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Towards building a sustainable future: Positioning ecological modelling for impact in ecosystems management

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Abstract

As many ecosystems worldwide are in peril, efforts to manage them sustainably require scientific advice. While numerous researchers around the world use a great variety of models to understand ecological dynamics and their responses to disturbances, only a small fraction of these models are ever used to inform ecosystem management. There seems to be a perception that ecological models are not useful for management, even though mathematical models are indispensable in many other fields. We were curious about this mismatch, its roots, and potential ways to overcome it. We searched the literature on recommendations and best practices for how to make ecological models useful to the management of ecosystems and we searched for "success stories" from the past. We selected and examined several cases where models were instrumental in ecosystem management. We documented their success and asked whether and to what extent they followed recommended best practices. We found that there is not a unique way to conduct a research project that is useful in management decisions. While research is more likely to have impact when conducted with many stakeholders involved and specific to a situation for which data are available, there are great examples of small groups or individuals conducting highly influential research even in the absence of detailed data. We put the question of modelling for ecosystem management into a socioeconomic and national context and give our perspectives on how the discipline could move forward.

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1 Introduction

Edward O. Wilson said that “It’s obvious that the key problem facing humanity in the coming century is how to bring a better quality of life—for 8 billion or more people—without wrecking the environment entirely in the attempt”[1]. Many ecosystems and agro-ecosystems around the globe are disrupted (Messerli and Murniningtyas, 2019), species extinctions exceed the basic rate more than a hundred times, and crises and regime shifts are becoming frequent phenomena (Ceballos et al., 2015). Scientifically based, consistent, and sustainable ecosystem management is required to avert global disaster. We share with others the conviction that a management task of this scale and importance needs to be based on a rigorous theory and mathematical modelling (Karunaratne and Asaeda, 2002; De Lara and Doyen, 2008; Fulford et al., 2020). We say this despite a common perception that mathematical models for ecological processes are not as useful and widespread as their counterparts in other areas (Peters, 1991; Sagoff, 2016). The goal of our work is to evaluate this perception and to identify ways in which mathematical models have been, and can continue to be, instrumental in generating understanding of ecological systems in general and of sustainable ecosystem management in particular.

Mathematical models have a long and distinguished history in ecological theory and have been applied to questions of endangered species conservation (Lebreton and Clobert, 1991; Green et al., 2005; Williams et al., 2004), biological invasion (Shigesada et al., 1995; Petrovskii and Li, 2005; Lewis et al., 2016) and many others. Such models come in many different forms, from simple statistical correlation or differential equation models to complex simulation scenarios. The inherent complexity of ecological systems and processes is one reason why mathematical models are of key importance. A model can act as a ‘virtual laboratory’ (Caswell, 1988; Milton and Ohira, 2014), where hypotheses can be tested and various scenarios and different management strategies can be investigated under controlled conditions, safely and at relatively low cost compared to experiments and empirical work (DeAngelis et al., 1998; Francis and Hamm, 2011; Österblom et al., 2013; Dietze, 2017). However, the use of mathematical models in ecosystems management is not as widespread as in many other areas, such as aerospace engineering, finance, hydrology, power grid regulation, disaster preparedness, etc. (Sengupta and Bhumkar, 2020; Howison et al., 1995; Singh and Woolhiser, 2002; Deng et al., 2015; Steward and Wan, 2007), where they have become indispensable tools to managers. Nonetheless, prominent success stories do exist, a fraction of which we revisit in this paper, and inspire us to study ways in which mathematical modeling can be better integrated into ecosystems management.

We focus on mechanistic mathematical models that describe how the state of a system and the fate of its constituent species and substances evolve over time. Recent advances in modeling, analysis and computing capabilities have increased the emphasis and usefulness of mechanistic models. This can include models formulated as traditional dynamical systems in the form of (potentially stochastic) differential and difference equations, or, more recently emerging interacting particle and agent-based models (Bousquet and Le Page, 2004; Parrott et al., 2011).

Despite all recent advances and successes, only a small portion of ecological modelling research is used in management, regulatory, and decision-making processes. Given the sheer magnitude of the challenges that we face and the success of mathematical models in other areas, this disconnect seems surprising, to say the least. It also indicates a great untapped potential in dealing with some of the foremost challenges of our times. In this study, we endeavour to gain insight into this disconnect. We give examples of mechanistic ecological models that have had great impact in management and decision making. We give insights to modelers for how to make their work more

[1]As told to Fred Branfman “Living in Shimmering Disequilibrium” Salon.com, April 22, 2000. https://www.salon.com/2000/04/22/eowilson/

relevant for applications to sustainable ecosystem management, and pave the way for mechanistic ecological models to take a prominent role in supporting decision making for a sustainable future. To affect the decision-making process, one has to know its components and their interplay. We do not explicitly study it here in detail because this has been done elsewhere, see, e.g., Dafoe (2003) and references therein. We do, however, mention various aspects of this process throughout our work where this context information is necessary.

It is sometimes helpful to categorize the broad variety of process-based models according to various criteria, but such a classification is neither obvious nor unique. Classification according to mathematical criteria (e.g., deterministic or stochastic, discrete or continuous) can be helpful for experts but gives little information about predictive or explanatory power. We will refer to the distinction that Holling (1966) proposed between *strategic* models, which are simple yet capable of revealing potential explanatory generalities, and *tactical* models, which are designed to predict the dynamics of specific systems and tend to be more complex. Such distinctions about models are not always so clear, and sometimes the classification may refer to an objective. Other classifications exist, for example by Levins (1966) who rated models on the three axes of generality, realism and precision; see Evans et al. (2013) for a review and discussion of this and other approaches.

We begin by reviewing the current literature on the topic from both academic and government sources, and we highlight their recommendations in terms of presentation, collaboration, and type of model to use. Then we critically analyse several success stories, where mechanistic models, published in the scientific literature, had significant impact on policy and decision making. We consider a variety of attributes for each study, from simple article metrics and the type of model used to questions of model presentation and urgency of the problem. By contacting the authors, we also investigate the level of collaboration between researchers and managers or decision makers throughout the research process. We discuss a few specific "pathways to success" that are common in this area. We also reveal how the communication between the academic researcher community on the one hand, and the community of managers and decision makers on the other, is organized in different countries around the world, and how different standards can create obstacles for collaboration while other aspects can become opportunities for collaboration. We believe that our analysis and findings will prove helpful to theoretical ecologists and ecological modelers interested in learning how to facilitate the uptake of their research by decision makers.

2 Characteristics of models for environmental decision-making

Models have long been essential for ecological theory in explaining how ecological systems work and have been used in a more applied manner in special areas of environmental management, such as ecotoxicological risk assessment (Pastorok et al., 2003), integrated pest control (Huffaker, 1980), wildlife management (Norton and Possingham, 1993), fisheries (Collie et al., 2016), and invasive species (Epanchin-Niell et al., 2012; Liebhold et al., 2016).

