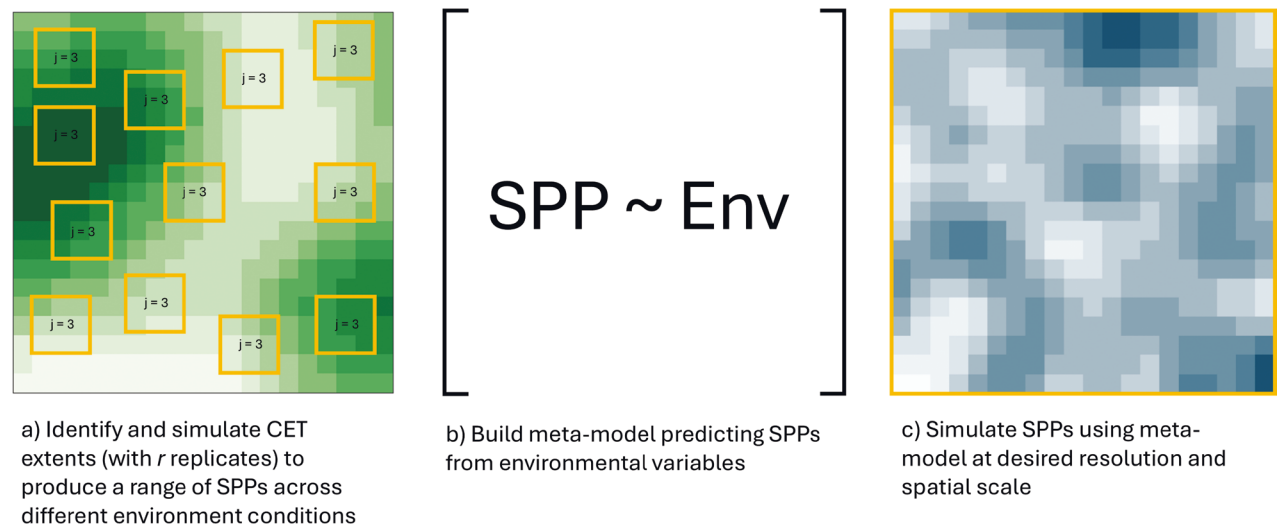


Figure 5. Illustrative example of the scaling up pipeline after identifying the CET for a given species and landscape. **a.** The landscape is sub-sampled into CET modules to ensure that sufficient environmental heterogeneity is represented. Values of key environmental variables (e.g. temperature, food availability, habitat composition) are shown in shades of green; **b.** IBM simulations of each module (for r replicates to capture stochasticity) are used to construct a meta-model linking environmental variables to standardised population patterns (SPPs); **c.** The meta-model is then applied across the full landscape to generate spatially explicit predictions of population dynamics (e.g. biomass, stage structure), shown in shades of blue. Colours in a) and c) distinguish environmental inputs (green) from population-level predictions (blue).

Step 3) Landscape-level inference

In the final step, the meta-model is applied across unsimulated regions of the landscape using spatial layers of environmental variables, generating spatially explicit predictions of population dynamics, species distributions or management outcomes at low computational cost (Fig. 5c). Crucially, this approach retains the fine-resolution biological realism of the IBM, while allowing landscape-level inference for decision support. Scaling up population patterns allows us to address land management questions, such as where pollinator populations are likely to thrive or decline under different crop management regimes, surrounding habitat configurations and pesticide use patterns, without the need to simulate billions of individuals. Identification of meta-modelling errors at the landscape level is critical at this stage to ensure proportionate interpretation of the results. For example, errors may include the averaging of detailed environmental data, parameter uncertainty from limited calibration sites and extrapolation beyond training conditions. Spatial uncertainty maps, confidence intervals and validation across habitat types can help reveal where the model performs poorly. Clear communication of meta-model limitations ensures that results are used appropriately and that decision-making accounts for confidence levels in model outputs.

Discussion

Here, we introduce STEBS, a framework for producing mechanistically informed population predictions at policy-relevant spatial scales. Across sub-fields of ecology, modelling approaches employ spatial strategies to balance biological realism and broad-scale prediction, typically involving aggregation of processes or states to manage computational costs (Table 1, Fig. 2; Fritsch et

al. 2020). Aggregation, however, can obscure the lower-level mechanisms that generate emergent dynamics and is prone to failure under novel environmental conditions (Johnston et al. 2019). STEBS addresses this gap by making the scale of emergent system behaviour stabilisation explicit through estimation of CET. In effect, the CET identifies where the marginal benefit of adding mechanistic detail and environmental heterogeneity, to capture multiple emergent patterns, no longer outweighs computational cost (Grimm et al. 2005). Framed this way, predictive power and practical utility can be co-optimised to support environmental decision-making (Wang et al. 2024). Conceptually, STEBS is, thus, analogous to the Medawar Zone, indicating the level of effort that yields the greatest scientific return (Grimm et al. 2005).

