



# A guide to ecosystem models and their environmental applications

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**Applied ecology has traditionally approached management problems through a simplified, single-species lens. Repeated failures of single-species management have led us to a new paradigm — managing at the ecosystem level. Ecosystem management involves a complex array of interacting organisms, processes and scientific disciplines. Accounting for interactions, feedback loops and dependencies between ecosystem components is therefore fundamental to understanding and managing ecosystems. We provide an overview of the main types of ecosystem models and their uses, and discuss challenges related to modelling complex ecological systems. Existing modelling approaches typically attempt to do one or more of the following: describe and disentangle ecosystem components and interactions; make predictions about future ecosystem states; and inform decision making by comparing alternative strategies and identifying important uncertainties. Modelling ecosystems is challenging, particularly when balancing the desire to represent many components of an ecosystem with the limitations of available data and the modelling objective. Explicitly considering different forms of uncertainty is therefore a primary concern. We provide some recommended strategies (such as ensemble ecosystem models and multi-model approaches) to aid the explicit consideration of uncertainty while also meeting the challenges of modelling ecosystems.**

Applied ecology has historically approached management with a narrow view, using a simplified single-species or single-threat frame for decision problems<sup>1</sup>. Such approaches to ecosystem management have been exposed as inadequate in many fields, as they lead to poor and even perverse outcomes in fisheries<sup>2</sup>, conservation<sup>3</sup>, invasive species management<sup>4</sup> and biocontrol<sup>5</sup>. The management of ecosystems is a ‘wicked problem’, involving a complex array of interacting organisms, processes, social and policy dimensions, and scientific disciplines<sup>6</sup>. Accounting for interactions, feedback loops and dependencies between ecosystem components is therefore fundamental to understanding and managing ecosystems<sup>7,8</sup>. This includes spatial and temporal dynamics, interactions between organisms and disturbances, anthropogenic impacts<sup>9–11</sup>, and complementarities across species. The limited information base available for analyses that integrate these relationships has historically precluded the implementation of complex ecosystem modelling. This has gradually changed over recent decades, particularly in the past 10 years, and now ecosystem modelling approaches are in high demand.

Although there have been considerable efforts to model marine and terrestrial ecosystems, these have largely been in isolation, with little cross-pollination between the two realms. Here, we provide a synthesis of general ecosystem modelling techniques that covers both terrestrial and marine ecosystems. Our aim is to provide guidance for potential ecosystem modellers in selecting an approach that suits their system, objectives and constraints. We outline a selection of currently available approaches and the key considerations for selecting ecosystem modelling methods. Although they are not

exhaustive, the approaches discussed are representative and provide a good indication of the possible and commonly used approaches available to ecosystem modellers. We place these methods in the context of applied management problems and discuss how particular ecosystem modelling techniques can help to embrace the uncertainty associated with complex systems.

## What is an ecosystem model?

Ecosystem models attempt to incorporate ecosystem components (for example, populations, species, functional groups) and processes (for example, predator–prey interactions, large and small perturbations, dispersal) into one modelling framework. We define an ecosystem model as a model that describes the interactions between at least two ecosystem components (for example, a species or functional group), whereby the interactions are real ecological processes (for example, predation, dispersal or perturbations). Ecosystem models are parametrized using field-collected, experimental and/or expert-elicited data to make inferences about specific components (for example, individual species), the entire ecosystem, or even a large part of the coupled socio-ecological system<sup>12,13</sup>. The models are often visualized as networks, where nodes denote interacting ecological components, and the causal relationships between them are shown by edges (Box 1). These models were developed because ecologists needed to disentangle, and therefore predict, the outcomes of complex interactions between ecosystem components in a meaningful way<sup>12,14,15</sup>. Such models have been used extensively in fisheries and other marine contexts<sup>16</sup>, and their use is increasing in terrestrial ecosystem management<sup>17</sup>, including scenario prediction<sup>18–20</sup>.

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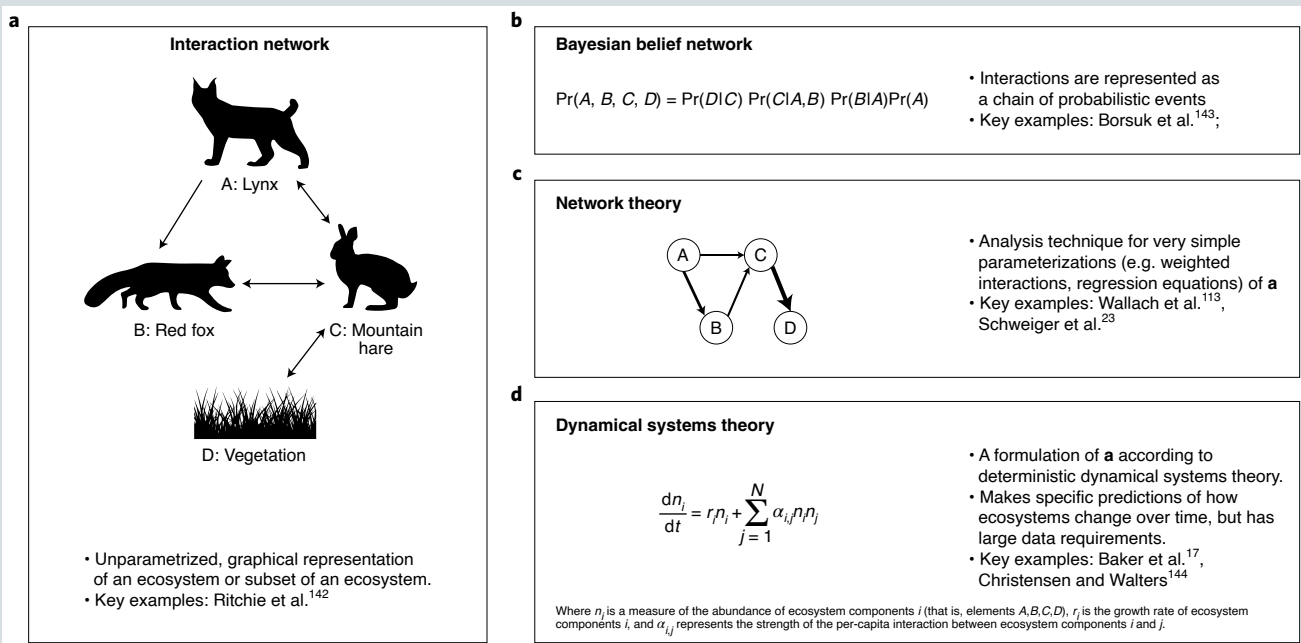
**Box 1 | The mathematics of applied ecosystem modelling**

The term ‘ecosystem model’ incorporates a wide variety of representations of ecosystems, with the common thread of representing interactions between ecosystem components and/or processes (for example, species, functional groups and/or perturbations). To illustrate the different mathematical approaches to and representations of ecosystem models, we use a simple food web from Central Europe containing an apex predator (Eurasian lynx), a mesopredator (red fox), a herbivore (mountain hare) and vegetation, adapted from the structural equation model developed by Elmhagen et al.<sup>141</sup>. Ecosystems are commonly represented as conceptual interaction networks (panel a of the figure), which are unparametrized illustrations of interaction networks. These models are essentially diagrammatic and are used as a starting point for more complex ecosystem models<sup>142</sup>. For instance, qualitative models using signed digraphs can be used to explore pulse–press perturbations for small-to-moderate network sizes<sup>30</sup>.

Bayesian belief networks represent ecosystem interactions as a chain of probabilistic events, showing how changes in the probability of one ecosystem component flow through to affect the probability of another ecosystem component changing. These models can be represented as a graphical structure, or a chain of probabilities (panel b of the figure). For example, Bayesian networks were used to model the effects of eutrophication in the Neuse estuary, North Carolina<sup>143</sup>. Bayesian networks have the advantage of their ability to incorporate expert and stakeholder judgements alongside field-collected data. However, their predictive use can be severely hampered by the inability to easily capture feedback dynamics and cyclical mechanistic flows.

Network theory encompasses a broad collection of ecosystem modelling approaches predicated on simple parametrizations of interaction networks (panel c of the figure). These can range from weighted networks<sup>98,113</sup> to structural equation models<sup>23</sup>. For instance, fuzzy cognitive maps are increasingly used for semi-quantitative prediction of the outcomes of changes (for example, reintroductions, invasive species control) on ecological networks<sup>31</sup>.

Ecosystem models that take a dynamical systems theory approach (panel d of the figure) use a deterministic approach to predict how ecosystems change over time. Such models are typically based on Lotka–Volterra equations, or similar, and can have demanding data requirements, especially if the model is complex. These approaches have been used to predict the ecosystem-wide effects of species reintroductions<sup>17</sup>, seed dispersal on islands<sup>94</sup> and the outcomes of invasive species control<sup>63</sup>, and could have broader applications<sup>144</sup>.



Building ecosystem models typically involves trade-offs between approaches that are highly complex and cannot be extrapolated beyond the sample system, and those that sacrifice some complexity to allow extrapolation to other ecosystems and situations<sup>21,22</sup>. For example, the structural equation model developed by Schweiger et al.<sup>23</sup> to manage wetland condition in the Rocky Mountain National Park, United States, is very complex and parametrizes the model with field-collected data, but its specificity means that the inferences would probably not be easily and generally transferable to other systems<sup>22</sup>. The main sources of uncertainty in ecosystem models are parameter (for example, the parameter estimates applied to the model structure) and structural (for example, ecosystem components included in the model, and the relationships between them, as well as completely missing processes). As the structure of

models becomes more complex, uncertainty in model predictions typically increases<sup>24</sup>. Because of this, constructing a single ecosystem model that incorporates all possible complexities is rarely advised, as the model outputs are too uncertain to inform decision making<sup>25</sup>. However, less complex models can also have limitations, particularly related to parameter uncertainty, potential omission of key processes (a critical issue where these govern response rates and delays in the system), inappropriate scales and the shape of relationships between components (for example, linear versus nonlinear relationships). This is why ensemble modelling — which can explicitly consider both parameter and structural uncertainty — is fast becoming ‘best practice’ amongst marine ecosystem modelling groups, particularly when addressing large-scale questions such as the effects of climate change (for example, ref. <sup>26</sup>).