Some of the first ecological models used in the realm of legal decision-making were linear compartmental models (ordinary differential equations). Such models can be used to trace the fate of a substance through the environment (Sheppard, 1948). Motivated by the fallout of radionuclides from nuclear weapons testing, food chain compartment models were developed to follow the movement and concentration of those and, later, other contaminants. Reichle and Auerbach (2003) note that "Food chain models have had important application in developing regulatory standards for environmental exposures (ingestion) and in developing risk analysis for chemical release", although these models did not simulate the dynamics of these food chains, only the movement of chemicals through the static chains.

Nevertheless, applications of mechanistic models in important environmental management decisions have remained rare. Skepticism still exists among many ecologists and managers on the usefulness of ecological models in management (Clark and Schmitz, 2001; Lester, 2019). According to Bunnell (1989), this problem of trust has emerged from numerous failures of models to provide useful information to environmental problems. He identifies some of the main reasons for this failure, including models not addressing managers' real questions, there not being an actual user envisioned at the start of model development, and model complexity exceeding what can be supported by data, leading to models not being adequately evaluated. Wright et al. (2020) found that there is often a big gap between finding an optimal solution for a given conservation challenge and implementing it. It is therefore possible that the perceived lack of usefulness of models in conservation decisions is attributable to challenges in implementation and not to the models themselves.

A number of authors have made recommendations for how to improve ecological modeling designed for decision-making. A few key pieces of advice can be summarized. First, there is broad agreement that a clear statement of the model objective is needed (Pastorok et al., 1997; Starfield, 1997; Clark, 2010; Nichols, 2001; Glaser and Bridges, 2007; Grimm et al., 2020). Formulation of a clear objective includes deciding what the key variables are, the types of outputs, and the data requirements to attain the objective. Second, there must be close coordination between environmental decision makers and modelers to develop a common understanding so that the science can be transferred to managers (Swannack et al., 2012; Schuwirth et al., 2019) and other stakeholders (Parrott, 2017; Schmolke et al., 2010). Third, only those features that are essential to the objective should be included in the model (Nichols, 2001). Fourth, clear measures should be identified to evaluate the model's success in attaining its objective (Starfield, 1997). Fifth, as noted by Bunnell (1989), working in teams is important, as most management problems are multidisciplinary and require several types of expertise. However, some of our examples will show that large interdisciplinary teams are not necessary for producing high impact papers.

A systematic strategy for using models for environmental decision support is proposed by Schmolke et al. (2010). In addition to the principles noted above, they stress the importance of an initial conceptual model formalization that includes all of the assumptions and a careful selection of the appropriate complexity level for the problem. They list the standard processes of parameterization, verification of the correct formulation, sensitivity analysis, uncertainly quantification, validation, and thorough documentation of steps.

Government agencies charged with making decisions about the environment have often developed their own standardized protocols for model development and application. Swannack et al. (2012) describe this process for ecological restoration by the U.S. Army Corps of Engineers. In theory, the modeling process develops smoothly from the conceptual model development through the quantitative model and evaluation to application. In practice, the process is more iterative, with both conceptual and quantitative models being changed as problems are met or new ideas arise along the way. Problems may include data gaps for key parts of the model, which may have to be filled with expert opinion (Lester, 2019). Such a process of successive model elaboration and refinement has also been described by Getz et al. (2018).

In such agency models, documentation and communication are essential parts of the process (Swannack et al., 2012). Communication is essential at all stages of the modeling process, including a clear statement of the objectives to stakeholders at the outset (see above). Cartwright et al. (2016) give a comprehensive guide on how to effectively communicate each aspect of the process, including schematics for presentations. To assist in decision-making, complex output must be communicated effectively. Communication with stakeholders may be improved by linking mental models of the stakeholders in the simulation models themselves (Elsawah et al., 2015).

There are many styles of ecological models, and there has been debate over which approaches are best for models aimed at decision-making. Norton and Possingham (1993) provide a taxonomy of various kinds of wildlife models. They felt that dynamic spatial simulation models were best for projecting various management scenarios and responses of systems to climate change. The most appropriate models for projecting novel situations may be process-driven models, which are based on a theoretical understanding of relevant ecological processes (Evans et al., 2013; Cuddington et al., 2013; Schuwirth et al., 2019). If knowledge of the basic processes is available, especially at the level of individuals, these models can project the response of an ecological system to changing land use and climate. They can help distinguish among the relative benefits of management alternatives and test hypotheses (Glaser and Bridges, 2007; Lester, 2019). Process models have also been useful in providing and suggesting 'optimal' ways to apply management in these areas (Clark, 2010; Huffaker, 1980; Buongiorno and Gilless, 1987). However, data at the level of detail needed are not always available. As an alternative, Sutherland et al. (2012) propose that models for decision-making use an empirically driven approach; that is, use phenomenological relationships. Even though processes are modeled explicitly, they are simplified as transitions between coarse-grained states, so the demand on data is reduced.

Robson (2014) observed that "ecological models only provide management-relevant predictions of the behaviour of real systems when there are strong physical (as opposed to chemical or ecological) drivers." Such a statement reflects the fact that planning frequently serves the goal of controlling a system by engineered structures and processes. Hydrology is one example of a strong physical driver in freshwater systems. An example is the massive Everglades restoration project, where highly detailed and validated hydrological models and physical structures are used to predict and regulate water flow, water depth, and other aspects. Management impact on biological populations is then evaluated according to habitat suitability models, which are, in their simplest form, statistical correlation models based on natural history (Beerens et al., 2015). Linking hydrology to population dynamic models has been rarer, but an apple snail population model by Darby et al. (2015) is currently officially accepted and implemented by the U.S. Army Corps of Engineers who oversee the project. Models such as these, that combine physical and ecological components, sometimes referred to as 'hard science–soft science' models (Ziman, 2002), could be an avenue for mechanistic ecosystem models to gain importance in planning and management as in Darby et al. (2015).

Similarly, river flow regulation and water extraction permits are typically based on instream flow needs, which, in turn, use habitat suitability models for fish and stream invertebrates (Gibbins et al., 2007). Phosphorous is considered the main driver for phytoplankton dynamics in lakes, and the control of algal blooms is typically based on restrictions for nutrient loading in tributary rivers. In all these cases, there exist mechanistic models for populations and communities for some of the species involved, and such models provide interesting insights into their sometimes complex dynamic behavior, but they are rarely included in official management plans and practice (Anderson et al., 2006a). More recently, predictions of how populations respond to climate change are based on climate envelope models that couple the physical drivers (e.g., temperature) with habitat suitability correlations (Elith and Leathwick, 2009). More mechanistic models exist that reveal dynamics other than those predicted by climate envelope models (Harsch et al., 2017) but we are unaware of management applications.

