

The Finite Element method to aid modelling of complex ecological systems

Klementyna A. Gawecka* & James M. Bullock

UK Centre for Ecology & Hydrology

* corresponding author (klementyna.gawecka@gmail.com)

Abstract

Predicting how biodiversity responds to environmental change and management interventions remains a major challenge in ecology. Ecological systems are shaped by the interplay of demographic processes, species interactions, dispersal, and spatial heterogeneity across landscapes. Yet, many existing modelling approaches face a trade-off between spatial and ecological complexity, which limits their ability to realistic settings. Reaction-diffusion-advection (RDA) models – a class of partial differential equations (PDEs) – provide a flexible framework for describing community dynamics in continuous space and time. Despite their conceptual appeal, the application of RDAs to realistic ecological systems has been constrained by the computational difficulty of solving coupled nonlinear PDEs on heterogeneous landscapes. Here, we argue that the Finite Element (FE) method provides a practical and scalable solution to this challenge. Widely used in engineering and applied sciences, the FE method enables efficient numerical solutions of spatially explicit PDEs on irregular domains. We outline how combining RDA models with FE methods can expand the predictive capacity of ecological models by allowing realistic representation of landscape structure, dispersal, and species interactions. We also discuss key challenges, including parameterisation, software accessibility, and training, and provide a practical workflow for implementing FE-based ecological models. Broader adoption of FE approaches could substantially strengthen predictive ecology and help bridge the gap between ecological theory and applications.

1 Introduction: predictive bottleneck in ecological modelling

The natural world is facing a convergence of crises with profound consequences for biodiversity, ecosystem services and human well-being. Climate change, habitat loss, invasive species and disease emergence all pose escalating risks (IPBES, 2019, Isbell et al., 2023). Addressing these challenges requires not only understanding ecological processes, but also the ability to predict how biodiversity will respond to management, conservation, and restoration interventions across space and time.

Prediction in ecology remains difficult because ecological systems are inherently complex, both spatially and biologically. Landscapes are heterogeneous mosaics of habitat types, within which communities are shaped by the interplay of demographic processes, interspecific interactions and dispersal. These processes interact across spatial and temporal scales in ways that are difficult to observe empirically and even harder to predict (Mougi and Kondoh, 2016, Twining et al., 2022, Gawecka et al., 2025). Yet, the effectiveness of management, conservation and restoration actions depends on anticipating such complex responses (Bullock et al., 2022, Maes et al., 2024, Montoya et al., 2025). As a result, limited predictive capacity continues to constrain ecological decision-making, often leading to inefficient or even failed interventions (Lubiana Botelho et al., 2025, Zurell et al., 2026, but see Lewis et al., 2023).

A major obstacle to prediction lies in the spatial-ecological complexity trade-off in ecological modelling. Existing approaches typically simplify reality by focusing on certain aspects of complexity. For example, spatially-realistic models often focus on a single species (e.g., Bocedi et al., 2014, Gardner et al., 2024), while community dynamics models frequently ignore spatial processes or landscape structure (e.g., Rohr et al., 2014, Horn et al., 2020). Attempts to combine spatial and biological complexity usually rely on strong simplifying assumptions, such as discretising landscapes into patches or limiting interaction types (Ryser et al., 2021, Gawecka and Bascompte, 2023, Bhandary et al., 2026). Many such models are also computationally intensive or inflexible, restricting their applicability across different organisms, processes, and landscapes. Consequently, ecology effectively lacks predictive models that can simultaneously represent spatial structure, demographic processes, and species interactions while remaining scalable and computationally efficient (Fulton et al., 2019, Zurell et al., 2022, Zurell et al., 2025).

We argue that this limitation is not conceptual but computational: the mathematical frameworks needed to represent complex ecological systems already exist, but efficient numerical methods for solving them in realistic settings have been lacking.

In particular, reaction-diffusion-advection (RDA) formulations provide a natural mathematical backbone for addressing this challenge. RDA models are a class of partial differential equations (PDEs) that couple local population dynamics (*reaction* terms) with movement through space via random and directed processes (*diffusion* and *advection* terms). As such, they are well suited for simulating demographic, interspecific and dispersal processes (DeAngelis and Yurek, 2017). RDA models have a long history in ecology, providing insights into invasion dynamics, pattern formation, and range expansion (Holmes et al., 1994, Okubo and Levin, 2002). However, their application has largely been restricted to analytically tractable cases, simplified landscapes, or small numbers of interacting species (Cantrell and Cosner, 2004, Petrovskii, 2022). Extending RDA models to realistic landscapes and communities has remained computationally challenging, which limits their use for predictive ecology.

Here, we explore how the Finite Element (FE) method can enable more realistic applications of spatial PDEs such as RDA models, and thus facilitate the modelling of complex ecological systems. The FE method is a powerful and mature numerical approach for solving coupled, nonlinear PDEs on complex geometries. While widely used in engineering and applied sciences to simulate fluid flow, heat transfer, and structural mechanics (e.g., Bergheau and Fortunier, 2008, Zienkiewicz et al., 2014a), it has seen limited adoption in ecology. By enabling efficient solutions on heterogeneous landscapes and for interacting species, the FE method makes it possible to move beyond the traditional trade-off between spatial and ecological complexity. We outline how this approach can overcome the predictive bottleneck in ecological modelling and help bridge theory and application across biodiversity management, conservation, and restoration.

2 Reaction-diffusion-advection framework for spatial ecology

RDA models provide a powerful framework for describing population and community dynamics in continuous space and time. Mathematically, they are a class of PDEs. Unlike

spatially implicit approaches (e.g., island biogeography or classical metapopulation models, MacArthur and Wilson, 1967, Levins, 1969), RDA models explicitly represent what occurs at a given location and time. In contrast to patch-based or cellular automata models, they treat space as continuous, allowing realistic representation of environmental variation and avoiding assumptions such as discretised dispersal or simple suitable-unsuitable habitat classification. This makes them particularly well suited for capturing complex landscape geometries (Touboul et al., 2025). Their continuous-time formulation enables the study of transient dynamics and species with overlapping generations, while remaining applicable to organisms with discrete life stages when considered at appropriate temporal scales (Cantrell and Cosner, 2004).

RDA models describe populations in terms of densities rather than tracking individual organisms or simple occupancy states. This density-based formulation avoids the high computational costs of individual-based models, which rapidly become prohibitive as species richness increases (but see Cornell et al., 2019). Although often formulated deterministically, RDA models can incorporate stochasticity in dispersal or demography (Méndez et al., 2014, Erban and Chapman, 2019). Crucially, they allow explicit inclusion of different forms of species interactions (Holmes et al., 1994), an aspect that is frequently neglected in other spatially explicit modelling approaches (Bocedi et al., 2014, Gardner et al., 2024).