Frequency of use	Always	Objective of model development			Spatial and temporal patterns		Ecosystem component			Ecosystem processes					
	Often	Describe and understand current ecosystem	Forecast/hindcast scenarios	Decide on management actions	Incorporate multiple spatial scales	Temporally dynamic	Population (size, age) structure	Individual species	Aggregates/groups of taxa	Ecosystem condition/state	Species interactions	Dispersal	Single-node perturbations	Whole-of-ecosystem perturbations	
	Sometimes	Ecosystem modelling approach													
	Rarely														
		Conceptual model													
		Loop analysis													
		Fuzzy cognitive map													
		Bayesian belief network													
		Graph-theoretic network analysis													
		Co-occurrence analysis													
		Structural equation model													
		Multi-species population dynamic model													
		State-transition model													
		Mass-balance models													
		Agent-based/individual-based model													
		Models of intermediate complexity (MICE)													
		Ensemble ecosystem model*													
		End-to-end ecosystem model													

Increasing data/resources/knowledge required

**Fig. 1 | Ecosystem modelling methods and their frequency of use for specific purposes.** Schematic outlining potential ecosystem modelling approaches (rows) and the frequency (rarely, sometimes, often and always) with which each approach is used for different purposes (columns). Modelling approaches further to the bottom of the table increase in complexity, data, resources and knowledge required to implement. This figure can be used to determine which modelling approach is most appropriate for particular purposes and contexts. \*Ensemble ecosystem model in this context refers to ensembles of models of one type. For ensembles of ecosystem models of multiple types (for example, an ensemble of MICE and mass-balance models), refer to each of the model-specific rows.

**Choosing an ecosystem model**

For ecosystem models to be useful, their qualities and structure must be matched to the decision problem or management application<sup>13</sup>. The key elements or qualities of ecosystem models can be summarized into four broad categories: the objective of model development, the spatial and temporal patterns represented, and both the ecosystem components and ecosystem processes modelled. In this section, we outline a range of broad approaches that are commonly used in applied contexts and assess their frequency of use in each category (Fig. 1, and with more detail in Supplementary Table 1).

**Objectives of model development.** Setting clear objectives is a fundamental requirement for successful ecosystem management<sup>27</sup>. Matching the modelling approach to the objectives and decision context is therefore an important consideration. Doing so ensures the model inferences are relevant to management goals and are an appropriate use of the available data. For example, the inferences that can be drawn from species co-occurrence models are highly dependent on the type of data used — presence-only or presence-absence species records or abundance data — and whether causal inferences can be made from correlative models<sup>28</sup>. In an applied

context, there are typically three broad — sometimes complementary — objectives of ecosystem models (Fig. 1).

*Objective 1: Describe and understand the current ecosystem.* Ecosystem models are regularly used to describe and understand the system in question. Most often, this occurs initially as a conceptual model that shows plausible cause-and-effect relationships between important ecosystem components (for example, populations of different species). As increasing amounts of data are collected, the parametrization of these models moves towards a quantitative, rather than schematic, description (Fig. 1). For example, models of signed digraphs, built on early qualitative modelling by Levins<sup>29</sup>, assign interactions between ecosystem components as either positive or negative<sup>30</sup>. Going further, recent fuzzy cognitive maps describe the impact of a change in one ecosystem component on another as high, medium or low<sup>31</sup>. Fuzzy cognitive maps can then be used to predict semi-quantitatively how changes to one ecosystem component can flow through to affect other components<sup>32</sup>. Where field-collected data or expert judgements are available, semi- and fully quantitative descriptions of the relationships between ecosystem components can be drawn by using network-based

techniques such as Bayesian belief networks, structural equation modelling, dynamical systems theory and network analysis. For instance, extinction cascade models make predictions of how the extinction of one species from a system could then lead to secondary extinctions through chain reactions<sup>33,34</sup>.

Ecosystem models geared toward describing ecosystems can also be complex. For example, individual-based modelling has led to the development of the Madingley model, which describes the global dynamics of the biomass of terrestrial and marine ecosystems<sup>35</sup>. Similarly, end-to-end ecosystem models attempt to capture most ecosystem components and processes in some way<sup>36</sup>. In these instances, however, models that aim to represent a large portion of an ecosystem are necessarily coarse in their representation of some components, such as using functional groups rather than individual species. At more constrained scales, considering only planktonic parts of a system, nitrogen–phytoplankton–zooplankton–detritus (NPZD) ecosystem models are one example that links the concentration of each of these ecosystem components through dynamic equations<sup>37</sup>. The strength of these techniques lies in their ability to use sequences of direct causal pathways, to reveal indirect interactions between ecosystem elements and propagate single events through to multiple consequences (for example, extinction or trophic cascades). For instance, Bayesian belief networks that are parametrized using expert judgement, experimental and field data can be used to represent the current understanding of an ecosystem and inform adaptive management<sup>38</sup>. Smaller-scale models (like the NPZD or models of intermediate complexity) can also be run quickly — even effectively in near real time for response and day-to-day operational management.

Just as capabilities differ between approaches, each model type has different limitations. For example, Bayesian belief networks cannot easily represent the feedback loops that are crucial for maintaining ecosystem equilibria, or for generating cyclical dynamics (for example, predator–prey cycles). The lack of feedback loops means that they have limited capacity to model complex systems, compared with larger end-to-end models that account for feedbacks as well as multiple ecosystem states and scales but are computationally expensive (Fig. 1).

**Objective 2: Forecast or hindcast scenarios.** Making predictions about ecosystems and their components under possible past, future or novel scenarios is a key goal for many ecosystem models — particularly in relation to disturbance trajectories or management regimes<sup>39</sup>. The models typically do this by inputting estimates of future or historical conditions (such as weather, productivity, disturbance) and extrapolating model outputs to these conditions. For example, Lester and Fairweather<sup>40</sup> used state-transition models of an estuarine ecosystem to predict how disturbances and water-quality perturbations could shift the system into different biotic assemblage states. The same method was then applied to predict the outcome of whole-of-ecosystem perturbations, such as climate change and anthropogenic water extraction<sup>41</sup>. Ecosystem forecasting has been used widely in fisheries management<sup>42</sup>, using approaches such as mass balance models (for example, Ecopath<sup>43</sup>) and individual-based models to forecast the productivity of individual fisheries<sup>44</sup>, through to multi-model projections of spatially resolved fish biomass at global scales under alternative climate change scenarios<sup>26</sup>. Tulloch et al.<sup>45</sup> used a ‘model of intermediate complexity for ecosystem assessment’ (known as MICE) paired with climate change scenarios to forecast the effects of climate change on baleen whales due to reduced prey availability. Ecosystem modelling approaches are useful to assess the expected trajectory of ecosystem condition and function or the risk of ecosystem collapse under the International Union for Conservation of Nature (IUCN) Red List for Ecosystems criteria<sup>46</sup>; and interaction network analysis has been used to explore the role of humans in ecosystems, including hindcasting with

historical datasets (for example, the removal of First Nations People from food webs in Australia after European contact<sup>47</sup>).

Extrapolation into new scenarios is likely to require predictions outside the scope of model parameters, which can be highly uncertain<sup>17,48</sup>. Thus, to avoid misinterpretation, modellers must be explicit about the assumptions being made about those parameters and their uncertainty. Failing to communicate these uncertainties when forecasting or hindcasting ecosystems can lead to misinformed management decisions. For example, forecasts of northern cod stocks in Newfoundland, Canada, were overestimated owing to inflated abundance estimates, leading to substantial overfishing and subsequent collapse of the fishery<sup>49,50</sup>. Similarly, there are unknowns regarding how species will respond to future combinations of environment state, anthropogenic stress and climate<sup>39</sup>, as well as changes in ecosystem structure and composition as new species mixes arise with differential shifts in species distributions<sup>51</sup>. These ecological shifts and responses have led to an increasing need for models that account for range-extending invaders (or extirpations) and parameters that are allowed to change along spatial or temporal gradients<sup>52</sup>. As dynamic approaches are new and computationally challenging, more tractable approaches have been paired with scenario analysis techniques that draw parameter estimates from probability distributions to understand the likelihood of different ecosystem states<sup>53,54</sup>. Approaches that allow for this kind of future-casting are useful because they can aid in the identification of the potential causal pathway that led to an undesired state, provided that uncertainty is explicitly dealt with and allowed to propagate through to model predictions<sup>55,56</sup>.

**Objective 3: Decide on management actions.** Evaluating alternative management strategies is a fundamental component of environmental and conservation decision-making<sup>57</sup>, which has been adopted in fields such as fisheries management and strategic planning (Box 2). Ecosystem models that are able to meet this objective have two abilities: (1) to incorporate or compare multiple management options (that is, anthropogenic processes), and (2) to evaluate each option against a clearly defined objective, such as improving the sustainability or profitability of particular catchments or minimizing a species’ probability of extinction<sup>43,44</sup>. Many management decisions are informed by very complex models, with end-to-end ecosystem models<sup>16</sup>, ensemble ecosystem models<sup>17</sup>, individual-based models and MICE regularly used to guide decisions<sup>58</sup>. One approach to informing decisions based on process-based simulations of one or more system operating models is management strategy evaluation<sup>59</sup>, which Edwards et al.<sup>60</sup> used to determine sustainable quotas for a trophy-hunted lion population. Management strategy evaluation approaches that incorporate ecosystem models have been used extensively in fisheries and have incorporated multiple model types — from extended single-species models, such as modelling stock population dynamics to determine reef line fishing priorities in the Great Barrier Reef region in Australia<sup>61</sup>, to MICE<sup>45</sup>, through to end-to-end models<sup>44</sup>.

Simple ecosystem models of interacting species and limited sets of other ecosystem components, often based on predator–prey dynamics (for example, Lotka–Volterra models), can guide management decisions where a small number of species interact very strongly<sup>62,63</sup>. Computational qualitative modelling<sup>64</sup>, qualitative loop analysis<sup>30,65</sup> and ensemble ecosystem modelling<sup>66</sup> are techniques that can be used to identify which ecosystem components are most important to manage, for the persistence of important species for a given length of time<sup>39</sup>. Bayesian belief networks have been used to test the outcomes of alternative scenarios of ecosystem perturbation, often combined with process-based models of key ecosystem components<sup>67,68</sup>. Evaluating management strategies — rather than predicting ecosystem outcomes — can sometimes avoid the challenges of parameter uncertainty and inaccurate predictions.

