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BRITISH ECOLOGICAL SOCIETY Methods in Ecology and Evolution

PERSPECTIVE

Empirical ecology to support mechanistic modelling: Different objectives, better approaches and unique benefits

Steven F. Railsback[1] | Cara A. Gallagher[2,3] | Volker Grimm[4] | Matthew A. McCary[5] | Bret C. Harvey[6]

[1]Lang Railsback & Associates, Arcata, California, USA; [2]Department of Ecoscience, Aarhus University, Roskilde, Midtjylland, Denmark; [3]Department of Plant Ecology and Nature Conservation, University of Potsdam, Potsdam, Germany; [4]Department of Ecological Modelling, Helmholtz Centre for Environmental Research-UFZ, Leipzig, Germany; [5]Department of BioSciences, Rice University, Houston, Texas, USA and [6]US Forest Service, Pacific Southwest Research Station, Arcata, California, USA

Correspondence
Steven F. Railsback
Email: steve@langrailsback.com

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Abstract

1. Modern ecological management problems are characterized by large scales, rapid environmental change, multiple stressors and conflicts between local and global conservation objectives. These problems are too complex to address with field studies alone, and statistical models that assume past system behaviours can predict future responses are risky when systems are changing rapidly. Mechanistic simulation models, though, can avoid that assumption while accommodating important natural complexities.
2. Making mechanistic models credible requires empirical studies, but traditional study topics and designs often do not support them well. The models we use for modern problems need empirical studies that provide understanding of life history and autecology of study species, identify general patterns useful for model design and evaluation, collect data of kinds that models show are important and develop submodels and theory for individual-level mechanisms.
3. Ecologists can better produce such knowledge via research that: (a) is interdisciplinary and across-level, often designed to understand just enough about individuals to support individual-based models of populations and communities; (b) is designed to quantify relationships across broad ranges, instead of testing statistical hypotheses; (c) emphasizes relevance and realism over precision; and (d) includes stressful conditions relevant to modern management challenges.
4. Supporting complex management models is rewarding to research ecologists: Modelling identifies crucial yet understudied research topics; models can be used as virtual ecosystems for experiments (including tests of theory) that would be impossible in reality; and supporting models ensures that our work has high impact and contributes to critical issues.

KEYWORDS
applied ecology, empirical ecology, mechanistic modelling, study design

1 | INTRODUCTION: WHY 21ST-CENTURY ECOLOGY NEEDS MECHANISTIC MODELLING

Ecology, as a profession and academic discipline, is adapting rapidly to address the difficult yet urgent management challenges of the 21st-century, the complex problems that result from ever-increasing human influences on ecosystems. These problems are characterized by large scales, rapid change in climate and other environmental conditions, multiple stressors on multiple species and, often, conflicts between global benefits (e.g. of renewable energy) and local conservation. A key characteristic of 21st-century problems is that they push us into unexplored territory: We must make decisions now about futures when conditions will be very different from anything we have observed. Assuming that ecological systems are in equilibrium, reflecting the 'balance of nature' paradigm, is no longer a useful heuristic (Grimm et al., 2025). Instead, transient dynamics in response to disturbances or ongoing change 'are the norm rather than the exception under conditions of global change' (Jeltsch et al., 2025). They can last for decades, as in the case of 'extinction debts' with ongoing loss of species after, for example, habitat has been lost or changed (Jeltsch et al., 2025; Krauss et al., 2010).

These 21st-century challenges require ecologists to adapt our methods to be more relevant and productive. Traditional study approaches depend on field data and statistical analysis or relatively simple models, for example, looking for 'significant' relationships in datasets, fitting population models to census data and developing static models of 'suitable habitat' and species distributions. Traditional approaches are useful for many problems but have limited ability to handle complexities like interacting effects of multiple stressors, variability and interaction among individuals, species interactions and the effects and feedbacks of adaptive behaviour (Agrawal et al., 2007). Novel conditions are another major concern: Models fit to system-level data without considering underlying mechanisms implicitly assume that those underlying mechanisms will remain unchanged, a risky assumption when making predictions of a rapidly changing world. Even short-term and local management issues often involve too many variables for simple models or field experiments alone to address with adequate certainty.