In two-dimensional space, the general form for species i can be written as:

$$\frac{\partial N_i(x, y, t)}{\partial t} = f_i(\mathbf{N}) + D_i \left(\frac{\partial^2 N_i}{\partial x^2} + \frac{\partial^2 N_i}{\partial y^2} \right) + \left(v_{i,x} \frac{\partial N_i}{\partial x} + v_{i,y} \frac{\partial N_i}{\partial y} \right) \quad \text{Eq. 1}$$

Here, N_i denotes the density of species i at spatial coordinates (x, y) and time t . The reaction term $f_i(\mathbf{N})$ captures local population dynamics and may depend on the densities of other species represented by the vector \mathbf{N} . The diffusion term represents Brownian random motion, with D_i as the diffusion coefficient. The advection term describes directed movement, with velocity components $v_{i,x}$ and $v_{i,y}$ in x and y directions, respectively.

Importantly, the exact form of each term is context-dependent, making the RDA framework highly flexible. The reaction term may range from simple density regulation (e.g., logistic growth) to complex interaction networks involving competition, predation, parasitism, or mutualism (e.g., Lotka-Volterra systems). Diffusion terms can be parameterised using empirically informed dispersal kernels. Advection can capture directed movement driven by

landscape features, wind or water currents, or external stimuli. Moreover, parameters can vary across space and time, allowing explicit representation of spatial heterogeneity and environmental change.

RDA models have a long history in theoretical ecology, where they have been used to study dispersal-mediated coexistence, ecological invasions, pattern formation, wavefront propagation, and critical thresholds in habitat size and connectivity (e.g., Holmes et al., 1994, Fagan et al., 1999, Okubo and Levin, 2002, Prima et al., 2018). However, most applications have relied on homogeneous or discretised habitats, simplified species interactions, or idealised dispersal kernels (Cantrell and Cosner, 2004, Petrovskii, 2022). These assumptions have enabled analytical tractability and fundamental insights, but they have limited the applicability of RDA models to real-world ecological systems.

Importantly, these limitations are not inherent to the RDA framework itself. By design, RDA models can accommodate complex spatial structure and multispecies interactions. What has constrained their broader use in predictive ecology is the computational difficulty of solving coupled, nonlinear PDEs in realistic settings. This gap motivates the need for numerical approaches capable of utilising the full potential of the RDA framework.

3 The finite element method as numerical solution to RDA problems

To realise the potential of RDA models, numerical methods capable of handling nonlinear dynamics on complex landscapes are required. The FE method meets this need by enabling efficient solutions of coupled PDEs on irregular domains (Johnson, 2009), making it well suited for realistic ecological applications.

The FE method discretises space into a mesh of small, simple elements (triangles or quadrilaterals), over which the solution is approximated using basis functions. Rather than solving the PDEs directly, the equations are reformulated in a weak (integral) form, yielding a system of algebraic equations that can be solved numerically across the entire domain. This formulation naturally accommodates nonlinear dynamics, spatially varying parameters, and complex geometries.

The FE method is widely used across engineering and applied sciences, including fluid dynamics, heat transfer, and structural mechanics (e.g., Potts and Zdravković, 1999, Bergheau

and Fortunier, 2008, Zienkiewicz et al., 2014a, Zienkiewicz et al., 2014b). Within biology, FE approaches have been applied extensively in biomechanics (e.g., stress and strain analysis in bones; Rayfield, 2007, Cox et al., 2011, Curtis et al., 2019) and developmental biology, where reaction-diffusion systems represent morphogenesis and tissue growth (e.g., Brodland, 1994, Murea and Hentschel, 2007, Laussu et al., 2025).

In ecology, the FE method has been used more sparingly, but existing studies demonstrate its use for modelling spatial population dynamics, dispersal, and genetic spread in heterogeneous environments (e.g., Richter, 2008, Wyse et al., 2018, Ward et al., 2023, and examples in Box 2). The limited adoption of FE in ecology likely reflects historical rather than conceptual constraints: early spatial RDA models focused on idealised domains where analytical solutions sufficed, FE solvers were once computationally expensive, and access to flexible FE software has been limited, with little exchange between engineering and ecological modelling communities.

Although the RDA-FE framework offers flexibility for modelling spatial ecological systems, it is not universally appropriate. Some ecological problems are better addressed using alternative modelling approaches depending on the processes of interest, or spatial and temporal scales considered. Situations where RDA and FE methods may not be the most suitable choice are summarised in Box 1.

From an ecological perspective, implementing an FE-based RDA model involves a three-step workflow (Figure 1). (1) *Inputs*: four key components are required: (a) spatial data describing landscape structure, typically as vector polygons representing habitat types; (b) species-specific demographic, dispersal, and interaction parameters, potentially varying by habitat; (c) initial conditions specifying species distributions and densities; and (d) simulation settings, including boundary conditions, temporal resolution, and simulation duration. (2) *Analysis*: generating a finite element mesh and solving the RDA equations over the landscape (see Box 3). (3) *Outputs*: spatio-temporal predictions of species densities, which can be visualised as maps, trajectories, or derived summary metrics relevant to ecological questions.