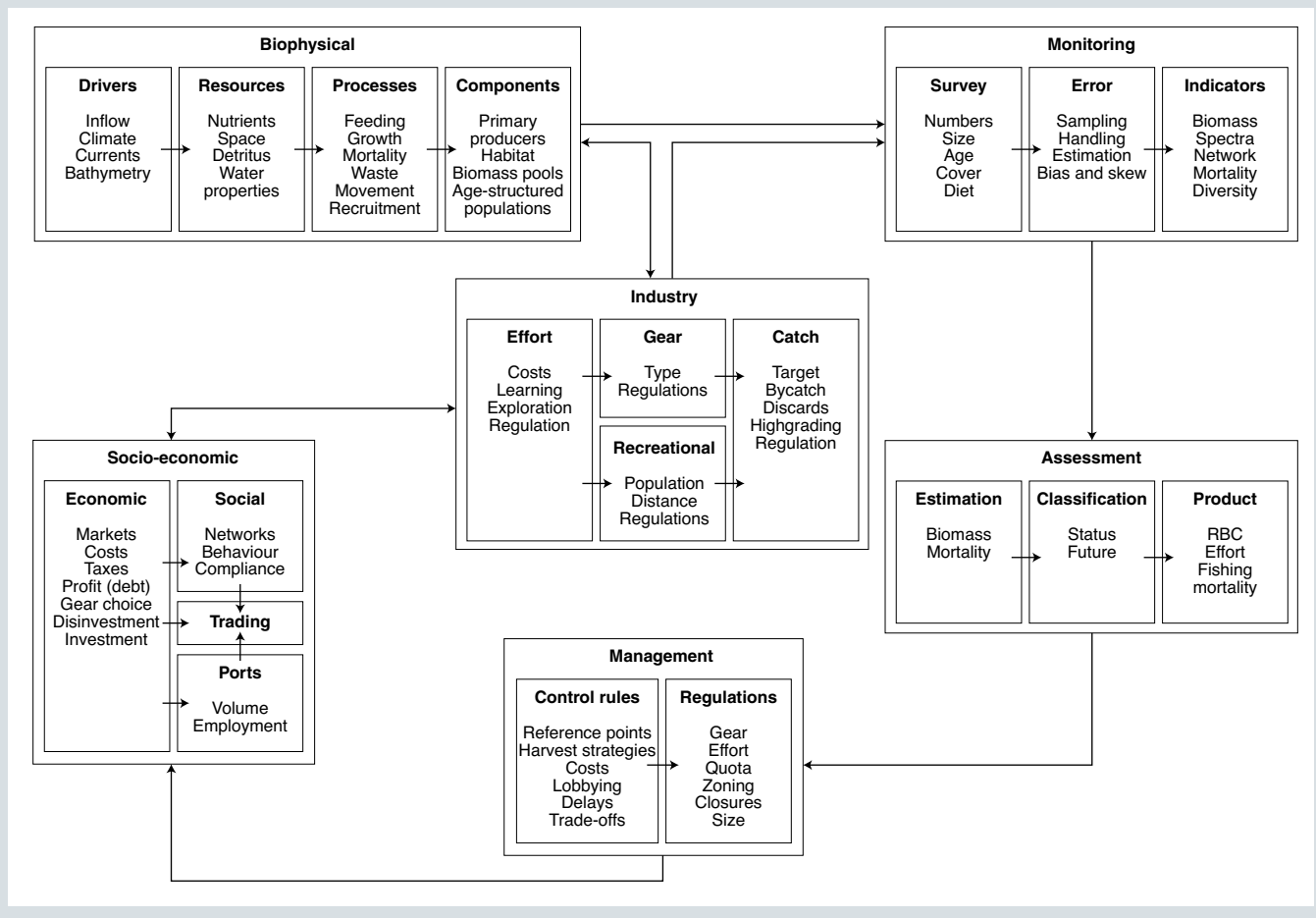
**Box 2 | End-to-end ecosystem models and their application in fisheries management**

End-to-end ecosystem models attempt to include all the major parts of ecosystems — biophysical, economic and social. Atlantis is a deterministic whole-of-ecosystem model used to support marine ecosystem-based management, system understanding and management strategy evaluation<sup>54</sup>. The simulation framework is based on modelling each part of the adaptive management cycle, through dynamic, two-way coupling of all system components (see figure for a conceptual illustration; modified from Fulton et al.<sup>36</sup>; RBC, recommended biological catch).

Atlantis models are used for strategic insight into system function and the consequences and potential trade-offs associated with different combinations of management strategies, providing information for strategic planning and decision support. Owing to the complexity of such models, they are generally inappropriate for use as tools for setting tactical management measures such as quotas, as absolute values are far less reliable than the patterns and relative distributions produced.

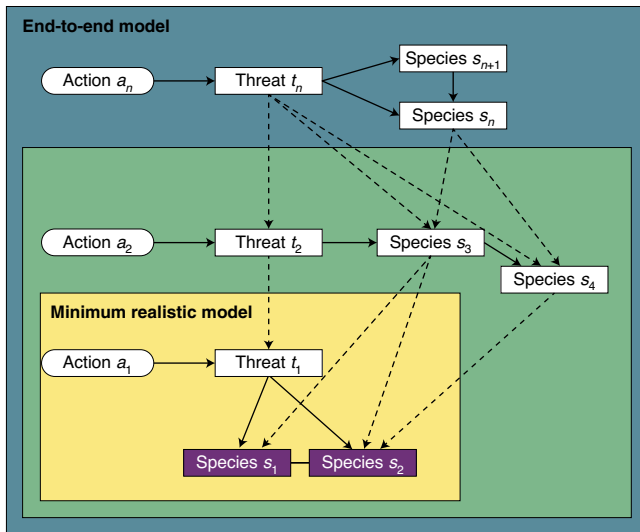
A good illustrative example comes from Atlantis-SE<sup>44</sup>, which was used as the basis for a whole-of-ecosystem management strategy evaluation (MSE) in support of a strategic restructuring of southeast Australian federal fisheries. This study developed and tested ecosystem-based management solutions for a complex of multispecies and multi-gear fisheries to predict ecosystem-scale responses to the consequences of alternative management scenarios. Strategies focused on different types and combinations of management including alternative quota management, spatial management and gear controls. MSE allowed quantitative comparison of the different future management scenarios: although no single management scenario outperformed the others across all ecological and economic objectives, outputs showed that successful management of such large and complex fisheries requires trade-offs to balance various input, output and technical management levers<sup>44</sup>.

MSE outputs were not intended to be prescriptive management advice, rather used as a decision-support for understanding potential futures of the ecosystem given different scenarios. The model is one of the most complex dynamic ecosystem models for fisheries ever developed, with uncertainty a crucial consideration — the quantitative MSE was performed across a bounding set of parameters that covered the range of plausible biomasses and dynamics. Structural uncertainty was minimized through the use of network analysis tools in developmental stages of the project, but human behavioural uncertainty produced unanticipated outcomes of management decisions. The whole-of-fishery and whole-of-ecosystem scale approach not only helps to highlight key processes requiring further study, but also, and most importantly, identifies integrated rather than piecemeal solutions to complex fishery management problems.



Decision theory holds that it is generally easier to rank a finite set of outcomes (that is, choose the best management action) than it is to accurately predict any one of those outcomes<sup>69</sup>.

**Spatial and temporal patterns.** Representation of spatial and temporal patterns is a relatively common feature of ecosystem models. Temporal patterns are common in all but the simplest ecosystem



**Fig. 2 | Varying levels of ecosystem model complexity.** Conceptual illustration of varying levels of ecosystem model complexity for an ecosystem model with an objective of maximizing the abundance of species  $s_1$  and  $s_2$ . Solid lines indicate interactions that occur between ecosystem components in a single level of the model; dashed lines indicate interactions between components across model levels. A minimum realistic model considers only the species, threats and actions (and the interactions between them) that directly influence the objective species ( $s_1$  and  $s_2$ ) (solid lines). Components can then be added to the ecosystem model that have increasingly distal interactions with the objective, building a model with increased complexity. Some components could represent individual species, and some could represent groups of species or other ecosystem components. An 'end-to-end' or 'whole-of-ecosystem' model would consider all components and interactions that occur in an ecosystem.

models (for example, conceptual models) and typically represent the outcomes of interactions between different components over time. This is regularly done using coarse representations, such as a limited number of non-descript time steps seen in fuzzy cognitive mapping<sup>31</sup> or state-transition models<sup>70</sup>. At the other end of the spectrum, models of intermediate complexity and end-to-end ecosystem models can incorporate and provide outputs at much finer temporal resolutions (for example, hours, days, months or years).

Although spatially explicit ecosystem models are relatively few, spatial heterogeneity in ecosystems is an important consideration for management decisions, even in simple systems<sup>71</sup>. For example, the CORSET ecosystem modelling approach successfully combines spatially explicit connectivity modelling and dynamic interactions between trophic levels to inform coral reef management<sup>72</sup>. Spatially explicit approaches that can incorporate interactions between ecosystem components, such as spatially explicit population dynamic models<sup>73</sup>, are increasingly applied to this objective. Fordham et al.<sup>74</sup> used metapopulation models to forecast Iberian lynx spatial distribution and likelihood of extinction under climate change, accounting for trophic interactions (for example, prey availability and disease dynamics). Individual and agent-based models are also regularly used to answer similar questions, incorporating ecosystem components such as functional groups<sup>35</sup> or species<sup>75</sup>.

**Ecosystem components.** Ecosystem models can be built to represent ecosystem components at a range of resolutions, including in the same model. Models used in fisheries management (for example, EcoPath, Atlantis) regularly use a mix of functional groups along with detailed species-level representations (which may include explicit size and age classes), as this guides decisions around specific

fishing quotas within a broader ecosystem or food-web context. Individual-based and population dynamics models are increasingly used to build whole-ecosystem models where species-scale predictions are required, but their use is more labour-intensive as they require demographic and behavioural information (such as dispersal, home range, birth rates and death rates) about all species modelled<sup>76,77</sup>, as well as information about the pairwise interactions between all species. They are also often very computationally expensive (struggling if they reach high numbers of agents), which can hamper their application.

Where high-resolution data are not available, or the questions being asked of the model do not require species-specific answers, ecosystem components can be represented as broader groups. For instance, biomass pool representations, functional or taxonomic groups, or whole-of-ecosystem condition scores are commonly used to represent ecosystem components. Techniques such as individual-based models and mass-balance models regularly represent ecosystems as functional groups. Other models only report generalized ecosystem condition scores. For example, state and transition models of grassland ecosystem condition have married both expert-elicited estimates and field-collected data to inform management<sup>70</sup>. The choice of how to represent each component in an ecosystem should be determined by two considerations: the objective of the model and the availability of data at the appropriate resolution.