The framework presented here promises to advance both theory, by formalising CET as a stabilisation point and practice, by embedding mechanistic insight within scalable prediction tools for robust decision support. Unlike brute-force scaling that simply extends mechanistic IBMs over larger domains via high-performance computing (Cipriotti et al. 2016; Fritsch et al. 2020), STEBS provides an ecologically grounded rule for when and how to scale up using more efficient meta-modelling techniques. By identifying biologically meaningful thresholds beyond which extra computation adds little information, it avoids arbitrary choices of model extent or resolution. Therefore, even if the upfront investment required to estimate CETs outweighs downstream efficiency gains, STEBS can still provide value as a flexible tool for model design and scaling decisions. Although our focus here (Figs 3–5) is scaling mechanistic IBMs to landscape-level population predictions, the same principle can help embed greater biological realism in models targeting higher ecological levels and other subfields (Table 1, Fig. 2).

STEBS supports calls for mechanistically grounded, landscape-level ecological risk assessments that reflect fragmented and managed environments (Tara-zona et al. 2024). By simulating individual-level exposure and effects of plant protection products, STEBS could enable prediction of emergent population responses under heterogeneous and multi-stressor scenarios. For example, STEBS could be applied to pollinator risk assessment by identifying the CET for key species (Figs 3, 4), simulating pesticide exposure across CET-sized modules and predicting impacts across an agricultural region using a landscape-level meta-model (Fig. 5). Crucially, because the CET derived from a mechanistic IBM is species- and context-specific, the framework accommodates variation in both intrinsic species traits (e.g. movement distance, home range size) and extrinsic landscape features (e.g. patch distribution, heterogeneity) (Box 1). STEBS can, therefore, support the scaling up of models designed for diverse species to the same scenarios, for instance, to predict population responses for multiple species of functional importance or conservation concern to novel land management interventions or habitat configurations. While our framework currently focuses on multiple response variables from a single model (Fig. 4), future extensions could explicitly incorporate more than one objective function by evaluating multiple metrics across several models simultaneously, thereby identifying multi-objective CETs. This would enable STEBS to capture trade-offs between diverse population and ecosystem-level outputs, further enhancing its relevance for decision support. STEBS as presented here, however, is a theoretical blueprint and future research will need to address several questions to test and refine the framework as an operational and transferrable tool (Box 2).

While STEBS offers a promising pathway to reduce the computational burden of landscape-level simulation, its utility depends on several key assumptions. Most critically, the framework assumes that a CET can be reliably identified, but for highly complex systems or particularly computationally demanding models, the limits of tractability may be exceeded before reaching the spatial extent of emergent system behaviour stabilisation (Fig. 4). In such instances, however, STEBS is no less tractable than brute-force simulation with the additional benefit of indicating whether scaling decisions are ecologically justified. Conversely, there is a possibility of false-positive CET identification – cases where intermediate-scale emergent patterns stabilise although broader landscape patterns have not. False positives could occur when larger-scale processes (e.g. long-distance dispersal, disturbance regimes, habitat connectivity) have been omitted from the IBM, leading to premature convergence. Moreover, different life stages within a species may exhibit different CETs due to contrasting drivers of movement or resource use, while CETs estimated for one landscape or management scenario may not be transferrable to another. These risks highlight that STEBS will not always provide a universal scaling solution and misidentification of CETs could result in misleading extrapolations. However, the process of identifying the CET (Fig. 3) offers a valuable opportunity to evaluate how the IBM structure (e.g. process implementation, representation of environmental scenarios) influences emergent system dynamics. Systematic sensitivity analyses across these alternatives can reduce reliance on hidden assumptions and help ensure that detected CETs represent real ecological thresholds rather than artefacts of model design (Bocedi et al. 2012; Gegr and Chan 2015).

A meta-model can only reflect relationships between environmental variables and population patterns that emerge from the mechanisms and processes encoded in the original model and so the landscape-level predictions yielded by STEBS will also depend on the IBM structure. The inclusion of key individual-level mechanisms (e.g. physiology, movement behaviour) should ensure flexibility (Evans et al. 2013; Johnston et al. 2019), but if the original model is overfitted to certain patterns or scenarios, the range of possible outcomes will be restricted (Gallagher et al. 2021). Another central challenge is ensuring the representativeness of the landscape modules used to estimate the CET and train the meta-model (Fig. 3). The ability to accommodate spatial heterogeneity by including landscape configurations that drive unique emergent population patterns is a key benefit of the STEBS framework. To support accurate and generalisable landscape-level predictions, the landscape modules must encompass key ecological drivers and spatial heterogeneity, characteristic of the broader landscape. Spatial autocorrelation in environmental variables can influence CET detection and sensitivity testing with varying levels of autocorrelation is strongly recommended. The successful implementation of STEBS will, therefore, depend on thoughtful landscape sampling (e.g. stratified sampling reflecting variance of environmental factors) and careful interpretation of emergent pattern generalisability.