Modern challenges can, however, be addressed with mechanistic models that are supported by empirical research. Useful predictions of novel conditions are possible with models that contain enough mechanism to reflect how drivers such as food availability, predation risk and disturbance interact with behaviour and interactions among individuals to produce ecological dynamics (Boult & Evans, 2021; Stillman et al., 2015). Such models are often individual-based and incorporate wide ranges of empirical knowledge, much observed with relative certainty at the individual level (Grimm et al., 2017; Grimm & Railsback, 2005). Individual-based models (IBMs) contain 'submodels' that, ideally, represent how environmental conditions affect individual fitness. These submodels can use theory, for example, for metabolic processes and trade-off decisions, or encode observations from the laboratory or field. IBMs can be validated in many ways, including via 'pattern-oriented' analysis to show how well a model reproduces multiple patterns observed at multiple levels and scales and, therefore, how well it captures critical mechanisms (Grimm et al., 2005; Grimm & Railsback, 2012). While the uncertainty of simple system-level models increases with the number of parameters fit to limited system-level data, the uncertainty of mechanistic IBMs depends less on the number of parameters and more on the mechanisms they contain and—the topic addressed here—the ecological knowledge used to model those mechanisms (DeAngelis & Mooij, 2003; Wiegand et al., 2003). Empirical research guides decisions about which mechanisms to include and how to represent them.

This paper is not about models but about the empirical ecology we need to support them. Our objective is to illustrate two points about how ecologists address the world's most pressing problems. First, we need to adapt the study topics and methods we use in basic research: Traditional study approaches are not always the best for supporting the mechanistic models required for these problems. Second, addressing 21st-century problems with new kinds of research is rewarding: It makes our work relevant and important and often identifies opportunities for important discoveries, both empirical and theoretical.

We first describe four research programmes that address important, complex, modern ecological management issues using models and empirical studies. These examples are provided to support the conclusions discussed in the subsequent sections on (1) roles and objectives of empirical research supporting mechanistic modelling, (2) methods that make such research more useful for complex models and (3) the scientific and career benefits of model-oriented empirical research.

2 | EXAMPLES OF ECOLOGY FOR 21ST-CENTURY PROBLEMS

Here, we present four example research programmes that vary widely in scope and duration, but all include both mechanistic models and empirical studies. We describe the models only briefly and instead focus on the rewards of linking ecological research with management modelling, especially how modelling identified important gaps in existing knowledge and provided ways to address questions that could not be addressed with field studies alone.

Methods in Ecology and Evolution

2.1 | Example 1: Marine mammals and offshore energy development

The effects of noise from offshore wind energy development on marine mammal populations is a quintessential 21st-century problem: Balancing the benefits of renewable energy against its ecological costs involves spatial and temporal processes at scales from individual physiology to regional foraging dynamics. The DEPONS model (Figure 1; Gallagher et al., 2022; Gallagher, Grimm, et al., 2021; Nabe-Nielsen et al., 2018) simulates the effects of noise on individual porpoise foraging behaviour and success and their consequences for survival, reproduction and population dynamics. The development and validation of DEPONS used a wide range of captive-animal and field studies. Individual morphometrics were evaluated from long-term datasets on porpoise strandings. A locomotion parameter was estimated from respirometry data collected from captive porpoises (Otani et al., 2001). The maintenance energy cost submodel was based on a study using isotopic data and ventilation rates obtained from captive and wild porpoises (Rojano-Doñate et al., 2018). Behavioural responses to noise were based in part on field observations (Nabe-Nielsen et al., 2018).

Key results include that noise impacts are highly seasonal, so potentially can be mitigated through construction timing, and that a common, simple metric of noise impact—the number of porpoises exposed to noise—is not a good indicator of population impacts. Its mechanistic nature makes DEPONS useful for broader and more general purposes than its primary application to noise impacts. Gallagher et al. (2022) used the model to investigate two likely effects of climate change—changes in prey size and spatial distribution—on porpoise feeding behaviour and population dynamics. Results suggest that climate-induced changes in prey structure may threaten predator populations and that the additional energy