**Ecosystem processes.** Models regularly include ecological processes that influence ecosystem trajectory and alternating states (dynamics), particularly interactions between individuals of different species (for example, trophic dynamics), dispersal, perturbations that impact individual components (for example, management interventions) or the entire ecosystem (for example, large disturbances). For example, climatic regimes and trophic interactions are fundamental components of marine and freshwater ecosystem models (such as MICE or end-to-end models; Fig. 1)<sup>45,78</sup>. Despite this, coupling trophic interactions with other environmental components to create models of terrestrial ecosystems has not been widely adopted<sup>35,39</sup>. However, dynamic global vegetation models have recently been linked with population models of grazers to predict long-term trends in vegetation<sup>79</sup>. So far, the models that regularly combine trophic interactions and other environmental components include MICE, ensemble ecosystem models and structural equation models (Fig. 1). This is an important step forward, as modelling food webs can provide considerable insight into improving the understanding and management of ecosystems<sup>80,81</sup>, especially when considered in tandem with other processes such as climate dynamics<sup>82,83</sup>.

Perturbations are fundamental processes in ecosystems, and those caused by humans are increasingly important<sup>84,85</sup>. Consequently, incorporating anthropogenic effects into models of socio-ecological systems is becoming more common, and most often these effects are represented as human-induced stressors and the actions undertaken to combat them<sup>86,87</sup>. Therefore, modelling techniques that allow for the inclusion of single-node perturbations and whole-of-ecosystem perturbations are of increasing utility. Including perturbations allows modellers to go beyond simply understanding ecosystems and predicting future ecosystem states, to making comparisons between alternate management scenarios and identifying optimal management regimes. Ideally, such scenario analysis or comparison of management strategies will involve explicit consideration of the costs of management<sup>88</sup>. Given the increasing influence of humans on ecosystems, being able to incorporate anthropogenic effects will also increase a model's realism<sup>9</sup>.

### Matching model complexity with applications

Ecosystem models, by definition, are required to have a reasonable level of complexity. This is particularly true when the objectives of

model building extend beyond simply understanding the ecosystem in question. With increasing computational power and data collection capacity (field, and expert-based), there are a growing number of approaches that can straddle a combination of the aforementioned objectives. Despite this, models that aim to capture as much complexity as possible tend to sacrifice utility and tractability, as model outputs can be uncertain and difficult to interpret<sup>25</sup>. Therefore, careful consideration of the number of ecosystem components included is required<sup>89</sup>, particularly given that increased model complexity results in reduced predictive capacity<sup>90</sup>. Whole-of-ecosystem models are most useful for long-term strategic planning<sup>44</sup> but are less useful for directing management strategies at operational scales (for example, year to year) which require more accurate predictions. MICE attempt to operationalize ecosystem models for tactical management by balancing these two objectives — principally by focusing only on those ecosystem components and scales relevant to a particular decision context and undertaking rigorous model fitting<sup>91</sup>.

Ecosystem model development therefore requires a balanced complexity approach, in which the model being developed is only as complex as the modelling objective requires and the available data allow. Minimum realistic models attempt to model the fewest ecosystem components and processes directly related to the model objective (Fig. 2)<sup>92</sup>. Such a model may have considerable structural uncertainty, due to missing ecosystem components, but will have minimized parameter uncertainty, and this partitioning of uncertainty will be acceptable for particular situations (for example, tactical or operational management decisions<sup>93</sup>). For example, Pesendorfer et al.<sup>94</sup> used ensemble ecosystem models to evaluate the optimal management of seed dispersal mechanisms to aid oak recovery in the Channel Islands. Although the model could have incorporated many additional ecosystem components, it focused only on the key structural and process elements (for example, dispersal dynamics of oak seeds) required to answer the management problem with enough certainty. Decisions to include particular ecosystem components and the spatial and temporal scales to model should be guided by the management objective and model capacity (for example, number of components, data availability)<sup>95</sup>, focusing on the components being directly affected by an action or related to the objective of an action<sup>96</sup>. In instances where a parameter is known to be important but has large uncertainty, models that can be parametrized using expert elicitation in a Bayesian framework or structural sensitivity analyses may be of use (see section 'Dealing with uncertainty'). In many instances, a complementary set of minimum realistic models is preferable to constructing a single, highly complex ecosystem model that captures all desired components and processes<sup>25</sup>. Each minimum realistic model can then be explored using structural sensitivity analyses that sample across structurally different, but equally complex models to assess the impact of structural uncertainty on model predictions.

For situations in which the objective is also to consider a broader set of components and processes (for example, predator–prey interactions across multiple trophic levels, single-node and whole-of-ecosystem perturbations; Fig. 1), a more complex model with increasingly distal processes and components is necessary. The Atlantis end-to-end ecosystem model is an example of this, as it incorporates many types and scales of interactions (for example, predator–prey, and human–species) to inform strategic, long-term management decisions (Box 2). In this instance, adding to the model complexity will reduce the structural uncertainty (as more of the ecosystem is represented). However, structurally complex models are difficult to parametrize and so can have considerable parameter uncertainty. Predictions and outputs may need to be made at a coarser resolution to ensure that model complexity and utility are balanced. In practice, this might mean aggregating species into functional groups or reducing the spatial and temporal

resolution of the model. This may be an acceptable trade-off when only a conceptual or qualitative illustration of the system is required (that is, strategic questions pertaining to the general form of management to use).

Emerging modelling techniques and increasing computational power allow increasingly complex ecosystem models with fine-resolution outputs to be built, meaning the trade-off between model complexity and tractability is becoming less restrictive (though modellers should still be careful to consider model content carefully rather than becoming complacent or including model components 'just because they can'). Instead, predictions made by ecosystem modellers are most likely to be limited by the data available to parametrize or constrain model outputs<sup>97,98</sup>. Two recent examples suggest that even with long-term monitoring data available to constrain ecosystem model outputs, model predictions remain highly uncertain due to the noise inherent in field datasets<sup>17,90</sup>. Therefore, minimum realistic models and MICE may remain the best approaches to achieve balanced complexity, particularly in tactical management situations that require relatively precise predictions. These trade-offs have seen the emergence of techniques that are hybrids of some of the methods outlined in Fig. 1. For example, 'Islands DSS' incorporates population dynamics models with conservation planning to help to prioritize invasive species management on islands, while also incorporating temporal dynamics<sup>99</sup>. However, even such hybrid methods can be difficult to parametrize. Smart use of hybrid approaches can make the representation of a whole system much easier — by representing the different components of a system 'in their native currency' and focusing on key scales and processes for that component, rather than shoe-horning the diversity of an ecosystem into one formulation.

Ongoing research effort should be given to targeted data collection for model parametrization. However, environmental and conservation decisions often cannot wait for new data. Alternative methods for learning, imputing or inferring components and processes with sparse data that allow managers to act without waiting for more data are crucial<sup>90,98</sup>. This might mean settling for models that have complex structures but give only the direction of parameter outputs<sup>31</sup>, rather than precise estimates, or using management strategy evaluation approaches to rank scenarios. However, developing models that can incorporate complex ecosystem dynamics in a temporally and spatially explicit manner is also highly desirable<sup>100</sup>. One means of allowing more complex end-to-end representations and relatively fine spatial resolutions is to make use of general ecological principles such as size spectra, which have been found to be a unifying description of many key ecological processes<sup>101,102</sup>. Another approach is to incorporate adaptive management techniques such as Markov decision processes that incorporate non-stationary transition models<sup>103</sup>. Most importantly, balanced complexity is best achieved when ecosystem models are developed to answer well-defined management problems, and where model outputs are well matched to the decision context<sup>30</sup>.

### Dealing with uncertainty

Ecosystem models trade off three key qualities — generality (can the model be applied to a variety of scenarios?), realism (does the model realistically reflect the target ecosystem?), and accuracy and precision (do the model outputs have a high degree of certainty?)<sup>29</sup>. Uncertainty is a fundamental component of managing complex systems, and therefore good ecosystem models must allow for and embrace it<sup>89,104</sup>. The field of near-term ecological forecasting provides a robust framework for achieving this, by explicitly partitioning different types of uncertainty and iteratively updating model parameters by validating near-term forecasts with observations<sup>105</sup>.

Ecosystem models can make uncertainty more explicit by identifying key sources and consequences of it. For the purposes of this Review, we identify four distinct types of uncertainty: parameter,

**Table 1 | Recommended strategies for explicitly considering and dealing with different types of uncertainty in ecosystem modelling**

Uncertainty source and type	Definition	Suggested strategies according to degree of uncertainty		Applied case studies
<b>Inputs</b>				
Parameter	Uncertainty related to quantifying the input parameters (for example, interaction coefficients, initial value estimates) from actual observed data, or uncertainty about the observations (for example, sources such as field-collected data compared with expert judgements or guesses)	High	Parameter sensitivity analysis using emulator-based approaches <sup>127</sup> Formal model skill assessment <sup>117</sup> Bootstrap resample from uncertain parameter distributions and show model predictions as distributions <sup>128</sup>	Ensemble ecosystem models <sup>90</sup> Emulator-based ecosystem models <sup>127</sup> Management strategy evaluation <sup>129</sup>
		Medium	Propagate all input uncertainty through to generate prediction envelopes Fit model to data, parameter estimation Reference sets of alternative models	Models of intermediate complexity <sup>58,130,131</sup> Management strategy evaluation <sup>57</sup>
		Low	Formal model skill assessment <sup>117</sup>	Reporting of model skill metrics <sup>117</sup>
Process	Uncertainty caused by the inherent variation and stochasticity present in ecosystems	High	Ensembles of ecosystem models that use a variety of structural assumptions and/or modelling methods	Models of intermediate complexity <sup>91</sup> Bayesian belief networks
		Medium	Explicitly simulate stochasticity in model inputs using a defined distribution of stochastic processes	Stochastic simulation modelling <sup>74</sup> CORSET biophysical model <sup>72</sup> Multispecies stochastic dynamic programming <sup>132,133</sup> Management strategy evaluation
		Low	Typically captured in other uncertainty handling (for example, parameter, structural, scenario)	Not applicable
Model/ structural	Uncertainty related to the structure of the ecosystem model, including: Model components Specific model interactions (that is, links between components) Shape of function describing model interactions	High	Build ensembles of ecosystem models with different structural assumptions (across modelling philosophy, formulations used and ecosystem connections)	Ensembles of models with different structural assumptions Structurally morphing models <sup>134</sup>
		Medium	Scenario analysis: identify and simulate multiple potential model structures, and contrast the predictions in a common format (for example, on a single set of axes) Trial different model formulations within the one modelling approach/software (and using one ecosystem interaction network/food-web structure) Consider multiple model configurations (that is, ecosystem interaction networks)	Management strategy evaluation <sup>135</sup> Atlantis <sup>36</sup> EcoPath with Ecosim <sup>136</sup> Models of intermediate complexity <sup>131</sup>
		Low	Evaluate whether the model provides ecologically plausible results under a discrete set of scenarios (for example, perturbations)	Any model with quantifiable outputs should be able to do this
<b>Outputs</b>				
Future/ scenario	Uncertainty related to the predictions made by the forecasts or hindcasts of the ecosystem model (for example, confidence intervals), including uncertainty about future conditions (for example, climate change, unknown future human decisions). Often a result of propagated uncertainty from input parameters	High	Build ensembles of ecosystem models across multiple scenarios. Sensitivity analysis/Markov chain Monte Carlo simulations to understand distribution of possible futures Explore a wide range of future conditions using scenario analysis	Ensemble ecosystem models <sup>39</sup> Emulator-based ecosystem models Models of intermediate complexity <sup>45,137,138</sup> Structural equation models <sup>82</sup>
		Medium	Explore a discrete set of future conditions using scenario analysis Management strategy evaluation	Structural equation models <sup>139</sup> Bayesian belief networks <sup>140</sup> Fuzzy cognitive maps <sup>31</sup>
		Low	Report results only in terms of how they vary across one other dimension of uncertainty (for example, parameter sensitivity analysis)	Any modelling approach with quantifiable outputs should be able to do this