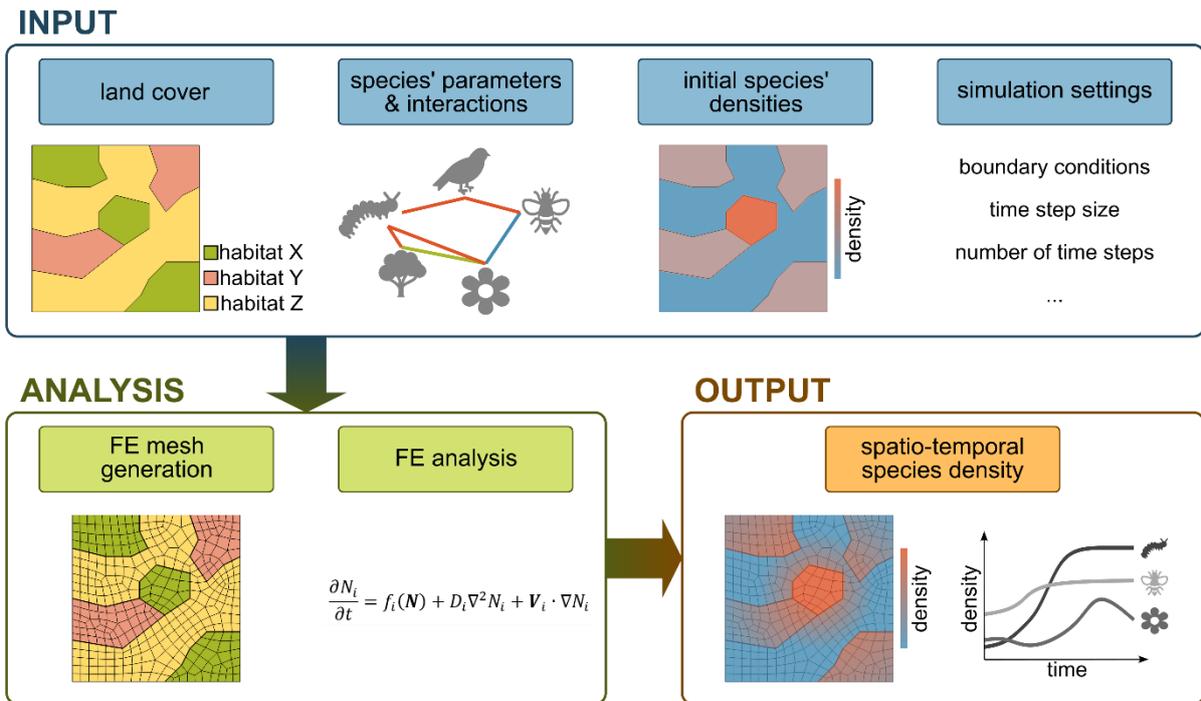


Figure 1 Generic FE modelling workflow for spatial ecological problems. Typical inputs include land cover data, species-specific and habitat-specific parameters and interactions, initial species distributions, and simulation settings. The landscape is discretised into small finite elements to approximate RDA dynamics across the landscape. Outputs are spatio-temporal predictions of species density, visualised as maps and summary plots.

Figure 2 illustrates a simple FE simulation of single-species reaction-diffusion dynamics on a hypothetical landscape with three habitat types (Figure 2A). Local population dynamics follow logistic growth ($f(N) = rN(1 - N/K)$), with four scenarios differing in how species parameters vary among habitats. In case 1, growth rate (r), carrying capacity (K), and diffusion coefficient (D) are identical across habitats. In cases 2-4, r , K , and D vary among habitats, respectively. The resulting dynamics (Figure 2B-C) demonstrate how spatial heterogeneity in demographic and dispersal parameters can strongly influence population patterns. These simple examples highlight the flexibility of the FE approach in incorporating habitat-specific variation, complementing previous applications in ecology (see Box 2), and provide an intuitive demonstration of how spatial complexity can be modelled.

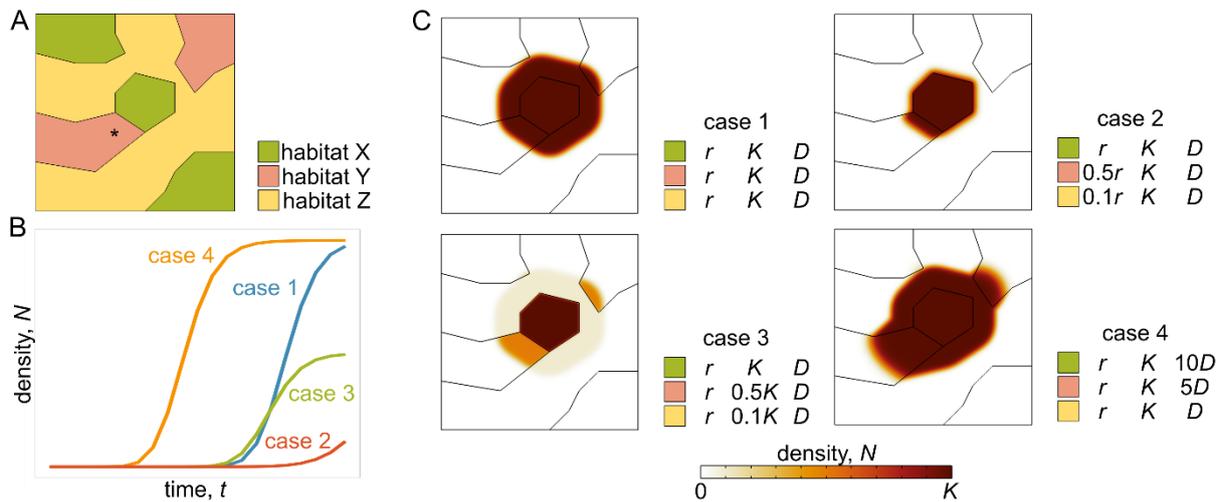


Figure 2 Results of four FE simulations predicting the spatio-temporal density of a species with various parameter combinations of a logistic growth equation: case 1 – the species has the same growth rate (r) carrying capacity (K) and diffusion coefficient (D) in all habitats; case 2 – r varies between habitats; case 3 – K varies between habitats; case 4 – D varies between habitats. (A) Landscape with three habitat types. (B) Change in species density with time at location marked * in (A). (C) Spatial species density at the end of simulation. At the start of the simulation, the species is present at low densities only in the central habitat X polygon.

Box 1 When RDA models and FE method are not appropriate

RDA models and the FE method are not universally applicable to all ecological questions and should be used where their assumptions are appropriate. RDA models are best suited to systems in which population densities can be treated as continuous variables and movement can be approximated at aggregate scales. Systems dominated by strong demographic stochasticity, discrete behavioural decisions, or individual-level interactions are often better addressed using individual-based or agent-based approaches. Likewise, populations with strongly seasonal dynamics may be more naturally modelled using integrodifference equations (Cantrell and Cosner, 2004, Lutscher, 2019).

FE methods are also unnecessary when spatial geometry is simple or homogeneous. For example, when habitats can be represented as discrete patches and the surrounding matrix plays a negligible role, patch-based metapopulation models or coupled map lattices may be more appropriate. Similarly, when population dynamics are simple and analytically tractable, low-dimensional numerical models may suffice.

Rather than replacing existing approaches, FE-based RDA modelling should therefore be viewed as a complementary tool, particularly well-suited to systems where spatial heterogeneity and multispecies interactions jointly shape ecological dynamics.

4 Ecological applications of the FE method

The ability to model ecological systems that are both spatially and biologically complex opens new opportunities for fundamental and applied ecology, helping to bridge the gap between ecological theory and real-world decision-making (Cadotte et al., 2017). By enabling continuous-space, multispecies simulations in realistic landscapes, FE method makes it possible to address questions that could not be answered with other modelling approaches.

From a fundamental perspective, FE-based RDA models allow investigation of, for example, (a) how landscape structure shapes community assembly, persistence, and collapse, (b) how dispersal interacts with local species interactions to determine biodiversity outcomes, or (c) how spatial, demographic and interspecific processes give rise to spatial patterns, coexistence mechanisms, or eco-evolutionary feedbacks. These questions have been difficult to explore jointly at realistic scales.