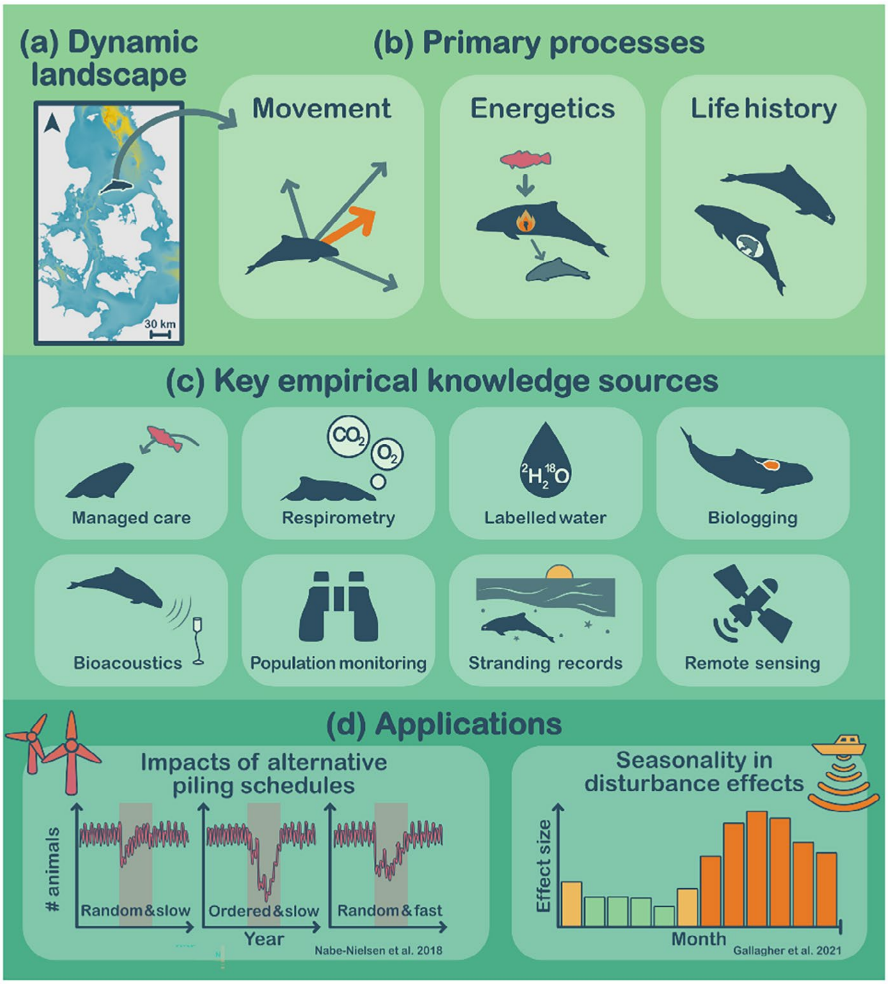

FIGURE 1 The DEPONS model predicts the effects of offshore development on harbour porpoise populations. It represents (a) the dynamics of the offshore environment and (b) the primary processes through which environment and disturbance affect individuals and populations. Submodels for those processes were built from empirical studies (c) conducted both in the field and on captive animals. Because it represents mechanisms instead of relying only on historic data, DEPONS can address novel conditions such as (d) alternative schedules for pile driving and related seasonal disturbances.

required to locate smaller and less aggregated prey is important when assessing impacts of decreased energy availability.

2.2 | Example 2: Stream salmonids and water diversions

InSTREAM (Railsback et al., 2023; Railsback, Ayllón, et al., 2021) is a complex IBM designed to support decisions allocating river flow between human uses (hydropower, water supply) and sustaining trout populations. Key mechanisms for simulated trout include: (1) Growth, represented via an energy balance of intake from feeding and metabolic costs; (2) mortality, especially predation, with risk that varies with habitat and fish variables; (3) behaviour—fish select when and where they feed, as a trade-off between growth and survival; and (4) spawning and egg incubation, to allow multigeneration simulations that include the effects of management on reproductive life stages.

InSTREAM's design is deeply rooted in empirical knowledge, with Railsback et al. (2023) using ~150 published studies to model the trout life cycle. Its 25 years of development and use have been supported by both laboratory and field studies. Myrick and Cech Jr. (2020) quantified salmonid metabolic and digestion rates at the higher temperatures that are often important for management but neglected in previous lab studies. Parameter uncertainty analysis indicated that the relation between water depth and predation risk (from birds) is critical to population dynamics, so Harvey and White (2017) conducted a field experiment evaluating that relation.