process, model/structural, and future uncertainty (Table 1). Some ecosystem models (such as conceptual models) do not explicitly consider uncertainty, thereby potentially giving a false sense of precision<sup>106</sup>. Given the inherent complexity of ecosystems (for example, many components and nonlinear interactions) and the limited and noisy nature of ecological data, in some instances ecosystem models may never be able to make predictions with sufficient certainty<sup>17,107</sup>. Irrespective of this, ecosystem models must be explicit about their uncertainty. In Table 1, we provide some recommended strategies and modelling approaches for dealing with this uncertainty. This includes, where possible, fitting or constraining models to real-world data<sup>17,54</sup>, building ensembles of models and identifying where they converge on common predictions<sup>108</sup>, and ensuring models have capacity to test the sensitivity to input parameters and/or alternative model structures, through the use of techniques such as Monte Carlo simulations<sup>109</sup>.

Because resolving uncertainties frequently requires further research, data collection or adaptive management that learns through action, it is often useful to conduct a priori analyses to determine which uncertainties are most important to resolve or account for. One approach to this is reviewing the dominant sources of uncertainty in similar (methodologically and/or ecologically) models<sup>105</sup>. However, to make this possible, increased investment in standardized, public reporting of ecosystem models is required. Another is using expert elicitation and/or existing data to quantify the expected improvement in the decisions made (for example, through value-of-information analysis) by resolving specific uncertainties<sup>110,111</sup>. Despite their benefits for informing knowledge acquisition, value-of-information analyses are rarely done at an ecosystem level but are more commonly applied to socio-ecological networks<sup>96</sup>. Hybrid, multi-scale ecosystem modelling methods are well suited to dealing with these challenges as they can use complementary methods to incorporate and combine disparate forms and scales of data<sup>112</sup>, such as species information (abundance time-series estimates), interaction rates (for example, diet analysis), and responses to environmental perturbations (for example, fire or drought).

Building ecosystem models that both adequately describe and predict nonlinear ecosystem dynamics is difficult and sometimes not possible. This is mostly driven by large data needs and a requirement from managers to answer highly specific (for example, species-level) questions, rather than more broad questions. As an example, Baker et al.<sup>17</sup> aimed to predict the impact of eastern quoll reintroduction on eastern bristlebird abundance in Booderee National Park, Australia, but found that their predictions were highly uncertain owing to multiple plausible interaction pathways. To illustrate this further, in Box 3 we present the results of simulated dingo management on the simple network described by Wallach et al.<sup>113</sup>, showing that model predictions become more uncertain as distance from the direct management action increases. As a consequence, most conservation decision problems will need to acknowledge and deal with some uncertainty and therefore risks of unexpected outcomes<sup>114</sup>.

Identification of where key knowledge gaps exist can also be achieved through ecosystem modelling approaches<sup>110</sup>. Important uncertainties can be paired with qualitative descriptions of ecosystems, using expert judgement to infer where knowledge gaps occur and also those that are most relevant for decision-making<sup>115</sup>. This needs to be done carefully because of the difficulty of considering multiple parameters simultaneously, and the nonlinearities of feedbacks. Ecosystem models can also be analysed to identify information gaps by using parameter or structural sensitivity analyses, information theory, and other techniques to identify the model parameters or structural elements that are most uncertain, or which have the greatest influence on management decisions, and therefore where further data collection is required<sup>39,54</sup>.

## Validating and refining ecosystem models

Ecosystem models are inherently difficult to validate, as optimal experimental designs for complex models could require many different treatment and control combinations, and considerable temporal and spatial (geographic) dimensions. Therefore, other approaches (such as 'inverse methods') that derive a parameter space from mathematical models and observed data are required<sup>90,116</sup>. Model skill assessments — testing the ability of ecosystem models to successfully make predictions — is emerging as a best-practice technique in marine fields and involves testing model hindcasts and forecasts against survey data<sup>117</sup>. When being used to inform decision making, model skill assessment should be targeted at the ecological components and processes most relevant to the decision context. Given that information uncertainty can influence outputs from conservation decision-support analyses<sup>118</sup>, this is a valuable component of some ecosystem modelling approaches (Table 1). Some sources of parameter uncertainty are best addressed by refining and validating ecosystem models using experimental or field-collected data (for example, resolving linked species' responses to natural disturbances through long-term monitoring of population dynamics that covers a range of environmental conditions<sup>119</sup>). This is particularly pertinent when the modelling objective requires explicit consideration, and therefore data on particular ecological processes. Structural uncertainty can be addressed through ecosystem manipulation or adaptive management (for example, node exclusion or removal experiments<sup>120</sup>), which can also improve parameter estimates (or plausible ranges) for models if supplemented by long-term monitoring<sup>121</sup>.

Some ecosystem models can explicitly identify sources of uncertainty, owing to their ability to partition the variance from different errors (for example, process versus observation<sup>122</sup>). Such models become intractable with very large state spaces. For very complex ecosystems, an easier approach for identifying the ecological components to which a decision problem is most sensitive is to pair ecosystem models with other decision theory practices. These range from structured decision making to management strategy evaluation, adaptive management and value of information analysis<sup>115</sup>. Value of information analysis is most useful when the relative expected value of new information is expressed in the units of the conservation objective, and in terms of its influence on a conservation decision<sup>111</sup>. For example, to what extent will improving our understanding of a given ecosystem component or process allow us to choose between two alternative decisions, and thereby reduce a target species' probability of extinction<sup>110,123</sup>?

Ensembles of models have been used in ecology, fisheries and other fields such as economics to navigate uncertainty, particularly in forecasting attempts<sup>124</sup>. Making inferences from multiple models can be advantageous, especially when two different approaches give contrasting results<sup>125</sup>. For example, Spence et al.<sup>108</sup> use a Bayesian framework for combining predictions from five separate ecosystem models on the impacts of cessation of fishing in the North Sea on the biomass of demersal fish species. Ensembles of ecosystem models have been used to predict the impacts of reintroductions on ecosystems in Australia where interactions between multiple components are uncertain<sup>17</sup>, and could be expanded to consider the impacts of other environmental perturbations (for example, fire). In particular, corroborating predictions using multiple modelling methods can be a powerful tool for reducing uncertainty in decision making<sup>126</sup>.

## Concluding remarks

Modelling is a central component of understanding and managing ecosystems<sup>20</sup>. As a result, there is an impetus for ecologists and managers to ensure that the modelling approach is appropriate for the decision or management problem, and its social and ecological constraints. These challenges mean that hybrid modelling approaches that explicitly consider different forms of uncertainty are becoming

**Box 3 | The propagation of uncertainty through ecosystem models**

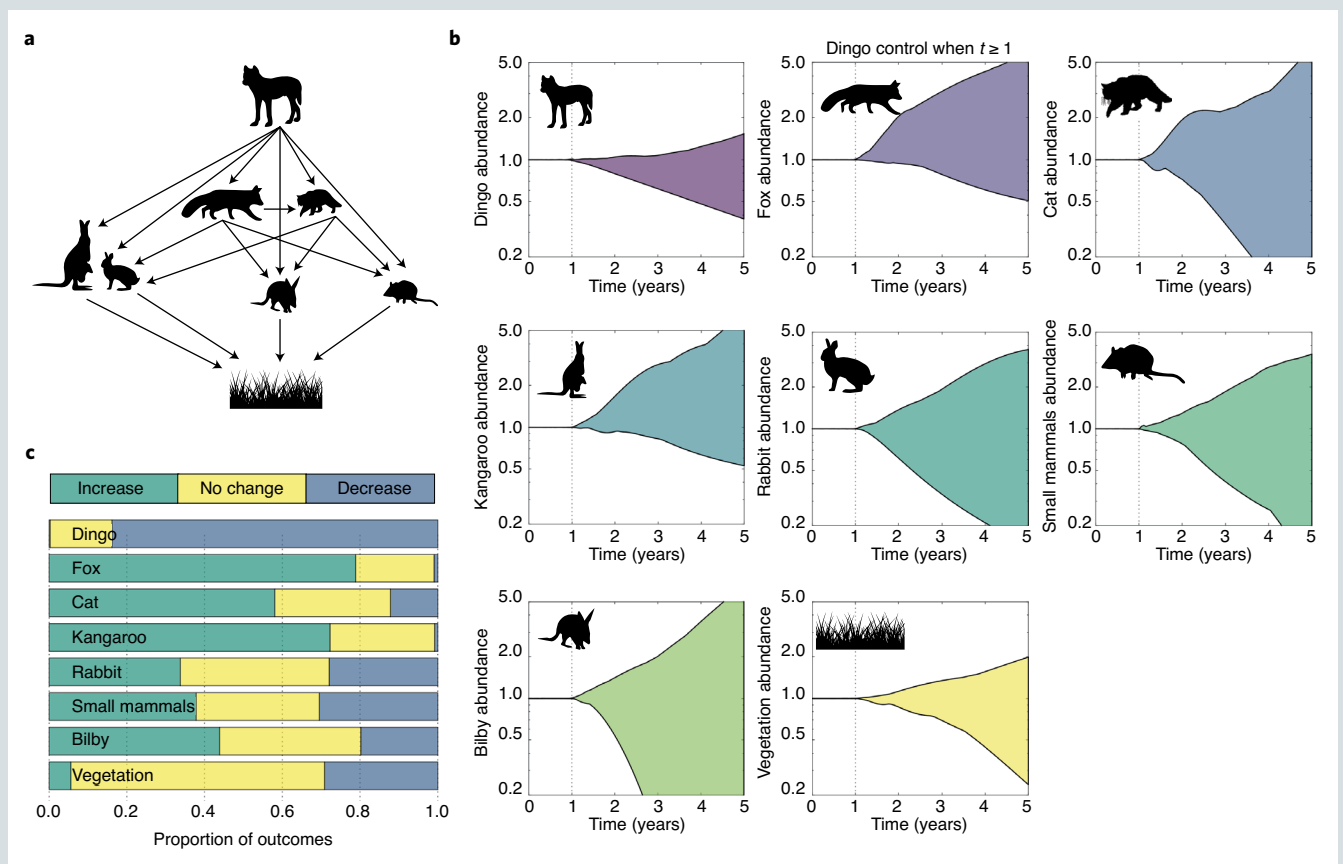
Ecosystems are complex and multi-dimensional, with many possible interaction pathways and permutations. Building models that accurately describe and predict nonlinear ecosystem dynamics for management can be very difficult, particularly when data are sparse (as is commonly the case). As the complexity of an ecosystem model increases, the number of interactions (and therefore the number of free parameters) will tend to increase as the square of the number of species being modelled.