At the same time, the FE method provides a framework for addressing a range of applied ecological questions that depend on spatial context and species interactions. Examples of ecological applications that can benefit from this approach are summarised in Box 2. These include land-use change such as habitat loss and restoration, species range shifts under climate change, biological invasions, and the emergence and spread of pests or diseases. In these settings, FE models allow mechanistic exploration of alternative scenarios.

Beyond academia, FE-based ecological models have the potential to function as decision-support tools for nature management, conservation and restoration, analogous to the role of numerical models in engineering design. By enabling scenario testing, sensitivity analyses, and spatially explicit predictions, such tools could support evidence-based ecological planning.

Box 2 Ecological applications enabled by the FE method

Across these applications, the FE method enables investigations of how landscape structure, species movement, demography, and interactions jointly determine ecological outcomes.

Land-use and habitat change

FE models can simulate temporal changes in habitat quality and configuration, predicting species collapse or recovery under degradation or restoration scenarios.

Examples: Grech et al. (2016) predicted seagrass recovery potential on the Great Barrier Reef by simulating hydrodynamics and propagule dispersal.

Climate-driven range shifts

FE method enables coupling of changing habitat suitability, climate-dependent demography, and species movement across realistic landscapes.

Examples: Richter et al. (2012) simulated warming-induced shifts in distributions of species with temperature-dependent growth rates; MacDonald et al. (2025) developed a model where habitats move under climate change.

Biological invasions

By coupling spatial and interspecific dynamics, FE models allow prediction of invasion speed and impact on the ecological community.

Examples: Pepper et al. (2019) simulated invasive species spread across a heterogeneous landscape in the Basque Country, Spain.

Disease emergence and spread

Coupling host or vector movement with species demography and interactions enables realistic disease spread modelling.

Examples: Keller et al. (2013) modelled rabies spread in raccoons in New York state, USA; Richter et al. (2022) simulated mosquito-borne disease spread in human populations in rural and urban landscapes in Vietnam.

Agriculture and pest management

FE models can integrate species interactions, dispersal, genetics, and management interventions.

Examples: Richter and Seppelt (2004) and Richter (2008) explored pest control and the spread of pesticide-resistant weeds in agricultural landscapes.

Beyond these applied examples, FE method has also been used to explore theoretical questions such as spatial pattern formation and multispecies coexistence (e.g., Upadhyay et al., 2016, Cangiani et al., 2018).

5 Challenges and next steps for FE ecological modelling

Here, we outline challenges associated with applying the FE method to ecological modelling and discuss ways of addressing them.

5.1 Computational cost

FE-based solutions to coupled RDA problems can be computationally demanding, particularly for multispecies simulations on fine meshes or large spatial extents. However, this challenge is increasingly tractable, especially with high-performance computing infrastructure becoming widely accessible.

Substantial gains can be achieved through efficient implementation, including the use of compiled, high-performance languages (e.g., C++), parallel domain decomposition, and adaptive mesh refinement that concentrates computational effort where it is most needed (Gilbert et al., 2017). The computational burden associated with large ensembles of simulations, for example in sensitivity analysis or uncertainty quantification, can be further reduced using surrogate models based on machine learning. These models approximate high-fidelity simulations at a fraction of the computational cost (Sánchez Fernández et al., 2025, Sheil et al., 2026, Yang et al., 2026). In practice, combining FE analysis with structured experimental design can further limit computational demands by focusing simulations on ecologically informative regions of parameter space.

5.2 Parameterisation

As systems of coupled nonlinear equations, RDA models can be sensitive to parameter values (see Figure 2 for an example). Yet, predictive modelling requires realistic, species-specific parameterisation. This is an especially challenging task in multispecies systems and heterogeneous landscapes, and a major bottleneck for spatially explicit ecological models.

Despite this challenge, substantial empirical information on dispersal, demography, and species interactions already exists across the literature and multiple databases. This creates an opportunity to integrate and harmonise these data into a coherent parameter resource for RDA models. First, information from existing databases (e.g., Stevens et al., 2010, Salguero-Gómez et al., 2015, 2016, Bullock et al., 2017, Uiterwaal et al., 2022, Fandos et al., 2023) can be

consolidated and standardised. Second, parameter estimates can be extracted from published empirical studies identified through systematic literature searches. Where sufficient data exist, parameters can be estimated using statistical frameworks that explicitly incorporate uncertainty (e.g., Bayesian approaches), providing distributions suitable for sensitivity and uncertainty analyses, which the FE method makes tractable.

Where empirical data remain sparse, three complementary strategies can be employed: (1) targeted expert elicitation to obtain informed parameter estimates (Gardner et al., 2024), (2) trait-based approaches that allow parameters to be partially pooled across related species or functional groups (Aslan et al., 2019, Chalmandrier et al., 2021), and (3) the generation of virtual species by statistically reconstructing multidimensional trait space and the covariation among traits from incomplete datasets, allowing plausible parameter combinations to be simulated (Santini et al., 2016).

5.3 Validation

Validation is essential for establishing the credibility of spatially explicit RDA models and for determining when they can be used for prediction rather than exploration. Validation is particularly challenging in complex ecological systems, where dynamics unfold over large spatial and temporal scales and controlled replication is often impossible (Synes et al., 2016). However, these challenges are not unique to RDA models and can be addressed using complementary validation strategies.

First, existing laboratory, mesocosm, and field experiments provide valuable benchmarks for model testing, particularly where landscape structure, dispersal, or community dynamics have been explicitly manipulated (e.g., Saade et al., 2022, Rayfield et al., 2023). Second, experimental design can be guided by modelling needs, ensuring that future experiments generate data suitable for model parametrisation and validation, rather than solely for hypothesis testing (Railsback et al., 2025). Third, validation need not rely exclusively on exact quantitative agreement. Pattern-oriented and qualitative validation can provide robust evidence that key mechanisms are captured correctly (Grimm et al., 2005). Such pattern-based validation is especially relevant for scenario analysis and decision support, where the goal is to compare alternative futures rather than to predict precise outcomes.

5.4 Software access and training

Despite their potential, FE methods remain largely inaccessible to ecologists due to a mismatch between existing software design and ecological modelling needs, combined with limited training opportunities.

Most existing FE software has been developed for engineering and applied science applications and is not tailored to ecological problems. Commercial software such as COMSOL Multiphysics, as well as open-source tools such as FEniCS (Logg et al., 2012) and MoFEM (Kaczmarczyk et al., 2020), provide powerful and general computing platforms for solving PDEs using the FE method. However, their engineering-focused design requires substantial expertise in numerical methods and scientific computing, creating a barrier for many ecologists. As a result, the primary limitation is not the utility of these tools, but their accessibility. Although robust FE infrastructure already exists, the gap between numerical capability and practical usability for ecological applications has limited broader adoption in spatial ecological modelling.