Studies combining simulation with field experiments have been especially productive because they both supported the model (by testing and improving it, establishing its credibility) and made important contributions to stream ecology. Harvey et al. (2014) not only validated InSTREAM's ability to predict individual growth responses to flow diversion but also showed that a feeding mode generally neglected in salmonid research (searching instead of sit-and-wait) is important under low-flow conditions (Harvey & Railsback, 2014). Persistence of a real trout population when InSTREAM predicted extinction due to turbidity-reduced feeding success (Harvey & Railsback, 2009) led to the discovery of a different feeding mode critical under this stressor (White & Harvey, 2007). Harvey et al. (2024) demonstrated InSTREAM's ability to predict the effects of a habitat restoration project, while showing that real population responses can take years to stabilize; the model suggested the effects of vegetation regrowth on food production as a mechanism causing the instability.

InSTREAM has also been rewarding as a virtual ecosystem for experiments impossible in the field or laboratory. For example, Harvey and Railsback (2012) simulated wide ranges of habitat fragmentation to explore their effect on population abundance and stability properties. Railsback, Harvey, et al. (2021) used InSTREAM to illustrate the consequences of ignoring nocturnal and crepuscular periods, as most management studies and models do.

2.3 | Example 3: Plant invasions

The plant invasion study of McCary et al. (2019) illustrates that modern problems can also be addressed by shorter term projects such as PhD research. The study was designed to support invasive plant management by producing understanding of interactions among invaders, mycorrhizal fungi and soil ecosystems. It combined a relatively simple simulation model of garlic mustard invasions, empirical experiments and existing knowledge of plant and soil communities.

Empirical research (McCary & Wise, 2019) included field censuses of plants, soil fungi, fungivores and predators; and mesocosm experiments that manipulated plant species, soil history and fungicide application. Sensitivity analysis of the model identified mechanisms most strongly affecting native plant density after invasion.

Key findings of the combined field, lab and simulation experiments are that native plants with both low and high reliance on mycorrhizal mutualisms are more susceptible to allelopathic plant invaders than those with intermediate-strength mutualisms. The model was designed to also be a virtual mesocosm for additional research on how invasion success is mediated by species interactions such as plant–mycorrhizal mutualisms.

2.4 | Example 4: Honey bees, farming practices and pesticide regulation

Honey bee colony collapse is a potential global crisis believed to result from multiple stressors. BEEHAVE (Becher et al., 2014) is a colony model that assembles knowledge about the mechanisms through which stressors affect individual bees and colonies (Figure 2). It combines foraging in realistic landscapes with in-hive processes such as brood-rearing and coping with mite infestation. An optional module tracks pesticide transport into the hive and represents toxicity using ecotoxicological test results (Preuss et al., 2022). BEEHAVE also predicts the effects of forage gaps caused by modern farming methods that produce few crops (Horn et al., 2021). Satellite data are useful but not sufficient for mapping floral resources; citizen science data on flowering plants in semi-natural habitats and field margins fill the gaps. Because BEEHAVE identified pollen collection rate as especially important to colony performance, flight monitors are being developed to measure it in real hives.

Because honey bee ecology is so complex, BEEHAVE's mechanistic detail can provide a much broader understanding of general factors limiting colony success than could be obtained via empirical research alone. For example, Rumkee et al. (2015) simulated the relative effects of exposure to pesticide-contaminated nectar and pollen on different bee life stages to understand which life stage had the strongest effects on colony survival. Henry et al. (2017) analysed BEEHAVE to examine the cumulative effects of forager and larvae mortality from pesticides, *Varroa* mite infestation and distance to

FIGURE 2 The BEEHAVE decision-support system includes (a) an individual-based honey bee colony model with submodels representing the effects of *Varroa* mite infestation and beekeeper activities such as honey harvest and *Varroa* control; and (b) the BEESCOUT model (Becher et al., 2016) of how bee foraging success depends on land use and agricultural practices. Distributed science to support the system includes (c; from www.bienenkunde.rlp.de/Bienenkunde/Trachtnet/Waagenstandorte-Karte) remote monitoring of over 500 hives throughout Germany.

forage vegetation, a question far too complex to understand using field experiments alone.