To illustrate how this uncertainty can make predictions challenging, we built an ensemble ecosystem model, based on the network described in Wallach et al.<sup>113</sup> (panel a of the figure). The network is made up of eight species and species groups: the dingo, red fox, feral cat, kangaroo, bilby, a generic small mammal (for example, dunnart), the European rabbit, and vegetation. We assume that our knowledge about the interactions is restricted to their sign structure (that is, we know if interactions are positive or negative, but not their strengths). Although this may sound pessimistic, it is not an unreasonable assumption. Parametrizations of microcosm ecosystems, which are spatially and temporally homogeneous, and can be replicated and accurately measured, display high uncertainty, with coefficients of variation greater than 1.

Following the methods described in Baker et al.<sup>66</sup>, we constructed an ensemble of 100,000 plausible models that share this sign structure, but where the parameters have an unknown magnitude. The ensemble members must also be able to persist with all species present (since this is the current state of the ecosystem). We then simulated the control of the dingo (*Canis dingo*), by annually removing 25% of the remaining population, and reported the range of potential outcomes of the management action from the ensemble of models. The full method and interaction matrix used to build the model is in Supplementary Information section 2.

In the absence of quantitative parameter estimates, our model ensemble cannot provide certain advice about the outcomes of control for most species in the ecosystem (panel b of the figure shows the plausible range of abundances for each species over 4 years of dingo control; time shown in years). This uncertainty propagates through the ecosystem from the point of intervention and is greatest for species one or two interactions removed from the management action. Panel c shows the proportion of ecosystems in the ensemble for which each species increases in abundance (cyan), decreases in abundance (blue) and has no change in abundance (yellow). The model offers support for the prediction that dingo control will reduce dingo abundance and lead to an increase in fox abundance. However, both changes are of an unknown and potentially negligible size. The plausible ranges of responses by feral cats, rabbits, small mammals and bilbies include both positive and negative changes in abundance over the five time steps (panel c).

Without careful parametrization of ecosystem models, predictions will be highly uncertain. Indeed, even with considerable monitoring data, predicting the outcomes of management actions on species and potential flow-on interactions can be difficult<sup>17</sup>. For instance, a relatively well parametrized model exploring the effects of controlling rabbits in an arid Australian ecosystem still had uncertain outcomes for bilbies<sup>63</sup>.



more prominent<sup>112</sup>. Here we have provided an overview of which techniques are likely to best match different objectives and the desired outputs. Uncertainty is a fundamental reality of managing and making decisions for complex ecological systems<sup>104</sup>. The strategies outlined in this Review, such as model skill assessment, use of multiple models and management strategy evaluation, can help modellers explicitly acknowledge and integrate uncertainty while also informing good conservation and management decisions.

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## References

- Lindenmayer, D. et al. The complementarity of single-species and ecosystem-oriented research in conservation research. *Oikos* **116**, 1220–1226 (2007).
- Skern-Mauritzen, M. et al. Ecosystem processes are rarely included in tactical fisheries management. *Fish Fish.* **17**, 165–175 (2016).
- Geary, W. L., Nimmo, D. G., Doherty, T. S., Ritchie, E. G. & Tulloch, A. I. T. Threat webs: reframing the co-occurrence and interactions of threats to biodiversity. *J. Appl. Ecol.* **56**, <https://doi.org/10.1111/1365-2664.13427> (2019).
- Buckley, Y. M. & Han, Y. Managing the side effects of invasion control. *Science* **344**, 975–976 (2014).
- Zavaleta, E. S., Hobbs, R. J. & Mooney, H. A. Viewing invasive species removal in a whole-ecosystem context. *Trends Ecol. Evol.* **16**, 454–459 (2001).
- DeFries, R. & Nagendra, H. Ecosystem management as a wicked problem. *Science* **356**, 265–270 (2017).
- Carpenter, S. R. et al. Early warnings of regime shifts: a whole-ecosystem experiment. *Science* **332**, 1079 (2011).
- Evans, M. C., Davila, F., Toomey, A. & Wyborn, C. Embrace complexity to improve conservation decision making. *Nat. Ecol. Evol.* **1**, 1588 (2017).
- Dorresteyn, I. et al. Incorporating anthropogenic effects into trophic ecology: predator–prey interactions in a human-dominated landscape. *Proc. R. Soc. B*, <https://doi.org/10.1098/rspb.2015.1602> (2015).
- Didham, R. K., Tylianakis, J. M., Gemmill, N. J., Rand, T. A. & Ewers, R. M. Interactive effects of habitat modification and species invasion on native species decline. *Trends Ecol. Evol.* **22**, 489–496 (2007).
- Brown, C. J., Saunders, M. I., Possingham, H. P. & Richardson, A. J. Managing for interactions between local and global stressors of ecosystems. *PLoS ONE* **8**, e65765 (2013).
- Peters, D. P. C. & Okin, G. S. A Toolkit for ecosystem ecologists in the time of big science. *Ecosystems* **20**, 259–266 (2017).
- Fulton, E. A. Approaches to end-to-end ecosystem models. *J. Mar. Syst.* **81**, 171–183 (2010).
- Waltner-Toews, D., Kay James, J., Neudoerffer, C. & Gitau, T. Perspective changes everything: managing ecosystems from the inside out. *Front. Ecol. Environ.* **1**, 23–30 (2003).
- Evans, M. R., Norris, K. J. & Benton, T. G. Predictive ecology: systems approaches. *Philos. Trans. R. Soc. B* **367**, 163–169 (2012).
- Smith, A. D. M., Fulton, E. J., Hobday, A. J., Smith, D. C. & Shoulder, P. Scientific tools to support the practical implementation of ecosystem-based fisheries management. *ICES J. Mar. Sci.* **64**, 633–639 (2007).
- Baker, C. M. et al. A novel approach to assessing the ecosystem-wide impacts of reintroductions. *Ecol. Appl.* **29**, <https://doi.org/10.1002/eap.1811> (2018).
- Purves, D. et al. Ecosystems: time to model all life on Earth. *Nature* **493**, 295 (2013).
- Sutherland, W. J. Predicting the ecological consequences of environmental change: a review of the methods. *J. Appl. Ecol.* **43**, 599–616 (2006).
- Seidl, R. To model or not to model, that is no longer the question for ecologists. *Ecosystems* **20**, 222–228 (2017).
- Rastetter, E. B. Modeling for understanding v. modeling for numbers. *Ecosystems* **20**, 215–221 (2017).
- Yates, K. L. et al. Outstanding challenges in the transferability of ecological models. *Trends Ecol. Evol.* **33**, 790–802 (2018).
- Schweiger, E. W., Grace, J. B., Cooper, D., Bobowski, B. & Britten, M. Using structural equation modeling to link human activities to wetland ecological integrity. *Ecosphere* **7**, e01548 (2016).
- Evans, M. R. Modelling ecological systems in a changing world. *Philos. Trans. R. Soc. B* **367**, 181–190 (2012).
- Fulton, E. A., Smith, A. D. M. & Johnson, C. R. Effect of complexity on marine ecosystem models. *Mar. Ecol. Prog. Ser.* **253**, 1–16 (2003).
- Lotze, H. K. et al. Global ensemble projections reveal trophic amplification of ocean biomass declines with climate change. *Proc. Natl Acad. Sci. USA* **116**, 12097–12912 (2019).
- Lindenmayer, D. et al. A checklist for ecological management of landscapes for conservation. *Ecol. Lett.* **11**, 78–91 (2007).
- Guillera-Aroita, G. et al. Is my species distribution model fit for purpose? Matching data and models to applications. *Glob. Ecol. Biogeogr.* **24**, 276–292 (2015).
- Levins, R. The strategy of model building in population biology. *Am. Sci.* **54**, 421–431 (1966).
- Dambacher, J. M., Li, H. W. & Rossignol, P. A. Qualitative predictions in model ecosystems. *Ecol. Model.* **161**, 79–93 (2003).
- Baker, C. M., Holden, M. H., Plein, M., McCarthy, M. A. & Possingham, H. P. Informing network management using fuzzy cognitive maps. *Biol. Conserv.* **224**, 122–128 (2018).
- Dexter, N., Ramsey, D. S., MacGregor, C. & Lindenmayer, D. Predicting ecosystem wide impacts of wallaby management using a fuzzy cognitive map. *Ecosystems* **15**, 1363–1379 (2012).
- Dakos, V. & Bascompte, J. Critical slowing down as early warning for the onset of collapse in mutualistic communities. *Proc. Natl Acad. Sci. USA* **111**, 17546–17551 (2014).
- McDonald-Madden, E. et al. Using food-web theory to conserve ecosystems. *Nat. Commun.* **7**, 10245 (2016).
- Harfoot, M. B. et al. Emergent global patterns of ecosystem structure and function from a mechanistic general ecosystem model. *PLoS Biol.* **12**, e1001841 (2014).
- Fulton, E. A. et al. Lessons in modelling and management of marine ecosystems: the Atlantis experience. *Fish Fish.* **12**, 171–188 (2011).
- Priester, C. R., Melbourne-Thomas, J., Klocker, A. & Corney, S. Abrupt transitions in dynamics of a NPZD model across Southern Ocean fronts. *Ecol. Model.* **359**, 372–382 (2017).
- McCann, R. K., Marcot, B. G. & Ellis, R. Bayesian belief networks: applications in ecology and natural resource management. *Can. J. Res.* **36**, 3053–3062 (2006).
- Bode, M. et al. Revealing beliefs: using ensemble ecosystem modelling to extrapolate expert beliefs to novel ecological scenarios. *Methods Ecol. Evol.* **8**, 1012–1021 (2017).
- Lester, R. E. & Fairweather, P. G. Ecosystem states: creating a data-derived, ecosystem-scale ecological response model that is explicit in space and time. *Ecol. Model.* **222**, 2690–2703 (2011).
- Lester, R. E., Fairweather, P. G., Webster, I. T. & Quin, R. A. Scenarios involving future climate and water extraction: ecosystem states in the estuary of Australia's largest river. *Ecol. Appl.* **23**, 984–998 (2013).
- Dubois, D. M. A model of patchiness for prey–predator plankton populations. *Ecol. Model.* **1**, 67–80 (1975).
- Pauly, D., Christensen, V. & Walters, C. Ecopath, Ecosim, and Ecospace as tools for evaluating ecosystem impact of fisheries. *ICES J. Mar. Sci.* **57**, 697–706 (2000).
- Fulton, E. A., Smith, A. D., Smith, D. C. & Johnson, P. An integrated approach is needed for ecosystem based fisheries management: insights from ecosystem-level management strategy evaluation. *PLoS ONE* **9**, e84242 (2014).
- Tulloch, V. J. D., Plagányi, É. E., Brown, C., Richardson, A. J. & Matear, R. Future recovery of baleen whales is imperiled by climate change. *Glob. Change Biol.* **25**, 1263–1281 (2019).
- Rodriguez, J. P. et al. A practical guide to the application of the IUCN Red List of Ecosystems criteria. *Philos. Trans. R. Soc. B* **370**, 20140003 (2015).
- Crabtree, S. A., Bird, D. W. & Bird, R. B. Subsistence transitions and the simplification of ecological networks in the Western Desert of Australia. *Hum. Ecol.* **47**, <https://doi.org/10.1007/s10745-019-0053-z> (2019).
- Plaque, B. Projecting the future state of marine ecosystems, “la grande illusion”? *ICES J. Mar. Sci.* **73**, 204–208 (2015).
- Walters, C. & Maguire, J.-J. Lessons for stock assessment from the northern cod collapse. *Rev. Fish. Biol. Fish.* **6**, 125–137 (1996).
- García-Díaz, P. et al. A concise guide to developing and using quantitative models in conservation management. *Conserv. Sci. Pract.* **1**, e11 (2019).
- Morse, N. et al. Novel ecosystems in the Anthropocene: a revision of the novel ecosystem concept for pragmatic applications. *Ecol. Soc.* **19**, <https://doi.org/10.5751/ES-06192-190212> (2014).
- Fulton, E. & Gorton, R. *Adaptive Futures for SE Australian Fisheries & Aquaculture: Climate Adaptation Simulations* (FRDC/CSIRO, 2014).
- Kurz, W. A. et al. Mountain pine beetle and forest carbon feedback to climate change. *Nature* **452**, 987 (2008).
- Plagányi, É. E. *Models for an Ecosystem Approach to Fisheries* (FAO, 2007).
- Hunter, D. O., Britz, T., Jones, M. & Letnic, M. Reintroduction of Tasmanian devils to mainland Australia can restore top-down control in ecosystems where dingoes have been extirpated. *Biol. Conserv.* **191**, 428–435 (2015).
- Baker, C., Bode, M. & McCarthy, M. Models that predict ecosystem impacts of reintroductions should consider uncertainty and distinguish between direct and indirect effects. *Biol. Conserv.* **196**, 211–212 (2016).
- Bunnefeld, N., Hoshino, E. & Milner-Gulland, E. J. Management strategy evaluation: a powerful tool for conservation? *Trends Ecol. Evol.* **26**, 441–447 (2011).