Beyond software, FE analysis requires specialised training and experience to be applied correctly and interpreted responsibly. Wider uptake will therefore depend not only on improved tools, but also on training, documentation, and collaboration between ecologists, numerical modellers, and engineers. Developing open-source FE software with user-friendly interfaces, ecological defaults, and workflows aligned with common ecological questions would represent a critical step toward mainstream adoption.

For readers interested in implementing FE-based ecological models, we outline a simplified workflow highlighting the key steps involved in developing and analysing such models (Box 3).

Box 3 A practical workflow for implementing the FE method into ecological modelling.

1. Define the ecological model

Formulate the ecological processes of interest (e.g., population growth, species interactions, dispersal) as PDEs such as RDA equations.

2. Parameterise model equations

Estimate model parameters (e.g., growth rates, interspecific interactions, dispersal rates) using empirical data, trait databases, literature synthesis or expert knowledge. Parameters may be species-specific and can vary across habitat types.

3. Specify the spatial domain

Define the landscape geometry representing the ecological system of interest. Spatial domains can be constructed from GIS data, for example using vector polygons representing habitat types or barriers.

4. Discretise the spatial domain into a FE mesh

Divide the spatial domain into small elements (triangles or quadrilaterals). Many FE software can generate meshes automatically. Mesh resolution should be sufficiently fine to capture important spatial features, such as habitat boundaries or regions where steep gradients in population density are expected.

5. Define boundary conditions and simulation settings

Boundary conditions specify how the system behaves at the edges of the spatial domain. Common conditions for ecological RDA models include Dirichlet (fixed population density values) and Neumann boundaries (fixed flux across the boundary, often representing no dispersal across impermeable boundaries). Simulation settings such as time step size, solver choice and simulation duration must also be specified.

6. Solve the PDE system numerically

Use FE software (e.g., FEniCS, COMSOL) to solve the coupled PDE system through time and space.

7. Analyse model outputs

Evaluate model predictions, compare outputs with empirical observations, explore parameter sensitivity and uncertainty, and simulate alternative management scenarios.

6 Conclusion: toward wider adoption of FE modelling in ecology

The increasing availability of ecological data, computational resources and open numerical libraries create a timely opportunity to rethink how spatial and ecological complexity are represented in predictive models. The RDA framework provides a natural mathematical language for describing ecological processes in space and time, but their broader use has historically been constrained by computational and practical barriers.

The FE method offers a pathway to overcome these limitations by enabling efficient numerical solutions of spatial PDEs such as RDA models on heterogeneous landscapes. Realising this potential will require coordinated progress on several fronts: the development of accessible

ecological modelling software, the consolidation of species-specific model parameters, and stronger collaboration between ecologists and numerical modellers.

By lowering the barriers between ecological theory and advanced numerical methods, FE approaches could open a new generation of spatially explicit models capable of representing ecological complexity while remaining computationally tractable. Such models have the potential to strengthen predictive ecology and support more effective management, conservation and restoration strategies in an increasingly dynamic world.

Acknowledgements

We thank David M. G. Taborda for discussions.

Funding

This work was supported by the Marie Skłodowska-Curie Actions Postdoctoral Fellowship (grant EP/Z000831/1) to KAG and Natural Environment Research Council (NERC) consortium award 'Restoring Resilient Ecosystems' (grant NE/V006525/1) to JMB.

References

- Aslan, C., Beckman, N. G., Rogers, H. S., Bronstein, J., Zurell, D., Hartig, F., Shea, K., Pejchar, L., Neubert, M., Poulsen, J., Hillerislambers, J., Miriti, M., Loiselle, B., Effiom, E., Zambrano, J., Schupp, G., Pufal, G., Johnson, J., Bullock, J. M., Brodie, J., Bruna, E., Cantrell, R. S., Decker, R., Fricke, E., Gurski, K., Hastings, A., Kogan, O., Razafindratsima, O., Sandor, M., Schreiber, S., Snell, R., Strickland, C. & Zhou, Y. 2019. Employing plant functional groups to advance seed dispersal ecology and conservation. *AoB PLANTS*, 11(2), 1-14.
- Bergheau, J.-M. & Fortunier, R. 2008. *Finite element simulation of heat transfer*, Hoboken, USA, Wiley.
- Bhandary, S., Gawecka, K. A., Pedraza, F. & Bascompte, J. 2026. Landscape configuration and community structure jointly determine the persistence of mutualists under habitat loss. *Proceedings of the Royal Society B: Biological Sciences*.
- Bocedi, G., Palmer, S. C. F., Pe'er, G., Heikkinen, R. K., Matsinos, Y. G., Watts, K. & Travis, J. M. J. 2014. Rangesifter: A platform for modelling spatial eco-evolutionary dynamics and species' responses to environmental changes. *Methods in Ecology and Evolution*, 5(4), 388-396.
- Brodland, G. W. 1994. Finite element methods for developmental biology. *International Review of Cytology*, 150(1994), 95-118.
- Bullock, J. M., Fuentes-Montemayor, E., McCarthy, B., Park, K., Hails, R. S., Woodcock, B. A., Watts, K., Corstanje, R. & Harris, J. 2022. Future restoration should enhance ecological complexity and emergent properties at multiple scales. *Ecography*, 2022(4), 1-11.