We can say then that a great deal of advice has been provided on methodology for developing modeling relevant to environmental decision making. But actual applications to such decision making have been limited to relatively simple, largely non-mechanistic, modeling approaches. It is clear that, ultimately, precision, feasibility, and principles of engineering need to be matched with mechanisms and complexity of ecosystems for successful sustainable management. In the next section, we present our approach to identifying features of mechanistic models that had impact on management decisions and explain some of their characteristics.

3 Analysis of success stories

An early success story of the influence of mechanistic ecological models in legislation was the regulation of dichloro-diphenyl-trichloroethane (DDT). During the 1950s, growing concern about the effects of DDT on thinning bird eggshells and its possible carcinogenicity culminated in Rachel Carson's book "Silent Spring" in 1962. The concerns voiced in the book eventually led to a ban on the use of DDT in the United States by the U.S. Environmental Protection Agency in 1972 (Peterle, 1991). Before that, court actions had been initiated in Wisconsin to classify DDT as a pollutant. In these court proceedings during 1968-69, charts and equations were presented that described the bioaccumulation of DDT in and through the trophic levels of an ecosystem (Loucks, 1972; Harrison et al., 1970). Although there was some later criticism of the lack of verification of the model, the result of the court proceedings was that the Examiner of the Wisconsin Department of Natural Resources ruled that DDT and its analogs were environmental pollutants (Henkin et al., 1971). Unfortunately, not many such success stories are documented in the literature.

We authors wondered why such success stories are rare and tried to find more examples while we all participated in a workshop entitled "New Mathematical Methods for Complex Systems in Ecology" at the Banff International Research Station for Mathematical Innovation and Discovery (BIRS)[2]. We were curious about what makes a modelling paper influential in management decisions, so we asked the workshop participants for suggestions of papers with such success stories. For each of the suggested papers, we compiled a number of factors that we expected could be relevant for work that has impact in management of ecosystems. We could determine each paper's performance with respect to several of these factors by consulting the published record, mostly standard metrics such as number of citations or the impact factor of the journal, and objective characteristics such as the type of model used or whether data was considered in the study. Other aspects that have been deemed crucial for success, such as clear communication and model presentation (see previous section), are somewhat subjective and more difficult to evaluate. Even more difficult to evaluate is the impact that a given publication has had. Rarely is this impact documented in the actual publication; at best it can sometimes be found in subsequent publications by the same author(s). When there was no clear documentation of impact, we contacted the authors directly and asked them about the impact of their work, the involvement of stakeholders and their contribution to success. Most authors replied to our requests and explained how management impact arose from their work. Table 1 lists the papers that we chose to highlight, together with some characteristics and metrics.

A first observation is that it is not easy to find modeling work in ecology that has explicit impact in ecosystem management. Few examples were provided by the workshop participants, and even for those, the nature of the impact was often not clear and rarely documented. In our opinion, this difficulty of finding examples and their documented impact reflects the fact that academic modellers and ecosystem managers/decision makers largely operate separately from one another and prevents each side from learning about the other's work and potentially collaborating where overlap exists. Perception of the necessity to bridge this gap was our main motivation for this study.

Our second observation, partly related to the first, is that the typical academic metrics used to judge a paper's value do not also indicate whether or not an ecological model has had management impact. This dichotomy is true for official metrics such as citation count, as well as for informal

[2] `https://www.birs.ca/events/2019/5-day-workshops/19w5108`

Main paper & *Topic*	Description	Model type	Data	Geo. extent	Citations
Harrison et al. (1970)* *DDT transport*	E	Cont. time (S)	Y	Global	94 (1.88)
Vollenweider (1975) *Lake eutrophication*	E	Cont. time (S)	Y	Global	1250 (27.77)
Carpenter et al. (1985)*† *Biocontrol of lakes*	A	Cont. time (S)	Y	Global	2990 (85.43)
Crouse et al. (1987) *Loggerhead sea turtles*	E	Disc. time (T)	Y	Global	1445 (42.52)
Lamberson et al. (1992)* *Northern spotted owl*	B	Disc. time (T) with stoch.	Y	Local	303 (10.82)
Hastings and Botsford (1999)*† *Marine reserves*	E	Disc. time (S)	N	Global	385 (18.33)
Matsuda et al. (1999) *Sika deer*	E	Disc. time (T) with stoch.	Y	Local	59 (2.81)
Watkinson et al. (2000)* *Genetically modified crops*	E	Disc. time (S) with stoch.	Y	Global	321 (16.05)
Krkošek et al. (2005)*† *Salmon sea lice*	C	Cont. time (T) with stoch.	Y	Global	330 (22)
Thomas et al. (2009) *Maculinea butterfly*	D	Disc. time (T) statistical	Y	Local	264 (24)
Rossberg (2012)* *Large fish*	D	Cont. time (T)	Y	Global	44 (5.5)
Railsback et al. (2013)*† *Salmon steam restoration*	D	IBM (T)	Y	Local	35 (5)
Becher et al. (2014)*† *Bee colony health*	D	IBM (T)	Y	Local	154 (25.66)
Lampert et al. (2014)† *Invasives, Spartina*	C	Disc.-Cont. (T) with stoch.	Y	Local	94 (15.66)
Hudjetz et al. (2014)† *Grassland management*	D	IBM (T)	Y	Local	9 (1.5)
Darby et al. (2015)† *Apple snail*	D	Disc. time (T)	Y	Local	15 (3)

Table 1: In the first column, $*$ indicates that the paper is the first in a series, and † indicates that we received direct input from the authors regarding the paper's impact on management or policy. The letters in column *Description* stand for: A Model not described mathematically, B Model in appendix without analysis, C Model and analysis in appendix, D Model in main text and analysis in appendix, E Model and analysis in main text. *Model type* indicates continuous or discrete time, strategic (S) or tactical (T) (see Introduction), potentially including stochasticity, and individual-based models (IBM). The *Data* column indicates whether the authors used (Y) or did not use (N) a specific data set in their work. Citation counts were taken from Google Scholar on 18/01/2021. Parentheses indicate the average number of citations per year since publication.

metrics such as the perceived rating of (some of) the authors in the academic community. For example, Harrison et al. (1970) was hugely influential in legislating a ban on DDT, but has fewer than 100 citations to date. For other papers, management and academic impact both occur, as for example in the study by Crouse et al. (1987) on the benefits of turtle excluding devices in fisheries, which has over 1,400 citations (see Table 1).

This dichotomy does not mean that these metrics are not important. When government representatives consult the academic literature, they may take such metrics as indicators for the scientific community's evaluation of the work and therefore decide to use the paper's results (Findlay, personal communication). There are, of course, many scientists working in government laboratories who use mathematical models (in our sense) as part of their toolbox when researching any given topic. The results may influence decision makers, but often do not see the light as academic publications and are therefore largely hidden from the academic community.