Multi-scale strategies that parallel the STEBS framework are commonly employed in climate modelling. Statistical downscaling, for instance, establishes empirical relationships between large-scale atmospheric predictors and local climate conditions, enabling the translation of coarse-resolution climate model outputs to fine-resolution, location-specific projections (Wilby et al. 2002).

Dynamical downscaling complements this by nesting fine-resolution regional climate models within global climate models to capture local climate features, while retaining global forcing conditions (Giorgi and Mearns 1999). These approaches allow climate modellers to balance computational efficiency and the representation of critical climate processes across multiple spatial and temporal scales. Similarly, hydrological modelling frequently applies parameter regionalisation techniques, transferring model parameters calibrated in well-monitored catchments to comparable physical attributes to enable prediction in data-sparse areas (Parajka et al. 2005). Hydrological models also increasingly adopt surrogate modelling techniques across extensive landscapes (Razavi et al. 2012). As in these disciplines, ecology increasingly requires models that deliver robust predictions to support policy and management decisions under uncertainty and environmental change.

Methodological advances in climate and hydrology offer both inspiration and caution for ecological modelling. Dynamical and statistical downscaling, parameter regionalisation and surrogate modelling techniques enable efficient cross-scale simulation, but also present challenges including scale mismatches, uncertainty propagation and risks of overfitting (Wilby et al. 2002; Parajka et al. 2005). The STEBS framework contributes to addressing these challenges by providing an intermediate modelling step that preserves mechanistic fidelity, while managing computational demands. However, as with other domains, its effective application will depend on rigorous model validation and transparent treatment of uncertainty to avoid distorting ecological predictions. Established frameworks like the ODD protocol (Grimm et al. 2010, 2020) and TRACE (Grimm et al. 2014) help to ensure clarity in describing model structure, assumptions and evaluation and, thus, form a foundation for reproducibility. Pairing these frameworks with practices that directly address validation requirements (i.e. formal sensitivity analysis, uncertainty quantification and cross-scale benchmarking) can provide the transparency and analytical rigour needed for the reliable application of STEBS and similar scaling frameworks.

Box 2. Future research needs and outstanding questions.

Transitioning the STEBS framework from a conceptual to an operational tool demands rigorous empirical testing and iterative refinement using well-validated mechanistic IBMs across diverse systems. Future research should target both model-based experimentation and cross-system application to address the outstanding questions below. Addressing these questions in future research will improve the reproducibility, transferability and practical value of STEBS in ecological modelling.

(1) How transferable is CET across species and landscapes? CET is inherently species- and context-specific, reflecting traits like body size, dispersal ability and behavioural plasticity, alongside landscape features, such as heterogeneity and resource distribution. Comparative studies across taxa and ecosystems are needed to explore how CET varies and whether general rules or trait-based scaling functions can predict CET under different conditions, including seasonal shifts and multi-stressor regimes.

(2) How sensitive are STEBS-based predictions to landscape structure? CET is derived from the principle that landscape configuration, composition and heterogeneity will significantly influence SPP convergence. Systematic exploration of landscape structures, for example, fragmented, patchy or continuous, will help define the robustness and limits of CET-based scaling.

(3) How does IBM organisation influence CET? Mechanistic IBMs vary widely in how they represent processes (e.g. resource competition, energy budgets, dispersal rules). It is essential to understand how model structure, such as the level of individual detail, behavioural algorithms or interaction complexity, affects the shape of emergence-area curves and the resulting CET.

(4) What STEBS extensions are needed for adaptive and decision support workflows? STEBS could be integrated into adaptive management and iterative modelling pipelines by utilising automation tools for CET estimation, dynamic updating as new data become available and interfaces with decision support systems. Balancing the up-front computational investment against downstream flexibility should remain a priority during STEBS development.

Outlook

The STEBS framework provides a practical solution to a longstanding trade-off in ecological modelling by enabling mechanistic simulations to provide predictions at the landscape level. This is achieved by identifying the CET, the smallest spatial extent at which emergent system behaviour stabilises, as the optimal scale for developing meta-models that preserve fine-resolution biological realism, while generating broad-scale predictions. The upfront investment required to estimate CETs is, in theory, offset by the simultaneous optimisation of ecological interpretability, predictive power and tractability compared to alternative scaling approaches. Advancing the conceptual STEBS framework outlined here to a fully operational and transferrable tool will require empirical testing with diverse species, refinement of methods for CET estimation, careful sensitivity analyses to landscape patterns and model structure and incorporating STEBS into adaptive modelling workflows. As ecological models become increasingly central to environmental policy and management, frameworks like STEBS will be vital for ensuring that detailed, mechanistic insights can be applied to large-scale decisions. By supporting computationally efficient and ecologically meaningful predictions, STEBS can become a cornerstone tool for biodiversity conservation, environmental risk assessment and land-use policy design in the face of global change.

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Additional information

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The authors have declared that no competing interests exist.

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Use of AI

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Data availability

All of the data that support the findings of this study are available in the main text.

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