- Bullock, J. M., Mallada González, L., Tamme, R., Götzenberger, L., White, S. M., Pärtel, M. & Hooftman, D. A. P. 2017. A synthesis of empirical plant dispersal kernels. *Journal of Ecology*, 105(1), 6-19.
- Cadotte, M. W., Barlow, J., Nuñez, M. A., Pettorelli, N. & Stephens, P. A. 2017. Solving environmental problems in the anthropocene: The need to bring novel theoretical advances into the applied ecology fold. *Journal of Applied Ecology*, 54(1), 1-6.
- Cangiani, A., Georgoulis, E. H., Morozov, A. Y. & Sutton, O. J. 2018. Revealing new dynamical patterns in a reaction–diffusion model with cyclic competition via a novel computational framework. *Proceedings of the Royal Society A: Mathematical, Physical and Engineering Sciences*, 474(2213), 20170608.
- Cantrell, R. S. & Cosner, C. 2004. *Spatial ecology via reaction-diffusion equations*, Chichester, UK, Wiley.
- Chalmandrier, L., Hartig, F., Laughlin, D. C., Lischke, H., Pichler, M., Stouffer, D. B. & Pellissier, L. 2021. Linking functional traits and demography to model species-rich communities. *Nature Communications*, 12(1), 1-9.
- Cornell, S. J., Suprunenko, Y. F., Finkelshtein, D., Somervuo, P. & Ovaskainen, O. 2019. A unified framework for analysis of individual-based models in ecology and beyond. *Nature Communications*, 10(1), 1-14.
- Cox, P. G., Fagan, M. J., Rayfield, E. J. & Jeffery, N. 2011. Finite element modelling of squirrel, guinea pig and rat skulls: Using geometric morphometrics to assess sensitivity. *Journal of Anatomy*, 219(6), 696-709.
- Curtis, A. A., Arbour, J. H. & Santana, S. E. 2019. Mind the gap: Natural cleft palates reduce biting performance in bats. *Journal of Experimental Biology*, 223(2), jeb196535.
- DeAngelis, D. L. & Yurek, S. 2017. Spatially explicit modeling in ecology: A review. *Ecosystems*, 20(2), 284-300.
- Erban, R. & Chapman, S. J. 2019. *Stochastic modelling of reaction–diffusion processes*, Cambridge, UK, Cambridge University Press.
- Fagan, W. F., Cantrell, R. S. & Cosner, C. 1999. How habitat edges change species interactions. *The American Naturalist*, 153(2), 165-182.
- Fandos, G., Talluto, M., Fiedler, W., Robinson, R. A., Thorup, K. & Zurell, D. 2023. Standardised empirical dispersal kernels emphasise the pervasiveness of long-distance dispersal in european birds. *Journal of Animal Ecology*, 92(1), 158-170.
- Fulton, E. A., Blanchard, J. L., Melbourne-Thomas, J., Plagányi, É. E. & Tulloch, V. J. D. 2019. Where the ecological gaps remain, a modelers' perspective. *Frontiers in Ecology and Evolution*, 7(424), 1-22.
- Gardner, E., Robinson, R. A., Julian, A., Boughey, K., Langham, S., Tse-Leon, J., Petrovskii, S., Baker, D. J., Bellamy, C., Buxton, A., Franks, S., Monk, C., Morris, N., Park, K. J., Petrovan, S., Pitt, K., Taylor, R., Turner, R. K., Allain, S. J. R., Bradley, V., Broughton, R. K., Cartwright, M., Clarke, K., Cranfield, J., Fuentes-Montemayor, E., Gandola, R., Gent, T., Hinsley, S. A., Madsen, T., Reading, C., Redhead, J. W., Reveley, S., Wilkinson, J., Williams, C., Woodward, I., Baker, J., Briggs, P., Dyason, S., Langton, S., Mawby, A., Pywell, R. F. & Bullock, J. M. 2024. A family of process-based models to simulate landscape use by multiple taxa. *Landscape Ecology*, 39(5), 1-26.
- Gawecka, K. A., Barbour, M. A., Bullock, J. M. & Bascompte, J. 2025. The roles of space and food-web complexity in mediating ecological recovery. *Ecology Letters*, 28(11), e70254.
- Gawecka, K. A. & Bascompte, J. 2023. Habitat restoration and the recovery of metacommunities. *Journal of Applied Ecology*, 60(8), 1622-1636.
- Gilbert, M. A., White, S. M., Bullock, J. M. & Gaffney, E. A. 2017. Speeding up the simulation of population spread models. *Methods in Ecology and Evolution*, 8(4), 501-510.

- Grech, A., Wolter, J., Coles, R., McKenzie, L., Rasheed, M., Thomas, C., Waycott, M. & Hanert, E. 2016. Spatial patterns of seagrass dispersal and settlement. *Diversity and Distributions*, 22(11), 1150-1162.
- Grimm, V., Revilla, E., Berger, U., Jeltsch, F., Mooij, W. M., Railsback, S. F., Thulke, H.-H., Weiner, J., Wiegand, T. & Deangelis, D. L. 2005. Pattern-oriented modeling of agent-based complex systems: Lessons from ecology. *Science*, 310(5750), 987-991.
- Holmes, E. E., Lewis, M. A., Banks, J. E. & Veit, R. R. 1994. Partial differential equations in ecology: Spatial interactions and population dynamics. *Ecology*, 75(1), 17-29.
- Horn, S., Coll, M., Asmus, H. & Dolch, T. 2020. Food web models reveal potential ecosystem effects of seagrass recovery in the northern wadden sea. *Restoration Ecology*, 29(S2), e13328.
- IPBES 2019. *Global assessment report on biodiversity and ecosystem services of the intergovernmental science-policy platform on biodiversity and ecosystem services*, Bonn, Germany, Zenodo.
- Isbell, F., Balvanera, P., Mori, A. S., He, J. S., Bullock, J. M., Regmi, G. R., Seabloom, E. W., Ferrier, S., Sala, O. E., Guerrero-Ramírez, N. R., Tavella, J., Larkin, D. J., Schmid, B., Outhwaite, C. L., Pramual, P., Borer, E. T., Loreau, M., Omotoriogun, T. C., Obura, D. O., Anderson, M., Portales-Reyes, C., Kirkman, K., Vergara, P. M., Clark, A. T., Komatsu, K. J., Petchey, O. L., Weiskopf, S. R., Williams, L. J., Collins, S. L., Eisenhauer, N., Trisos, C. H., Renard, D., Wright, A. J., Tripathi, P., Cowles, J., Byrnes, J. E. K., Reich, P. B., Purvis, A., Sharip, Z., O'Connor, M. I., Kazanski, C. E., Haddad, N. M., Soto, E. H., Dee, L. E., Díaz, S., Zirbel, C. R., Avolio, M. L., Wang, S., Ma, Z., Liang, J., Farah, H. C., Johnson, J. A., Miller, B. W., Hautier, Y., Smith, M. D., Knops, J. M. H., Myers, B. J. E., Harmáčková, Z. V., Cortés, J., Harfoot, M. B. J., Gonzalez, A., Newbold, T., Oehri, J., Mazón, M., Dobbs, C. & Palmer, M. S. 2023. Expert perspectives on global biodiversity loss and its drivers and impacts on people. *Frontiers in Ecology and the Environment*, 21(2), 94-103.
- Johnson, C. 2009. *Numerical solution of partial differential equations by the finite element method*, Cambridge, UK, Cambridge University Press.
- Kaczmarczyk, Ł., Ullah, Z., Lewandowski, K., Meng, X., Zhou, X.-Y., Athanasiadis, I., Nguyen, H., Chalons-Mouriesse, C.-A., Richardson, E., Miur, E., Shvarts, A., Wakeni, M. & Pearce, C. 2020. Mofem: An open source, parallel finite element library. *Journal of Open Source Software*, 5(45), 1441.
- Keller, J. P., Gerardo-Giorda, L. & Veneziani, A. 2013. Numerical simulation of a susceptible-exposed-infectious space-continuous model for the spread of rabies in raccoons across a realistic landscape. *Journal of Biological Dynamics*, 7(sup1), 31-46.
- Laussu, J., Michel, D., Magne, L., Segonds, S., Marguet, S., Hamel, D., Quaranta-Nicaise, M., Barreau, F., Mas, E., Velay, V., Bugarin, F. & Ferrand, A. 2025. Deciphering the interplay between biology and physics with a finite element method-implemented vertex organoid model: A tool for the mechanical analysis of cell behavior on a spherical organoid shell. *PLOS Computational Biology*, 21(1), e1012681.
- Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America*, 15(3), 237-240.
- Lewis, A. S. L., Rollinson, C. R., Allyn, A. J., Ashander, J., Brodie, S., Brookson, C. B., Collins, E., Dietze, M. C., Gallinat, A. S., Juvigny-Khenafou, N., Koren, G., McGlenn, D. J., Moustahfid, H., Peters, J. A., Record, N. R., Robbins, C. J., Tonkin, J. & Wardle, G. M. 2023. The power of forecasts to advance ecological theory. *Methods in Ecology and Evolution*, 14(3), 746-756.
- Logg, A., Mardal, K.-A. & Wells, G. (eds.) 2012. *Automated solution of differential equations by the finite element method*, Heidelberg, Germany: Springer.