58. Morello, E. B. et al. Model to manage and reduce crown-of-thorns starfish outbreaks. *Mar. Ecol. Prog. Ser.* **512**, 167–183 (2014).
59. Punt, A. E., Butterworth, D. S., de Moor, C. L., De Oliveira, J. A. A. & Haddon, M. Management strategy evaluation: best practices. *Fish. Fish.* **17**, 303–334 (2016).
60. Edwards, C. T. T., Bunnefeld, N., Balme, G. A. & Milner-Gulland, E. J. Data-poor management of African lion hunting using a relative index of abundance. *Proc. Natl Acad. Sci. USA* **111**, 539–543 (2014).
61. Mapstone, B. et al. Management strategy evaluation for line fishing in the Great Barrier Reef: balancing conservation and multi-sector fishery objectives. *Fish. Res.* **94**, 315–329 (2008).
62. Roemer, G. W., Donlan, C. J. & Courchamp, F. Golden eagles, feral pigs, and insular carnivores: how exotic species turn native predators into prey. *Proc. Natl Acad. Sci. USA* **99**, 791–796 (2002).
63. Lurgi, M., Ritchie, E. G. & Fordham, D. A. Eradicating abundant invasive prey could cause unexpected and varied biodiversity outcomes: the importance of multispecies interactions. *J. Appl. Ecol.* **55**, 2396–2407 (2018).
64. Raymond, B., McInnes, J., Dambacher, J. M., Way, S. & Bergstrom, D. M. Qualitative modelling of invasive species eradication on subantarctic Macquarie Island. *J. Appl. Ecol.* **48**, 181–191 (2011).
65. Levins, R. Discussion paper: the qualitative analysis of partially specified systems. *Ann. NY Acad. Sci.* **231**, 123–138 (1974).
66. Baker, C. M., Gordon, A. & Bode, M. Ensemble ecosystem modeling for predicting ecosystem response to predator reintroduction. *Conserv. Biol.* **31**, 376–384 (2017).
67. Amstrup, S. C. et al. Greenhouse gas mitigation can reduce sea-ice loss and increase polar bear persistence. *Nature* **468**, 955–958 (2010).
68. Trifonova, N., Maxwell, D., Pinnegar, J., Kenny, A. & Tucker, A. Predicting ecosystem responses to changes in fisheries catch, temperature, and primary productivity with a dynamic Bayesian network model. *ICES J. Mar. Sci.* **74**, 1334–1343 (2017).
69. McCarthy, M. A., Andelman, S. J. & Possingham, H. P. Reliability of relative predictions in population viability analysis. *Conserv. Biol.* **17**, 982–989 (2003).
70. Jamiyansharav, K., Fernández-Giménez, M. E., Angerer, J. P., Yadamsuren, B. & Dash, Z. Plant community change in three Mongolian steppe ecosystems 1994–2013: applications to state-and-transition models. *Ecosphere* **9**, <https://doi.org/10.1002/ecs2.2145> (2018).
71. Rayner, M. J., Hauber, M. E., Imber, M. J., Stamp, R. K. & Clout, M. N. Spatial heterogeneity of mesopredator release within an oceanic island system. *Proc. Natl Acad. Sci. USA* **104**, 20862–20865 (2007).
72. Melbourne-Thomas, J. et al. Regional-scale scenario modeling for coral reefs: a decision support tool to inform management of a complex system. *Ecol. Appl.* **21**, 1380–1398 (2011).
73. Briscoe, N. J. et al. Forecasting species range dynamics with process-explicit models: matching methods to applications. *Ecol. Lett.* **22**, 1940–1956 (2019).
74. Fordham, D. A. et al. Adapted conservation measures are required to save the Iberian lynx in a changing climate. *Nat. Clim. Change* **3**, 899–903 (2013).
75. Fedriani, J. M. et al. Assisting seed dispersers to restore oldfields: an individual-based model of the interactions among badgers, foxes and Iberian pear trees. *J. Appl. Ecol.* **55**, 600–611 (2018).
76. Breckling, B., Müller, F., Reuter, H., Hölker, F. & Fränze, O. Emergent properties in individual-based ecological models—introducing case studies in an ecosystem research context. *Ecol. Model.* **186**, 376–388 (2005).
77. Grimm, V., Ayllón, D. & Railsback, S. F. Next-generation individual-based models integrate biodiversity and ecosystems: yes we can, and yes we must. *Ecosystems* **20**, 229–236 (2017).
78. Walters, C., Christensen, V. & Pauly, D. Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. *Rev. Fish. Biol. Fish.* **7**, 139–172 (1997).
79. Pachzelt, A., Rammig, A., Higgins, S. & Hickler, T. Coupling a physiological grazer population model with a generalized model for vegetation dynamics. *Ecol. Model.* **263**, 92–102 (2013).
80. Pimm, S. L., Lawton, J. H. & Cohen, J. E. Food web patterns and their consequences. *Nature* **350**, 669–674 (1991).
81. Bodini, A. Reconstructing trophic interactions as a tool for understanding and managing ecosystems: application to a shallow eutrophic lake. *Can. J. Fish. Aquat. Sci.* **57**, 1999–2009 (2000).
82. Greenville, A. C., Wardle, G. M. & Dickman, C. R. Desert mammal populations are limited by introduced predators rather than future climate change. *R. Soc. Open Sci.* **4**, <https://doi.org/10.1098/rsos.170384> (2017).
83. Pasanen-Mortensen, M. et al. The changing contribution of top-down and bottom-up limitation of mesopredators during 220 years of land use and climate change. *J. Anim. Ecol.* **86**, 566–576 (2017).
84. Vitousek, P. M., Mooney, H. A., Lubchenco, J. & Melillo, J. M. Human domination of Earth's ecosystems. *Science* **277**, 494–499 (1997).
85. Bliège Bird, R. & Nimmo, D. Restore the lost ecological functions of people. *Nat. Ecol. Evol.* **2**, <https://doi.org/10.1038/s41559-018-0576-5> (2018).
86. Côté, I. M., Darling, E. S. & Brown, C. J. Interactions among ecosystem stressors and their importance in conservation. *Proc. R. Soc. B* **283**, 20152592 (2016).
87. Kuijper, D. et al. Paws without claws? Ecological effects of large carnivores in anthropogenic landscapes. *Proc. R. Soc. B* **283**, 20161625 (2016).
88. Moran, D., Laycock, H. & White, P. C. L. The role of cost-effectiveness analysis in conservation decision-making. *Biol. Conserv.* **143**, 826–827 (2010).
89. Evans, M. R. et al. Predictive systems ecology. *Proc. R. Soc. B* **280**, <https://doi.org/10.1098/rspb.2013.1452> (2013).
90. Adams, M. P. et al. Informing management decisions for ecological networks, using dynamic models calibrated to noisy time-series data. *Ecol. Lett.* **23**, 607–619 (2020).
91. Plagányi, É. E. et al. Multispecies fisheries management and conservation: tactical applications using models of intermediate complexity. *Fish. Fish.* **15**, 1–22 (2014).
92. Hui, C. & Richardson, D. M. How to invade an ecological network. *Trends Ecol. Evol.* **34**, 121–131 (2018).
93. Chadès, I., Curtis, J. M. R. & Martin, T. G. Setting realistic recovery targets for two interacting endangered species, sea otter and northern abalone. *Conserv. Biol.* **26**, 1016–1025 (2012).
94. Pesendorfer, M. et al. Oak habitat recovery on California's largest islands: scenarios for the role of corvid seed dispersal. *J. Appl. Ecol.* **55**, 1185–1194 (2017).
95. Schuwirth, N. et al. How to make ecological models useful for environmental management. *Ecol. Model.* **411**, 108784 (2019).
96. Davis, K. J., Chadès, I., Rhodes, J. R. & Bode, M. General rules for environmental management to prioritise social-ecological systems research based on a value of information approach. *J. Appl. Ecol.* **56**, <https://doi.org/10.1111/1365-2664.13425> (2019).
97. Mokany, K. et al. Integrating modelling of biodiversity composition and ecosystem function. *Oikos* **125**, 10–19 (2015).
98. Tulloch, A. I. T., Chadès, I. & Lindenmayer, D. B. Species co-occurrence analysis predicts management outcomes for multiple threats. *Nat. Ecol. Evol.* **2**, 465–474 (2018).
99. Lohr, C. A. et al. Modeling dynamics of native and invasive species to guide prioritization of management actions. *Ecosphere* **8**, e01822 (2017).
100. Nicol, S., Fuller Richard, A., Iwamura, T. & Chadès, I. Adapting environmental management to uncertain but inevitable change. *Proc. R. Soc. B* **282**, 20142984 (2015).
101. Blanchard, J. L., Heneghan, R. F., Everett, J. D., Trebilco, R. & Richardson, A. J. From bacteria to whales: using functional size spectra to model marine ecosystems. *Trends Ecol. Evol.* **32**, 174–186 (2017).
102. Andersen, K. H., Jacobsen, N. S. & Farnsworth, K. D. The theoretical foundations for size spectrum models of fish communities. *Can. J. Fish. Aquat. Sci.* **73**, 575–588 (2015).
103. Nicol, S., Sabbadin, R., Peyrard, N. & Chadès, I. Finding the best management policy to eradicate invasive species from spatial ecological networks with simultaneous actions. *J. Appl. Ecol.* **54**, 1989–1999 (2017).
104. Milner-Gulland, E. J., Shea, K. & Punt, A. Embracing uncertainty in applied ecology. *J. Appl. Ecol.* **54**, 2063–2068 (2017).
105. Dietze, M. C. et al. Iterative near-term ecological forecasting: needs, opportunities, and challenges. *Proc. Natl Acad. Sci. USA* **115**, 1424–1432 (2018).
106. Greg, E. J. & Chan, K. M. A. Leaps of faith: how implicit assumptions compromise the utility of ecosystem models for decision-making. *BioScience* **65**, 43–54 (2015).
107. Hill, S. L. et al. Model uncertainty in the ecosystem approach to fisheries. *Fish. Fish.* **8**, 315–336 (2007).
108. Spence, M. A. et al. A general framework for combining ecosystem models. *Fish. Fish.* **19**, 1031–1042 (2018).
109. Wood, S. N. & Thomas, M. B. Super-sensitivity to structure in biological models. *Proc. R. Soc. B* **266**, 565–570 (1999).
110. Runge, M. C., Converse, S. J. & Lyons, J. E. Which uncertainty? Using expert elicitation and expected value of information to design an adaptive program. *Biol. Conserv.* **144**, 1214–1223 (2011).
111. Bal, P. et al. Quantifying the value of monitoring species in multi-species, multi-threat systems. *Methods Ecol. Evol.* **9**, 1706–1717 (2018).
112. Fulton, E. A., Blanchard, J. L., Melbourne-Thomas, J., Plagányi, É. E. & Tulloch, V. J. D. Where the ecological gaps remain, a modelers' perspective. *Front. Ecol. Evol.* **7**, 424 (2019).
113. Wallach, A. D. et al. Trophic cascades in 3D: network analysis reveals how apex predators structure ecosystems. *Methods Ecol. Evol.* **8**, 135–142 (2017).
114. Ruscoe, W. A. et al. Unexpected consequences of control: competitive vs. predator release in a four-species assemblage of invasive mammals. *Ecol. Lett.* **14**, 1035–1042 (2011).
115. Bower, S. D. et al. Making tough choices: picking the appropriate conservation decision-making tool. *Conserv. Lett.* **11**, e12418 (2017).
116. Stouffer, D. B. All ecological models are wrong, but some are useful. *J. Anim. Ecol.* **88**, 192–195 (2019).