3 | NEW ROLES OF EMPIRICAL RESEARCH IN MODEL-BASED ECOLOGY

We now have decades of experience with mechanistic ecological models (e.g. Grimm & Railsback, 2005; Stillman et al., 2015) and a clear idea of how modellers use empirical literature and information. Those uses are rarely the original objectives of the empirical studies, which means that, if we want to address modern problems effectively, we need our research to address different objectives. Mechanistic models are often described as 'data-hungry', but really they are knowledge-hungry—building them requires diverse information including:

3.1 | Life history and autecology

Our four example studies illustrate the need to understand the study species' life stages, reproductive cycles and local interactions (e.g. with energy sources, predators, competitors, mutualists) to build mechanistic models. Studies that document the life history and autecology of modelled species with a focus on variation and adaptation are crucial and very often discover important new exceptions to what 'everyone knows' about a species.

3.2 | Patterns for model design and evaluation

'Pattern-oriented modelling' (POM) is a strategy for designing models with appropriate levels of detail and demonstrating their validity (Grimm et al., 2005; Railsback & Johnson, 2011). POM is especially important for showing that models adequately represent the mechanisms we think are essential. POM requires a diversity of patterns, often simple and qualitative, observed in real systems at both the individual and system levels; Gallagher, Chudzinska, et al. (2021) provide examples.

3.3 | Habitat and population data—Of new kinds

Mechanistic models typically require extensive field observations as input, but their focus on mechanisms often identifies types of data with more explanatory power than traditional census and habitat measures. For example, InSTREAM's representation of feeding and predator-avoidance behaviours uses three separate variables for what fish biologists typically lump together as 'cover': velocity shelter for feeding, predator escape cover and concealment places used when not feeding. More detailed census data, for example, size and age distributions in addition to abundance, are often useful for IBMs. More kinds of input can add uncertainty but can also reduce uncertainty by supporting submodels based on extensive knowledge (e.g. for trout feeding and behaviour) and by facilitating more thorough model calibration and evaluation.

3.4 | Theory and submodels for individual-level mechanisms

Mechanistic models contain submodels (e.g. for feeding, energetics, adaptive behaviour), which can be empirical or based on theory. Developing, testing and generalizing submodels is a major task of mechanistic modelling and modern ecology that even small studies can contribute to.

4 | RESEARCH APPROACHES TO SUPPORT MECHANISTIC MODELLING

Even though our models use empirical literature extensively, we often find studies that have been designed in ways that make results much less useful than they could have been. Empirical ecologists can make their work more useful for 21st-century problems as follows:

4.1 | Being interdisciplinary and across-level

Building and testing bottom-up models demands information over multiple ecological levels, from population or community ecology down to physiology and sometimes even genetics. We also need information that is inherently *across*-level: We do not need to know everything about individual behaviour but models of behaviour just detailed enough to represent how behaviour affects populations (Grimm & Railsback, 2005); we do not need 'realistic' models of physiology but submodels that capture just enough about the right physiology to produce useful individual behaviour, growth, reproduction and survival. Such research can be conducted by teams that include modellers and field and laboratory scientists (examples 1, 2 and 4, above), but also by individual researchers (example 3) who design both models and empirical studies to support them.

4.2 | Using mechanistic modelling instead of hypothesis testing as a conceptual framework

Traditional field and lab experiments address yes/no questions via statistical hypothesis testing: Do three levels of *X* produce significantly different values of response variable *Y*? Now, ecologists also commonly apply complex statistical models to large datasets. Neither of these approaches is very useful when the goal is understanding and modelling how systems work. Differences among discrete treatments are less useful than broad relationships: We need to know how *Y* changes as *X* varies over its full range of expected values (Figure 3). Statistical methods that identify 'significant' predictors from large datasets are rarely useful for modern problems because they cannot be assumed applicable to novel future conditions and do not elucidate the mechanisms driving responses (Limitations of hypothesis testing for supporting environmental decision-making have long been discussed; Suter, 1996; Hilborn, 1997.) We most need 'first principles' understanding:

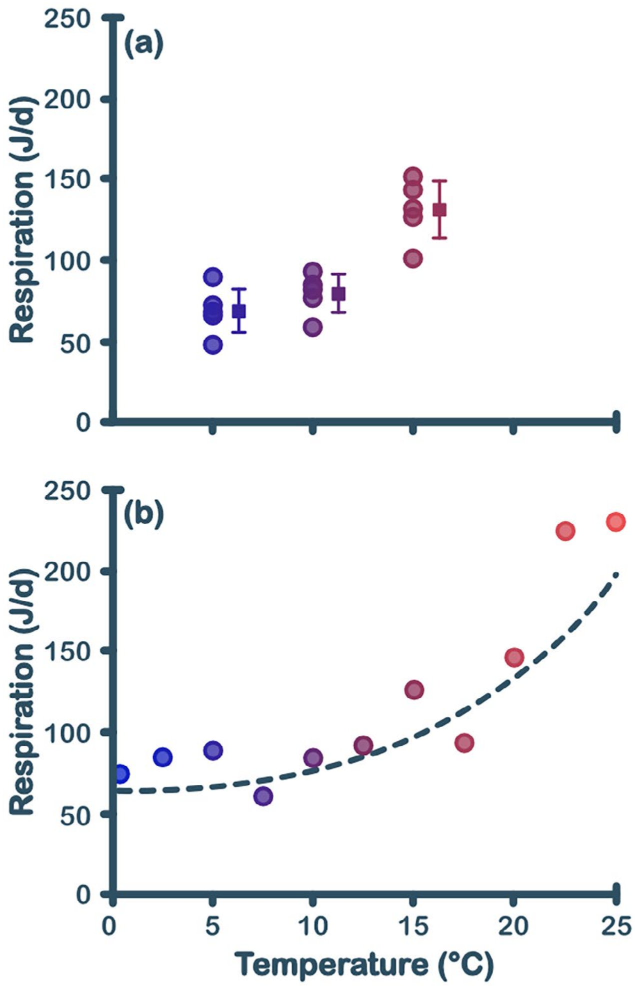

FIGURE 3 Illustration of laboratory study design to support modelling. (a) A traditional ANOVA using five replicates of three temperature treatments produces significantly higher trout respiration at 15° than at 5° or 10° ($p < 0.05$), but no clear guidance on modelling respiration below 5° or above 15°, or even between 5° and 10°. (Boxes and whiskers indicate the mean and standard deviation.) (b) The alternative of 11 unreplicated temperature treatments from 1° to 25° is noisy, but makes clear that respiration increases gradually up to ~18° but then at a sharply higher rate. The alternative design's results are much more useful for modelling respiration and, therefore, growth and behaviour, especially at stressful temperatures. ('Data' synthesized from the respiration submodel of Railsback et al., 2023, developed from ~10 lab studies.)

Experiments and theory that show how environmental factors and internal mechanisms (physiology, behaviour) affect individual fitness, for use in IBMs to predict population responses to novel futures.

4.3 | Emphasizing relevance over precision

Designing studies for precision (lower variance) supports the hypothesis testing framework: 'Noise' in data limits our ability to distinguish significant differences, so we simplify our experimental systems to reduce noise. However, in mechanistic as well as statistical modelling, decreasing variance is not good if the experiment is biased (Meng, 2018). Unfortunately, many ecological experiments use conditions so unnaturally simplified that results are biased with respect to real systems. For example, many studies of temperature effects on fish energetics use fish fed ad libitum; because food intake interacts with temperature, such studies do not represent energetics reliably under natural food conditions (Railsback, 2022). Enders and Boisclair (2016) review ways that simplified laboratory conditions have made fish physiology studies biased or irrelevant for management modelling. For management modelling, study conditions need to represent conditions being modelled while avoiding bias, even if that reduces precision.

4.4 | Including stressful conditions

Physiology and behaviour are often more variable under stressful conditions, so ecologists often avoid such conditions to avoid noisy data (and to avoid harming their subjects). However, useful models must predict responses to stressful conditions. We cannot understand population resilience, for example, without understanding how individuals perform under stress. Furthermore, behaviour is often driven by stress: Porpoises decide between abandoning offspring or starving, trout select habitat by balancing risks of starvation and predation. Modelling such behaviours requires knowing how stressful various conditions are. Therefore, it is especially important to include, not avoid, stressful and extreme conditions in study designs. Doing so may require stressing study animals more than we like, which makes it especially important to maximize the value of results for modelling.