Some of the papers that were suggested to us are published in very high impact journals (e.g., *Science*), but this academic prominence is not necessary for a paper to have management impact. For example, the Hokkaido Government in Japan adopted a management program for sika deer on the basis of Matsuda et al. (1999), published in *Population Ecology.* Even more surprising is the case of Vollenweider's work on lake eutrophication through the use of a mass balance and export model that seems simplistic from today's point of view but produces excellent predictions. According to the author's own account (Vollenweider, 1987), the most influential of his works, Vollenweider et al. (1970), was not even published in a peer-reviewed journal because the funding agency did not give its consent. The later, peer-reviewed work is Vollenweider (1975), and the impact of both is widely documented (Carpenter et al., 1985; Lowe and Steward, 2011). In other cases, it is not clear whether publication in a high-impact journal aided the application in management or, vice versa, (potential) important applications in management aided publication in high-impact journals. While some authors reported that there was a significant lag between model publication and its management action (Krkošek et al., 2005), others report that management action preceded publication (Hudjetz et al., 2014). Another feature we considered, that is, the geographical extent of the ecological problem, does not seem to affect its use in management. Table 1 contains numerous examples of both.

We were curious about model complexity and model realism in the studies that were suggested to us as success stories. There are, of course, many different types of (dynamic) mathematical models, such as differential equations, difference equations and in particular matrix models, individual- and agent-based models and others. We found influential examples from all different types, but there are differences, which we discuss now.

Matrix models are widely used and understood for discretely structured population dynamics (Caswell, 2000). Crouse et al. (1987) studied the effect of various factors on turtle reproductive success. Their work was instrumental in mandating turtle excluding devices in the United States. Matrix models are considered highly accessible to non-modellers and do play a significant role in conservation decisions and government reports, e.g., the evaluation of the status of boreal caribou in Canada under the COSEWIC status assessment report (Berglund et al., 2014). In fact, there are large data bases of life cycle dynamics (i.e., parameterized matrix models) of various organisms that can be used by researchers (e.g., the Compadre data base for plant species[3]).

Differential or difference equation models with only a few equations are sometimes seen as too simple, yet can be very useful, even if, or particularly when, parameter values are not known in site-specific detail. Despite their apparent simplicity, these models can easily yield complex dynamics. The potential for abrupt changes in behavior (e.g., tipping points) poses the question of parameter

[3] `https://www.compadre-db.org`

estimation and accuracy. The double-edged sword of general simplicity versus site-specific details and complexity is always present, but both types can have significant impact in management. For example, Hastings and Botsford (1999) used a simplistic, single-variable discrete time model to show that fisheries yield is equivalent with quota restrictions or with marine reserve regulation. This paper contains no specific data, but with its general insights helped pave the way for the concept of marine protected areas to enter the scientific and political debate (Saarman et al., 2013). While this publication is the only example in our list that does not contain specific data, other examples do exist, particularly in areas where data are difficult to come by. In these situations, qualitative trends and rules of thumb provide valuable conservation guidelines, for example, in terms of spatial scales (Gaines et al., 2010). Mumby et al. (2007) studied the resilience of coral reefs using a similarly simplistic model, which, despite being based on parameter values gathered from expert knowledge rather than data, also became instrumental in management. A more complicated discrete model by Lamberson et al. (1992) explored the population dynamics of the northern spotted owl (including mating, reproduction, dispersal and environmental stochasticity) in the presence of logging and habitat fragmentation, and contributed to significant legislation for protection of the species. In some cases, a suite of models, ranging from generic to specific, can be highly successful. For example, a key question regarding the health and management of inland and coastal waters is eutrophication. Basic research (Janse et al., 2010) demonstrated broadly that critical transitions from submerged aquatic to phytoplankton could occur in shallow lake ecosystems. For more specific applications, Janssen et al. (2019) used a generic lake ecosystem model to show how such critical transitions could occur in different ways in different lake types. While this approach provided advice regarding best practices for reversing eutrophication in particular lake types, the model was still fairly theoretical. A highly site-specific spatio-temporal explicit model (with hydrology) was developed over decades to determine effects of nutrient loading for the Everglades wetland, and it is used in decision making (Flower et al., 2019). In fisheries management, Collie et al. (2016) acknowledged the success of models for single-species management but calls for more tactical ecosystem models that include the dynamics of ecological and environmental features.

Individual-based models (IBMs) are often quite appealing to practitioners and non-scientists because these stochastic models are, or can be, formulated in terms of behavioural rules rather than mathematical equations. On the other hand, their detailed nature makes scientific reproducibility extremely difficult when small differences in implementation can lead to large differences in outcomes, which is why a protocol for their description was developed (Railsback and Grimm, 2019). Parameterization of individual-based models requires large amounts of data, but this effort can result in models that yield highly site-specific results and often allow visually appealing representation of those results. Examples of high-impact IBMs include the inSALMO model by Railsback et al. (2013), which is one of a series of papers on an individual-based model of the life cycle and behaviour of salmonids in rivers with the goal to allocate restoration efforts. This model was developed in a partnership between government research labs, academia, and industry in the United States and has been adopted by one laboratory of the National Marine Fisheries Service for management research in California (Dudley, 2018). The BEEHAVE model (Becher et al., 2014) was developed by an academic-industry partnership in the UK for use in pollinator risk assessment by industry and regulatory agencies. The European Food Safety Authority (EFSA) has evaluated BEEHAVE and found its design suitable for the development of a new model on its own and has decided to use BEEHAVE to define a reference "healthy" honeybee colony (EFSA, 2015). Yet another successful IBM, examining grassland dynamics in a German national park, was also developed in close collaboration with all stakeholders and its recommendations informed management actions before the corresponding article was published (Hudjetz et al., 2014).