- Lubiana Botelho, L., Jeynes-Smith, C., Vollert, S. A. & Bode, M. 2025. Calibrated ecosystem models cannot predict the consequences of conservation management decisions. *Ecology Letters*, 28(1), e70034.
- Lutscher, F. 2019. *Integrodifference equations in spatial ecology*, Cham, Switzerland, Springer International Publishing.
- MacArthur, R. H. & Wilson, E. O. 1967. *The theory of island biogeography*, Princeton, USA, Princeton University Press.
- MacDonald, J. S., Bourgault, Y. & Lutscher, F. 2025. A hybrid finite element method for moving-habitat models in two spatial dimensions. *ESAIM: Mathematical Modelling and Numerical Analysis*, 59(1), 331-362.
- Maes, S. L., Perring, M. P., Cohen, R., Akinnifesi, F. K., Bargués-Tobella, A., Bastin, J. F., Bauters, M., Bernardino, P. N., Brancalion, P. H. S., Bullock, J. M., Ellison, D., Fayolle, A., Fremout, T., Gann, G. D., Hishe, H., Holmgren, M., Ilstedt, U., Mahy, G., Messier, C., Parr, C. L., Ryan, C. M., Sacande, M., Sankaran, M., Scheffer, M. S., Suding, K. N., Van Meerbeek, K., Verbeeck, H., Verbist, B. J. P., Verheyen, K., Winowiecki, L. A. & Muys, B. 2024. Explore before you restore: Incorporating complex systems thinking in ecosystem restoration. *Journal of Applied Ecology*, 61(5), 922-939.
- Méndez, V., Campos, D. & Bartumeus, F. 2014. *Stochastic foundations in movement ecology*, Heidelberg, Germany, Springer.
- Montoya, D., Burón-Ugarte, A., Chrétien, L. T. S., Christensen García, C., Granjel, R. R., Holmes, M., Huang, M., Iglesias-Anciones, L., Larretxi-Gallastegi, I. & Porrás-Gómez, J. 2025. Complexity and interpretability in global change ecology. *PLOS Climate*, 4(3), e0000587.
- Mougi, A. & Kondoh, M. 2016. Food-web complexity, meta-community complexity and community stability. *Scientific Reports*, 6(1), 24478.
- Murea, C. M. & Hentschel, H. G. E. 2007. A finite element method for growth in biological development. *Mathematical Biosciences and Engineering*, 4(2), 339-353.
- Okubo, A. & Levin, S. A. 2002. *Diffusion and ecological problems: Modern perspectives*, New York, USA, Springer.
- Pepper, N., Gerardo-Giorda, L. & Montomoli, F. 2019. Meta-modeling on detailed geography for accurate prediction of invasive alien species dispersal. *Scientific Reports*, 9(1), 1-10.
- Petrovskii, S. (ed.) 2022. *Partial differential equations in ecology: 80 years and counting*, Basel, Switzerland: MDPI.
- Potts, D. M. & Zdravković, L. 1999. *Finite element analysis in geotechnical engineering: Theory*, London, UK, Thomas Telford.
- Prima, M. C., Duchesne, T., Fortin, A., Rivest, L. P. & Fortin, D. 2018. Combining network theory and reaction–advection–diffusion modelling for predicting animal distribution in dynamic environments. *Methods in Ecology and Evolution*, 9(5), 1221-1231.
- Railsback, S. F., Gallagher, C. A., Grimm, V., McCary, M. A. & Harvey, B. C. 2025. Empirical ecology to support mechanistic modelling: Different objectives, better approaches and unique benefits. *Methods in Ecology and Evolution*, 16(8), 1564-1573.
- Rayfield, B., Baines, C. B., Gilarranz, L. J. & Gonzalez, A. 2023. Spread of networked populations is determined by the interplay between dispersal behavior and habitat configuration. *Proceedings of the National Academy of Sciences*, 120(11), e2201553120.
- Rayfield, E. J. 2007. Finite element analysis and understanding the biomechanics and evolution of living and fossil organisms. *Annual Review of Earth and Planetary Sciences*, 35(1), 541-576.
- Richter, O. 2008. Modelling dispersal of populations and genetic information by finite element methods. *Environmental Modelling & Software*, 23(2), 206-214.