5 | THE VALUE OF MODERN MANAGEMENT MODELS FOR RESEARCH ECOLOGY

Supporting management modelling may seem an unlikely route to success as a research ecologist, but in our experience it offers unique opportunities to make basic discoveries, develop new theory and address crucial problems. The value of integrating modelling with empirical studies is well known; mechanistic models addressing difficult management questions have the additional benefits of:

5.1 | Identifying critical but understudied questions

In all our example projects, modelling identified information gaps that became important research topics. Models with more mechanisms are of course more likely to identify mechanisms that are more important than previously believed and, therefore, novel and valuable research topics (Wang et al., 2024). Such mechanisms are often found via analysis of model sensitivity to parameters or assumptions (Grimm & Berger, 2016). More detailed models also allow more detailed validation studies, which can reveal model weaknesses indicating that conventional understanding is inadequate (e.g. Harvey & Railsback, 2009, 2014).

5.2 | Identifying better variables to measure

Mechanistic models of how management affects populations often identify organism and habitat characteristics more directly related to individual fitness and population characteristics that better reveal underlying mechanisms. Such characteristics can be more important than the variables traditionally observed in field studies. Our third example study provides an illustration: When the model suggested that particular plant root traits (e.g. fine root turnover rate or root exudation) have especially strong effects on microbial activity, field measurements focussed on those traits had greater value for understanding and predicting mycorrhizal mutualisms than general root biomass estimates.

5.3 | Supporting theory development and testing

Theory for individual traits that explain population and community dynamics in IBMs is a largely unexplored field (Grimm & Railsback, 2005; Railsback & Harvey, 2020). IBMs also provide uniquely powerful ways to develop theory by testing alternative hypotheses against empirical observations in contexts that, while still simplified, can be more realistic than the highly simplified systems often used in empirical theory tests (e.g. Railsback et al., 2020).

5.4 | Providing virtual ecosystems

Our simulation experiments can address basic as well as applied problems. Using mechanistic models as virtual ecosystems lets us conduct experiments impossible in reality, for example, by turning mechanisms off to evaluate their importance. Ayllón et al. (2025)

used this advantage to evaluate the importance of a specific adaptive behaviour to the resistance of populations to climate change, contrasting long-term simulations with and without the behaviour.

5.5 | Ensuring research impact

Countless field and laboratory studies are rarely cited because their objectives, methods, endpoints, etc., have little relevance to larger questions. When we design studies specifically to support management models, we can be more confident that our results have a lasting impact because the model makes them relevant to ecology and to the management of important issues.

6 | CONCLUSIONS

Modern management problems often require models that represent the mechanisms that will drive ecological responses to novel future conditions, and those models require many kinds of empirical knowledge. Interdisciplinary programmes that combine modelling with empirical research are especially productive (Stillman et al., 2015). Yet any ecologist can contribute by addressing questions identified by modellers as important but understudied, and by designing their empirical or theoretical studies to support mechanistic models. Heinrichs et al. (2025) illustrate studies that develop broad relationships useful for modelling while still rigorously testing hypotheses. In our experience, working in these ways is professionally rewarding and benefits ecology as a science by keeping it relevant.

AUTHOR CONTRIBUTIONS

Steven F. Railsback: Conceptualization (equal), writing—original draft (lead), writing—review and editing (lead). Cara A. Gallagher: Conceptualization (equal), visualization (lead), writing—original draft (supporting), writing—review and editing (supporting). Bret C. Harvey: Conceptualization (equal), writing—original draft (supporting), writing—review and editing (supporting). Matthew A. McCary: Conceptualization (equal), writing—original draft (supporting), writing—review and editing (supporting). Volker Grimm: Conceptualization (equal), writing—original draft (supporting), writing—review and editing (supporting).

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

ORCID

Steven F. Railsback https://orcid.org/0000-0002-5923-9847
Volker Grimm https://orcid.org/0000-0002-3221-9512
Matthew A. McCary https://orcid.org/0000-0002-7846-7159

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