We observe that there is not one and only one way to conduct research on dynamic ecosystem

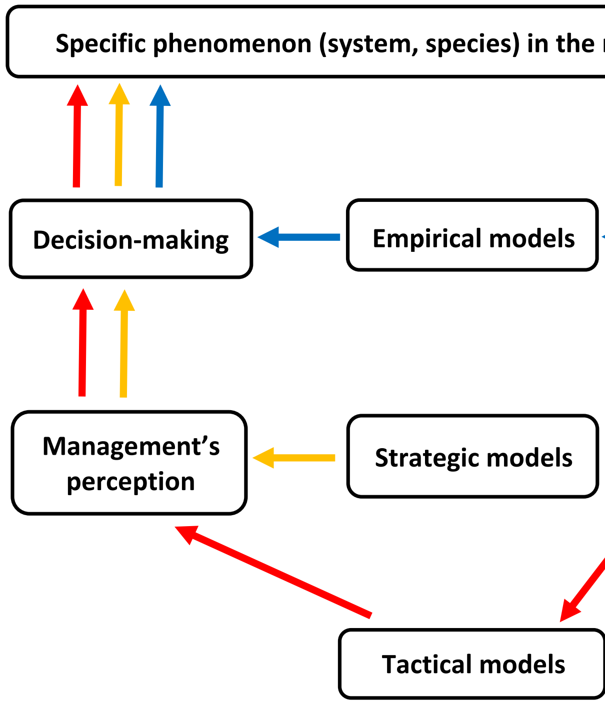

Figure 1: Different paths of the information flow resulting in decision-making supported by use of mathematical models. The blue, yellow and red paths (visualised by the corresponding chain of arrows) correspond to the use of models of increasing complexity as required by the complexity of the given natural system. Along the blue path, the approaches from a standard ecologist's toolbox are predominantly used. Use of less standard and/or more advanced mathematical techniques along the yellow and red paths introduces the crucial stage of manager perception where the modelling results should be linked to the real world using manager's terms (that often differ from the modeller's terms, see Sections 4.1 and 4.2 for a discussion of 'different cultures').

modelling and to disseminate its results in such a way that it is useful to ecosystem management. This could be seen as bad news in that we cannot offer one 'blue print' to follow for models to have impact on management. We consider it good news in that there are many different approaches that promise visibility and impact as long as some basic insights are respected. We distinguish three different 'pathways to success' that may be taken depending on the nature of the problem and the type of the modelling approach used, illustrated in Figure 1. The blue path may arise in the cases of relatively simple, low-dimensional dynamics, especially when predominantly linear predictor variables are used that can be deduced from the analysis of field data using statistical tools (Dietze, 2017), sometimes as simple as the linear regression (Vollenweider, 1975). No well-established ecological theory or mechanistic models are involved in this case; the predictors are usually (but not always) chosen based on biological knowledge. The yellow path arises in the cases of higher-dimensional ecological dynamics of intermediate complexity, where the predictor variables and their interactions are not deducible directly from data, but relevant ecological theory supplemented with conceptual, schematic models work well in describing the system's properties and suggesting a sustainable management practice (Hastings and Botsford, 1999; Lamberson et al., 1992; Matsuda et al., 1999). Following this path, the model sometimes can be formulated entirely qualitatively, using causal loop or stock-and-flow diagrams, without using any equations, cf. Carpenter et al. (1985). Arguably, even if only a trend can be predicted correctly, such models can still provide useful information to advise decision makers, for example for conservation purposes. The models arising in the yellow path would often be accessible to analytical investigation, although not necessarily be explicitly solvable. The red path arises in the cases of a high-dimensional system of high complexity, where conceptual theory and models are not capable of providing a meaningful description of the system's properties. Such models are usually investigated through extensive numerical simulations, e.g. Thomas et al. (2009); the corresponding field of research and methodology is known as computational ecology (Pascual, 2005; Petrovskii and Petrovskaya, 2012). We mention that the difference between 'strategic' models (yellow path) and 'tactical' models (red path) is often conditional rather than absolute and may even depend on the preferences and experience of the researchers. We also mention that the three colored paths are typical but not exclusive and some other, ad hoc or case-specific links and paths may be possible (not shown in the figure for the sake of clarity). For instance, observations and filed data may suggest, through management's perception, a straighforward approach to tackle the problem without any need for modelling. Conversely, use of non-standard empirical models may require the stage of management's perception and appreciation. Else, sometimes the red path may include the stage where strategic models are attempted before moving on to the use more detailed tactical models, in case the former are found to be too schematic.

In addition, the following points outline further responses that we obtained from the authors of the papers selected for the analysis.

1. The scientific question should be currently relevant to managers and decision makers, ideally the question would come directly from them. Sometimes theoretical models can have impact if the topic is currently highly debated in the community, e.g., Hastings and Botsford (1999).

2. The work should include all relevant aspects, which sometimes results in a series of papers that build our understanding of a given system, e.g., Krkošek et al. (2005); Railsback et al. (2013). Sometimes, however, a single paper is sufficient to influence policy strongly, e.g., Crouse et al. (1987).

3. Ideally, stakeholders are involved from the beginning of the modelling process; e.g., Becher et al. (2014); Railsback et al. (2013). However, this is, again, not necessary if the authors are highly familiar with the pressing issue, as in Hastings and Botsford (1999).

4. The use of data can be key to successful management outcomes. In models regarding the management of specific species or locations, data is essential for the analysis and parametrization, as in the turtle management arising from Crouse et al. (1987). Using Markov decision processes with data from the U.S. Fish and Wildlife Service, Johnson et al. (2016) explained the framework used to manage mallards in the United States and Canada.

Even if all of these recommendations and suggestions are followed, there is no guarantee that any particular research activity will have the desired influence on management and policy, or that it will have any impact at all. Policy and management decisions are made in the context of a societal environment, so that even excellent scientific work will not influence policy unless the goals and results of the research are aligned with this larger context. The discussion below includes some observations about this issue.

4 Discussion

4.1 Two communities, two cultures: managers' perception of modelling studies

Despite the long history of ecological models as heuristic tools in understanding ecological systems, there is disagreement over the impact of their applications to management and decision making. On the one hand, models have been said to "have played key roles in informing public debate and informing management decisions" (Harris et al., 2004). For example, the model by Epanchin-Niell et al. (2012) gave advice on allocating expenditures between surveillance and eradication of invasive species. Models have also shown the effectiveness of sterile insects techniques in invasives with specific features (Liebhold et al., 2016). The adaptive management modeling approach of Donovan et al. (2019) in collaboration with the Grand Canyon research staff gave recommendations on an endangered species, the humpback chub. On the other hand, models have also been criticized for their lack of predictive power and that "problems that ecology should solve are not being solved," e.g., Peters (1991). Such contradictory views might be explained by distinguishing two types of potential uses of models for environmental issues, namely 'exploratory/planning' and 'regulatory/legal', as defined by Harmel et al. (2014). The former type of model provides qualitative information that can be used to plan relevant research and influence opinion. Most ecological modeling that is termed 'applied' is of the exploratory/planning type, and the insights it provides often support the former point of view. However, models that directly guide important environmental decisions and are incorporated into management, that is, the regulatory/legal type, are much rarer, which tends to support Peters's negative opinion. That reflects the difficulty of ecological models to attain high predictive power, and therefore leads to continued reports of skepticism about the use of ecological models in decision-making, e.g., Clark and Schmitz (2001) and Lester (2019). Part of the problem is that contributing to regulatory/legal decisions is a multi-step process, and there is frequently a lack of funding for work that moves from exploratory or proof-of-concept studies to a point where the findings are relevant to regulators.