117. Olsen, E. et al. Ecosystem model skill assessment. Yes we can! *PLoS ONE* **11**, e0146467 (2016).
118. Cattarino, L. et al. Information uncertainty influences conservation outcomes when prioritizing multi-action management efforts. *J. Appl. Ecol.* **55**, <https://doi.org/10.1111/1365-2664.13147> (2018).
119. Greenville, A. C. et al. Biodiversity responds to increasing climatic extremes in a biome-specific manner. *Sci. Total Environ.* **634**, 382–393 (2018).
120. de Visser, S. N., Freymann, B. P. & Olff, H. The Serengeti food web: empirical quantification and analysis of topological changes under increasing human impact. *J. Anim. Ecol.* **80**, 484–494 (2011).
121. Curtsdotter, A. et al. Ecosystem function in predator–prey food webs — confronting dynamic models with empirical data. *J. Anim. Ecol.* **88**, 196–210 (2019).
122. Greenville, A. C., Nguyen, V., Wardle, G. M. & Dickman, C. R. Making the most of incomplete long-term datasets: the MARSS solution. *Aust. Zool.* **39**, 733–747 (2018).
123. Tulloch, A. I. T., Chadès, I. & Possingham, H. P. Accounting for complementarity to maximize monitoring power for species management. *Conserv. Biol.* **27**, 988–999 (2013).
124. Araújo, M. B. & New, M. Ensemble forecasting of species distributions. *Trends Ecol. Evol.* **22**, 42–47 (2007).
125. Bode, M., Bode, L., Choukroun, S., James, M. K. & Mason, L. B. Resilient reefs may exist, but can larval dispersal models find them? *PLoS Biol.* **16**, e2005964 (2018).
126. Tittensor, D., Coll, M. & Walker, N. D. A protocol for the intercomparison of marine fishery and ecosystem models: Fish-MIP v1.0. *Geosci. Model Dev.* **11**, 1421–1442 (2018).
127. Prowse, T. A. A. et al. An efficient protocol for the global sensitivity analysis of stochastic ecological models. *Ecosphere* **7**, e01238 (2016).
128. McGowan, C. P., Runge, M. C. & Larson, M. A. Incorporating parametric uncertainty into population viability analysis models. *Biol. Conserv.* **144**, 1400–1408 (2011).
129. Chee, Y. E. & Wintle, B. A. Linking modelling, monitoring and management: an integrated approach to controlling overabundant wildlife. *J. Appl. Ecol.* **47**, 1169–1178 (2010).
130. Plagányi, É. E. & Butterworth, D. S. The Scotia Sea krill fishery and its possible impacts on dependent predators: modeling localized depletion of prey. *Ecol. Appl.* **22**, 748–761 (2012).
131. Kinzey, D. & Punt, A. E. Multispecies and single-species models of fish population dynamics: comparing parameter estimates. *Nat. Resour. Model.* **22**, 67–104 (2009).
132. Bode, M. & Possingham, H. Can culling a threatened species increase its chance of persisting? *Ecol. Model.* **201**, 11–18 (2007).
133. Poudel, D. & Sandal, L. K. Stochastic optimization for multispecies fisheries in the Barents Sea. *Nat. Resour. Model.* **28**, 219–243 (2015).
134. Gray, R. & Wotherspoon, S. Increasing model efficiency by dynamically changing model representations. *Environ. Model. Softw.* **30**, 115–122 (2012).
135. Punt, A. E. & Hobday, D. Management strategy evaluation for rock lobster, *Jasus edwardsii*, off Victoria, Australia: accounting for uncertainty in stock structure. *N. Zeal. J. Mar. Freshw. Res.* **43**, 485–509 (2009).
136. Colléter, M. et al. Global overview of the applications of the Ecopath with Ecosim modeling approach using the EcoBase models repository. *Ecol. Model.* **302**, 42–53 (2015).
137. Angelini, S. et al. An ecosystem model of intermediate complexity to test management options for fisheries: a case study. *Ecol. Model.* **319**, 218–232 (2016).
138. Tulloch, V. J., Plagányi, É. E., Matear, R., Brown, C. J. & Richardson, A. J. Ecosystem modelling to quantify the impact of historical whaling on Southern Hemisphere baleen whales. *Fish. Fish.* **19**, 117–137 (2018).
139. Geary, W. L., Ritchie, E. G., Lawton, J. A., Healey, T. R. & Nimmo, D. G. Incorporating disturbance into trophic ecology: fire history shapes mesopredator suppression by an apex predator. *J. Appl. Ecol.* **55**, <https://doi.org/10.1111/1365-2664.13125> (2018).
140. Marcot, B. G., Holthausen, R. S., Raphael, M. G., Rowland, M. M. & Wisdom, M. J. Using Bayesian belief networks to evaluate fish and wildlife population viability under land management alternatives from an environmental impact statement. *Ecol. Manag.* **153**, 29–42 (2001).
141. Elmhagen, B., Ludwig, G., Rushton, S. P., Helle, P. & Lindén, H. Top predators, mesopredators and their prey: interference ecosystems along bioclimatic productivity gradients. *J. Anim. Ecol.* **79**, 785–794 (2010).
142. Ritchie, E. et al. Ecosystem restoration with teeth: what role for predators? *Trends Ecol. Evol.* **27**, 265–271 (2012).
143. Borsuk, M. E., Stow, C. A. & Reckhow, K. H. A Bayesian network of eutrophication models for synthesis, prediction, and uncertainty analysis. *Ecol. Model.* **173**, 219–239 (2004).
144. Christensen, V. & Walters, C. J. Ecopath with Ecosim: methods, capabilities and limitations. *Ecol. Model.* **172**, 109–139 (2004).

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### Author contributions

W.L.G. and E.G.R. conceived the ideas for the paper. W.L.G. led the writing. V.J.D.T. wrote Box 2. M.B. constructed and ran the model for Box 3. W.L.G., M.B., T.S.D., E.A.F., D.G.N., A.I.T.T., V.J.D.T. and E.G.R. all contributed to developing schematics and writing the paper.

### Competing interests

The authors declare no competing interests.

### Additional information

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