- Richter, O., Moenickes, S. & Suhling, F. 2012. Modelling the effect of temperature on the range expansion of species by reaction–diffusion equations. *Mathematical Biosciences*, 235(2), 171-181.
- Richter, O., Nguyen, A. & Nguyen, T. 2022. Application of reaction-diffusion equations for modeling human and breeding site attraction movement behavior of aedes aegypti mosquito. *Mathematical Biosciences and Engineering*, 19(12), 12915-12935.
- Richter, O. & Seppelt, R. 2004. Flow of genetic information through agricultural ecosystems: A generic modelling framework with application to pesticide-resistance weeds and genetically modified crops. *Ecological Modelling*, 174(1-2), 55-66.
- Rohr, R. P., Saavedra, S. & Bascompte, J. 2014. On the structural stability of mutualistic systems. *Science*, 345(6195), 416.
- Ryser, R., Hirt, M. R., Häussler, J., Gravel, D. & Brose, U. 2021. Landscape heterogeneity buffers biodiversity of simulated meta-food-webs under global change through rescue and drainage effects. *Nature Communications*, 12(1), 4716.
- Saade, C., Kefi, S., Gougat-Barbera, C., Rosenbaum, B. & Fronhofer, E. A. 2022. Spatial autocorrelation of local patch extinctions drives recovery dynamics in metacommunities. *Proceedings of the Royal Society B: Biological Sciences*, 289(1972), 1-10.
- Salguero-Gómez, R., Jones, O. R., Archer, C. R., Bein, C., De Buhr, H., Farack, C., Gottschalk, F., Hartmann, A., Henning, A., Hoppe, G., Römer, G., Ruoff, T., Sommer, V., Wille, J., Voigt, J., Zeh, S., Vieregg, D., Buckley, Y. M., Che-Castaldo, J., Hodgson, D., Scheuerlein, A., Caswell, H. & Vaupel, J. W. 2016. Comadre: A global data base of animal demography. *Journal of Animal Ecology*, 85(2), 371-384.
- Salguero-Gómez, R., Jones, O. R., Archer, C. R., Buckley, Y. M., Che-Castaldo, J., Caswell, H., Hodgson, D., Scheuerlein, A., Conde, D. A., Brinks, E., De Buhr, H., Farack, C., Gottschalk, F., Hartmann, A., Henning, A., Hoppe, G., Römer, G., Runge, J., Ruoff, T., Wille, J., Zeh, S., Davison, R., Vieregg, D., Baudisch, A., Altwegg, R., Colchero, F., Dong, M., De Kroon, H., Lebreton, J. D., Metcalf, C. J. E., Neel, M. M., Parker, I. M., Takada, T., Valverde, T., Vélez-Espino, L. A., Wardle, G. M., Franco, M. & Vaupel, J. W. 2015. The compadre plant matrix database: An open online repository for plant demography. *Journal of Ecology*, 103(1), 202-218.
- Sánchez Fernández, J., Ruiz López, A. & Tabora, D. M. G. 2025. A novel machine learning-based approach to thermal integrity profiling of concrete pile foundations. *Data-Centric Engineering*, 6(33), 1-27.
- Santini, L., Cornulier, T., Bullock, J. M., Palmer, S. C. F., White, S. M., Hodgson, J. A., Bocedi, G. & Travis, J. M. J. 2016. A trait-based approach for predicting species responses to environmental change from sparse data: How well might terrestrial mammals track climate change? *Global Change Biology*, 22(7), 2415-2424.
- Sheil, B., Anagnostopoulos, C., Buckley, R., Ciantia, M. O., Febrianto, E., Fu, J., Gao, Z., Geng, X., Gong, B., Hanley, K., He, P., Kolomvatsos, K., De C.F.L. Lopes, B., Ninic, J., Previtali, M., Rezaia, M., Ruiz-Lopez, A., Sun, J., Suryasentana, S., Tabora, D., Utili, S., Whyte, S. & Zhang, P. 2026. Artificial intelligence transformations in geotechnics: Progress, challenges and future enablers. *Computers and Geotechnics*, 189(2026), 107604.
- Stevens, V. M., Turlure, C. & Baguette, M. 2010. A meta-analysis of dispersal in butterflies. *Biological Reviews*, 85(3), 625-642.
- Synes, N. W., Brown, C., Watts, K., White, S. M., Gilbert, M. A. & Travis, J. M. J. 2016. Emerging opportunities for landscape ecological modelling. *Current Landscape Ecology Reports*, 1(4), 146-167.
- Touboul, J., Li, J., Patterson, D. & Levin, S. 2025. New challenges in spatial ecology. *Japan Journal of Industrial and Applied Mathematics*, 42(4), 1695-1714.

- Twining, J. P., Sutherland, C., Reid, N. & Tosh, D. G. 2022. Habitat mediates coevolved but not novel species interactions. *Proceedings of the Royal Society B: Biological Sciences*, 289(1966), 1-9.
- Uiterwaal, S. F., Lagerstrom, I. T., Lyon, S. R. & Delong, J. P. 2022. Forage database: A compilation of functional responses for consumers and parasitoids. *Ecology*, 103(7), e3706.
- Upadhyay, R. K., Roy, P., Venkataraman, C. & Madzvamuse, A. 2016. Wave of chaos in a spatial eco-epidemiological system: Generating realistic patterns of patchiness in rabbit-lynx dynamics. *Mathematical Biosciences*, 281(2016), 98-119.
- Ward, S. L., Robins, P. E., Owen, A., Demmer, J. & Jenkins, S. R. 2023. The importance of resolving nearshore currents in coastal dispersal models. *Ocean Modelling*, 183(2023), 102181.
- Wyse, A. P., Santos, A. J. B. D., Azevedo, J. D. S., Lima, J. S. D. & Faria, J. R. D. 2018. Modeling the spreading and interaction between wild and transgenic mosquitoes with a random dispersal. *PLOS ONE*, 13(10), e0205879.
- Yang, Y., Ruiz López, A., Tsiampousi, A. & Taborda, D. M. G. 2026. A novel adaptive sampling approach with batch selection for the automatic generation of surrogate models in geotechnical engineering. *Data-Centric Engineering*, 7(2), 1-29.
- Zienkiewicz, O. C., Taylor, R. L. & Fox, D. 2014a. *The finite element method for solid and structural mechanics*, Oxford, UK, Elsevier.
- Zienkiewicz, O. C., Taylor, R. L. & Nithiarasu, P. 2014b. *The finite element method for fluid dynamics*, Oxford, UK, Elsevier.
- Zurell, D., Albert, C. H., Bocedi, G., Briscoe, N. J., Buckley, L. B., Gascoigne, S. J. L., Gonzalez, A., Guillera-Arroita, G., Isaac, N. J. B., Karger, D. N., Lundquist, C. J., Merow, C., Cabral, J. S., Schifferle, K., Velazco, S. J. E. & Urban, M. C. 2026. Biodiversity science and policy need more model intercomparisons. *Nature Reviews Biodiversity*, 2(2026), 204-215.
- Zurell, D., Bocedi, G., Velazco, S. J. E., Gonzalez, A., Purvis, A., Wintle, B., Merow, C., Lundquist, C., Guillera-Arroita, G., Settele, J., Serra-Diaz, J. M., Cabral, J. S., Travis, J. M. J., Schifferle, K., Buckley, L., Briscoe, N. J., Isaac, N. J. B., Peres-Neto, P. R., Keuth, R., Gascoigne, S. J. L., Ferrier, S. & Urban, M. C. 2025. Predicting the way forward for the global biodiversity framework. *Proceedings of the National Academy of Sciences*, 122(41), 1-4.
- Zurell, D., König, C., Malchow, A. K., Kapitzka, S., Bocedi, G., Travis, J. & Fandos, G. 2022. Spatially explicit models for decision-making in animal conservation and restoration. *Ecography*, 2022(4), 1-16.