Arguably, one factor that hinders more efficient communication between ecological modellers and ecosystem managers are the 'cultural' differences between the corresponding communities. The set of indicators that managers routinely use to gauge the value of a model is considerably different from those of an academic; see Findlay (2019); Harris et al. (2004); Schuwirth et al. (2019); Swannack et al. (2012). For example, two factors that are often regarded by applied mathematicians as important in order to maintain their respect and ranking in the community of applied mathematicians are the journal where the paper is published and the 'elegance' of the model, e.g. whether it is investigated analytically. However, these issues matter little if at all for ecological managers. This narrow view of 'important' work in applied mathematics should be broadened to recognize more positively the value of collaborative research with multiple authors with a variety of viewpoints (possibly including managers).

4.2 Social Context

What matters for decision-makers in general is (i) whether the evidence provided by the model speaks directly to the issue/problem (all else being equal, indirect evidence is something that managers tend to down-weight) (Sutherland et al., 2012) and (ii) what the 'costs' are (economic, political due to public opinion and media coverage, etc.) of taking a decision based on the evidence provided by the model (Lortie and Owen, 2020). In Figure 2, we illustrate three key information streams that are considered in the development of policy, and discuss these elements below.

Since ecological research often points to management actions that are of benefit to humans in the long term, but look detrimental to profits or jobs in the short term (Hoffmann and Paulsen,

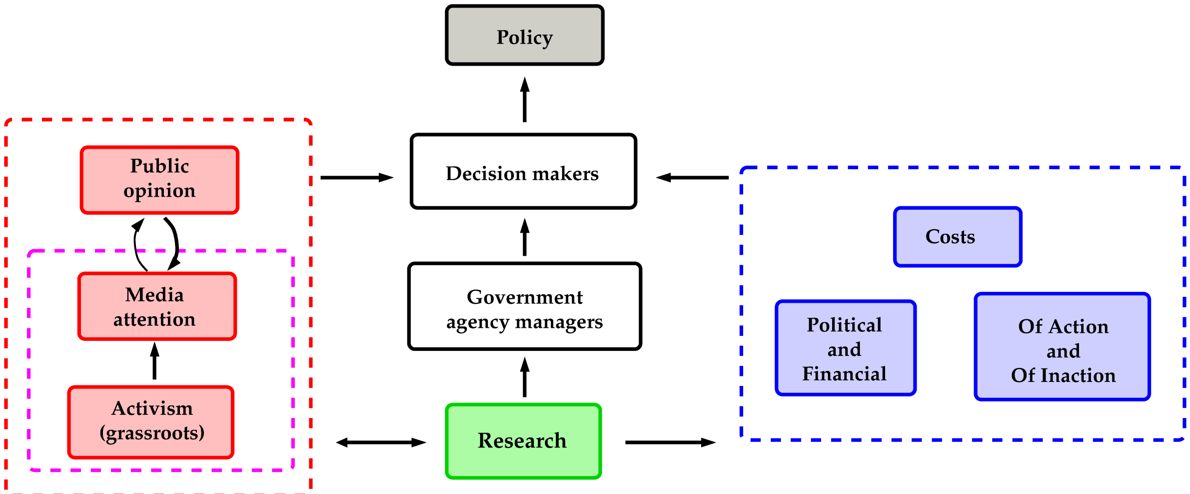

Figure 2: Three information streams that are key components of policy development. These three streams are important in determining whether or not research results will be used to inform policy. Decision makers must integrate information from government agency priorities (centre stream), costs (blue box), and public opinion (red box). Research (university, government, etc. – green box) informs all three streams. Public opinion is often rooted in media attention to grassroots issues (purple box). If there is sufficient public support of management actions recommended by research, and the costs (monetary costs and/or political costs of action and/or inaction) are favorable, the research can lead to policy action (gray box). There is a bidirectional relationship between research and activist organizations because the latter are not simply recipients of research knowledge, but can also be contributors by funding or co-funding, or—more recently—through citizen science.

2020; Caplan, 2016; Hyde and Vachon, 2019; Leonard, 2019; Scanlan, 2017), governments will be more likely to implement the recommendations of ecological research if public opinion supports such activity (Burstein, 2003). The required groundswell of public opinion is often created when grassroots organisations are able to obtain media attention and gain sufficient momentum to shape public opinion. This process can occur quickly, but can also involve decades of hard work (Bullard and Johnson, 2000; Fields, 2018; Bullard and Johnson, 2000), and the level of success is context-dependent (Foweraker, 2001). This activism is informed by research, some of it funded through the basic research programs of individual researchers, some co-funded by activist organisations.

Finally, decision makers also need to consider the associated costs of the management action (Lortie and Owen, 2020): costs of implementation, costs of doing nothing, the likelihood that the recommendation might be in error, and the consequences if the recommendation is in error. For illustration, consider two extremes: At one extreme are (a) inexpensive recommendations that are sure to lead a good outcome easily observed by the public, and at the other extreme are (b) very costly recommendations that may lead to a marginally better outcome or a good outcome that isn't apparent until many years have passed. Recommendations of type (a) are easy for policy-makers to adopt, while recommendations of type (b) are unlikely to be adopted. Recommended actions to reduce reliance on fossil fuels are definitely of type (b), and government appetite to implement such actions has only begun to develop momentum as the consequences of doing nothing become more obvious to industry and the public (Diringer and Perciasepe, 2020). Modelling work that includes an in-depth study of uncertainty (ideally going beyond the imprecision of parameter estimates, which is generally a relatively small source of uncertainty compared to other sources), and that can nonetheless demonstrate a high level of confidence in the predictions, will be more likely to inform management decisions (Cooke et al., 2020). Management of invasive species provides a superb illustration of many of the issues raised here. Monitoring can often prevent species from being introduced, but the cost may be high. Proper management for species that have been introduced depends on appropriate knowledge of the cost of damage by the invasive species (which can be very difficult to assess) (Epanchin-Niell and Hastings, 2010).

Several of our success story examples are caught between conservation goals and economic interests, e.g., the question of turtle-excluding devices (Crouse et al., 1987), the protection of the northern spotted owl (Lamberson et al., 1992), and the effect of fish farms on sea lice among wild salmon (Krkošek et al., 2005). Since such potential conflicts often garner media attention, modellers may find themselves in the spotlight and might require training for communicating with media outlets. Parrott (2017) considers such communication skills as one of many nonscientific skills that are as important as scientific skills for researchers aiming to help solve difficult ecological problems with substantial socio-economic implications in interdisciplinary teams.

4.3 Government research

As the use of science is important in the decision-making process, many if not most government bodies not only fund research but also operate their own research institutes. Hence, there is a lot of research done by government scientists, many of whom use complex models and support management decisions, but publish only in government reports. As academic researchers we could be more active about searching the gray literature in order to tie in with and contribute to this research activity. In this section, we showcase some selected opportunities for academics to connect with government research. Our aim is to illustrate the variability of different forms of government research and which role it can play. Along the way, we touch on modeling standards of in-house work of government authorities.

In the United States, the Environmental Protection Agency (EPA) is the main environmental regulatory agency and responsible for policy and regulatory decisions. Environmental models "[...] are becoming a key component of science that is used not only within the EPA but throughout federal agencies" (Borg, 2009). An example of a model used by EPA is the AQUATOX model, developed by a private company, which simulates an aquatic environment, tracking the fate and transport of pollutants and predicting the effects they will have on an ecosystem (Park et al., 2008; Galic et al., 2019; Forbes et al., 2017). Although AQUATOX is a complex model, it has been well enough peer reviewed and tested to meet the three issues of importance to regulatory decision-making: uncertainty, transparency, and consistency (Borg, 2009; Galic et al., 2019). The work by Springborn et al. (2016) was partially funded by USDA-APHIS and resulted in changes in inspection procedures at US ports. A list of all funding opportunities from federal agencies can be found on grants.gov, and are generally available to universities and private companies. The Cooperative Extension System provides funding to Land-Grant universities, in order to bring science directly to the regional and country level.

In Canada, mathematical models form an important part of agency decision making, especially in forestry and fisheries, which are two economically essential industries in Canada with significant conservation challenges. For example, the Department of Fisheries and Oceans employs the Habitat Ecosystem Assessment Tool to assess net change of habitat productivity, using habitat suitability as a surrogate. The Canadian Forest Service developed and continues to use several large-scale simulation models for forest management, fire regimes, or carbon cycling. The listing of species by the Committee of the Status of Endangered Wildlife in Canada uses a range of mathematical models, including matrix models for caribou (Berglund et al., 2014). There are funding opportunities by government agencies that are available to academic researchers (e.g., the Early Intervention Strategy program for spruce budworm), and there are government-academic research networks (e.g., FLUXNET).

In the European Union, the Joint Research Centre provides scientific advice to the European Commission and to EU member states. Notably, the Competence Center on Modelling was launched in 2017 to promote a responsible use of models in EU policy making. Among its key objectives are to increase the transparency, consistency, and quality of model use. There is an increasing trend in models being used in the Commission's Impact Assessments[4] from 2003–2018, reaching around 25–30% from 2015 onward (Acs et al., 2019). The policy areas with the highest number of model use are environment (including climate), internal market, transport, and energy. Descriptions of the models previously or currently used by the Commission are contained in the Modelling Inventory and Knowledge Management System (MIDAS), which is open to the public since December 2020.

In the United Kingdom, environment-concerned government institutions such as The Department for Environment, Food and Rural Affairs provide relatively little funding for academic research. Their interaction with academia seems occasional rather than regular and, as it stands, neither to inspire university researchers to make their results useful for managing environmental problems nor to provide a framework for that. Instead, environmental and ecological research in the UK, including that involving mathematical modeling, is usually done in a few government-funded research institutes such as Rothamsted Research and the Centre for Ecology and Hydrology. In spite of the apparent absence of any comprehensive system facilitating the interaction between academia and decision-makers, UK academics are in fact encouraged to explain how their research has "impact" upon the economy, society, public policy, culture, and the quality of life through the Research Excellence Framework.

In Germany, due to its federal political system, a host of federal ministries or state authorities grant research contracts, primarily to the government's own but also to other research institutions. For example, as wolves are re-invading and establishing in Germany, the Federal Agency for Nature Conservation ordered a study that developed habitat models to assess the potential number of wolf territories (Kramer-Schadt et al., 2020). A number of non-university research institutes have working groups on or using ecological modeling. The largest one may be the Department of Ecological Modelling at the Helmholtz Centre for Environmental Research, which has played a key role in individual-based models of ecological systems. The framework of joint appointments serves to strengthen connections between these non-university research institutes and universities.

In Russia, most ecological research is funded by the state, and research outcomes are often multidisciplinary. The Russian Academy of Sciences (RAS) is influential in making decisions on environmental policy and statutory regulation. For example, mathematical models have been developed for the sustainable management of Lake Ladoga and Lake Onego (L. Rukhovets and Filatov, 2010) or, in collaboration with nature reserves, of the European beaver (Petrosyan et al., 2016). An example of universities cooperating with the RAS is the EFIMOD model that is used for sustainable forest management (Komarov et al., 2003).

In Spain, central and regional authorities, sometimes with the support of EU funds, grant research contracts, whose outcomes help to make political decisions. One of the most intense conservation programs in the last decades has been the conservation of free-ranging Iberian lynx populations in the south of Spain and Portugal. Mathematical models have been used to infer and forecast population growth and the possible results of the management measures adopted (Heredia, 2008). In particular, metapopulation models have been used to understand the effect of habitat fragmentation and to design ecological corridors for the species (Gaona et al., 1998).

These examples are not aimed at providing a comprehensive overview of government research activities around the globe. Yet, they demonstrate a wide spectrum of agencies, authorities and

[4]Impact Assessments refer to the process of gathering and analyzing evidence to support policymaking.

programs with which academics could connect. While a thorough comparison of government funding opportunities around the globe and their uptake in the academic community could be of interest to academics and governments alike, it is beyond the scope of this work and would only increase the variability of research opportunities.

4.4 Modeling software and tools

For models to be used by practitioners like conservation biologists or agency staff members, an important tenet is the availability of user-friendly software. This can come, for example, in the form of R packages or off-the-shelf computer programs. They make models easily accessible to practitioners and save them from having to code models from scratch. Graphical user interfaces, tools for sensitivity or uncertainty analysis, and compatibility with geographic information systems (GIS) often come as added features. For example, the wide use of individual-based models may be fairly attributed to user-friendly modeling frameworks, making available code libraries and simplified programming language (e.g., NetLogo, Repast).

Process-based models play a prominent role in population viability analysis (PVA), which provides a broad suite of modeling and data-fitting methods that are well recognized as supporting decision-making especially in habitat conservation and recovery plans for threatened species (National Research Council, 1995). PVA programs differ in the model type they use. For instance, the commercial RAMAS packages use matrix population models, whereas the freely available VORTEX relies on individual-based simulations. For modeling marine and aquatic ecosystems, AQUATOX and EcoPath with EcoSim are commonly used tools, yet, the latter cannot completely handle age structure, and its use in tactical applications like setting regulations is scarce. For a review paper on integrating lake ecosystems modeling approaches, see Milton et al. (2010). While mentioning these software products as examples, we stress that there are many other options available, some of which are reviewed in Pastorok et al. (2001). Users should exercise caution in applying these tools (e.g. Ellner et al., 2002), yet they are recommended as valuable conservation tools by Brook et al. (2002). Certainly, users ought to be aware about the underlying assumptions of the models 'hidden' behind graphical interfaces. To this end, the book by Morris and Doak (2002) is aimed at training field biologists at using modeling in decision-making.

There exist many other tools and software packages, often in the area of statistics and optimization to support data collection, threat assessment, or the ranking of management options. Arguably one of the most influential and relatively recent mathematical developments is Marxan, which has been described in a number of papers as summarized in Watts et al. (2009). Marxan is a software program that implements an approximate mathematical solution to the optimization problem of siting reserves to maximize the number of species included. Although the problem is easy to state, exact solutions are not practical as the number of sites and species grows, so that the approximate solution to what is essentially a very high dimensional combinatorial problem is appropriate. It is easy to understand why this work has been so influential. The problem is easy to state and is one that decision makers are both familiar with and need to deal with. There is freely downloadable and easy to use software that allows end users to implement the methods with relatively little need to deal with the underlying mathematics. It is also informative to note what this work does not try to do. The real novelty lies in the application, and not in the mathematical development. The underlying modeling makes a number of assumptions leading to a problem of a form that arises in a large number of cases.

4.5 Epidemiological models

From a modeling perspective, epidemiology and ecology are two very close fields: the models as well as the tools for their analysis are very similar, and many academic researchers who work in one field also have keen interest in the other. Just like in ecosystems models, there are many more academic publications on epidemiological models than are used in decision making, and just as with ecosystems models, there is discussion on how to raise the visibility and use of models in policymaking (Woolhouse, 2011). Unlike ecosystems models, however, epidemiological modeling has long been instrumental in public health management, for example to control HIV (Anderson, 1988), malaria (Mandal et al., 2011), and the 2002–03 SARS epidemic (Anderson et al., 2006b; Brauer and Wu, 2009).

Before high-performance computing was widely available, results from mathematical models often lagged behind the rapid timeline for implementing public health measures during an epidemic. In the current SARS-CoV-2 pandemic, however, mathematical models are being updated daily and are highly influential in the development of policies aimed at controlling spread. Similar close integration of research and policy occurred during the 2001 outbreak of foot and mouth disease (FMD) in Britain; mathematical models and simulations provided invaluable guidance to decision makers about control efforts (Dafoe, 2003). Despite the many similarities, there are, of course, a number of significant differences between epidemiology and ecosystems science: public interest is much more easily roused by human health than by ecosystem health, and consequently much more funding is available for the former than for the latter. Data quality is usually also much better for public health questions, where, for example, influenza data can yield important insights even 100 years after an outbreak (He et al., 2013).

5 Conclusions

Ecological systems and processes are inherently complex, and ongoing global change only increases this complexity. In addition, management often needs to balance multiple stakeholder goals, for example in large-scale projects such as the restoration of the Everglades or the San Francisco Bay-Delta (Van Eeten and Roe, 2002). We believe that sustainable ecosystem management should therefore be based on rigorous ecological theory and verified by relevant mathematical models before being put into practice.

Despite the numerous examples where models of ecological dynamics have been used with great success to help ecosystem managers in the decision-making process, many theoretical ecologists and ecological modellers feel that their science has a much stronger potential to support evidence-based decision making than is currently being used. The question becomes how to facilitate a tighter integration of ecological modelling into decision-making processes. Our contribution to this question is to analyze several success stories and to reveal features that often lead to success. It is worth pointing out that there are common features of many of the success stories presented in Table 1. The papers listed deal with either a specific problem (e.g., spotted owl or DDT) or class of problems (e.g., eutrophication or overfishing), though of course the issues are often more general.

Like essentially all good science, each of the contributions we highlight do answer a question. We could also summarize these successes as cases where the contribution is more to explain how the problem can be solved rather than why it occurs. The latter is often a question that is pursued for academic reasons, and answering the how question does depend on answering first the why question. The example of the turtle exclusion devices illustrates this clearly where the why question of decline in turtle numbers was a basic one of demography while the issue how to achieve the desired result led to the proposed solution. Viewed this way, it is clear that the likelihood of impact can be enhanced by making use of ideas from social sciences and including appropriate costs.

Our findings refute the idea that success of a project as measured by academic criteria (e.g., citation metrics) is required for or leads to success in informing management decisions. Similarly, there is no unique way to develop a model and approach a problem that would guarantee its application in decision making. Instead, there are multiple pathways to success: the model need not necessarily be simple (conceptual) or complicated (realistic). However, the way in which it is presented to decision makers is indeed important. In fact, involving decision makers and ecosystem managers from the early stages of academic research increases the potential of the research to make impact. In that respect, we are encouraged by calls for increased training in theoretical foundations and aspects of ecology (Rossberg et al., 2019) as well as by the creation of numerous academic programs that provide multi-disciplinary training in sustainability and biological conservation. These programs include scientific, socio-economic, policy and legal perspectives. Graduates from these programs will know the value, advantages and limitations of such models. They will be able to moderate multi-stakeholder communication throughout the planning and research process.

A paradigmatic example for the involvement of managers and politicians is given by the campaign that resulted in banning DDT: "Before the show at Madison, Wisconsin was over, 32 persons ranging in occupation from politician, lawyer, and arborist, to bureaucrat, medical doctor and businessman had appeared to testify about DDT. Their knowledge—or lack of it—makes up the hearing transcript, a document that records some 2,500 pages of direct and cross-examination with a few thousand more pages of scientific, unscientific, and pictorial exhibits thrown in for good measure" (Henkin et al., 1971).

Yet, even in this respect, there is not only one way to have an impact, so that the above observation should not discourage theoretical ecologists and ecological modellers who are not directly involved with managers or politicians from aspiring to make an impact on decision making. It is one of our important findings that even the work done by an individual or a small group can affect decision making if a scientifically sound model is used to address an important ecological problem and the model and results are presented in a way accessible to decision makers.

Ecological modeling and theory are not static but constantly evolving and improving. Here we have showcased some success stories in a variety of areas. Other areas for future modeling work will arise like in ecotoxicology, as suggested by EFSA (2018). One of the reasons why ecological modeling has not been used as much as might be expected in environmental decision making is that models are often judged to have too much uncertainty. To increase the influence of their work in decision-making, mathematical ecologists should continue to improve theory and models, including testing them against the increasing stream of data (Dietze, 2017).

We considered the question of how science can be more helpful for decision making from the point of view of a mathematical modeller, while similar questions are being asked in other communities involved with sustainability and ecosystem health. Most come to the same conclusions that communication is key in the process: listening closely to stakeholders' needs and explaining in simple terms the scientific tools involved, their powers and their limitations (Parrott, 2017; Cooke et al., 2020; Will et al., in review). Many share with us the conviction that evidence-based decision making can make this world a better place for all.

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