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Process-based models are required to manage ecological systems in a changing world

K. Cuddington,[1,†] M.-J. Fortin,[2] L. R. Gerber,[3] A. Hastings,[4] A. Liebhold,[5] M. O'Connor,[6] and C. Ray[7]

[1]*Department of Biology, University of Waterloo, Waterloo, Ontario N2L 3G1 Canada*
[2]*Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, Ontario M5S 3G5 Canada*
[3]*School of Life Sciences, Arizona State University, Tempe, Arizona 85287 USA*
[4]*Department of Environmental Science and Policy, University of California, Davis, California 95616 USA*
[5]*Northern Research Station, United States Department of Agriculture Forest Service, Morgantown, West Virginia 26505 USA*
[6]*Department of Zoology, University of British Columbia, Vancouver, British Columbia V6T 1Z4 CDN*
[7]*Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, Colorado 80309 USA*

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Abstract. Several modeling approaches can be used to guide management decisions. However, some approaches are better fitted than others to address the problem of prediction under global change. Process-based models, which are based on a theoretical understanding of relevant ecological processes, provide a useful framework to incorporate specific responses to altered environmental conditions. As a result, these models can offer significant advantages in predicting the effects of global change as compared to purely statistical or rule-based models based on previously collected data. Process-based models also offer more explicitly stated assumptions and easier interpretation than detailed simulation models. We provide guidelines for identifying the appropriate type of model and level of complexity for management decisions. Finally we outline some of those factors that make modeling for local and regional management under global change a particular challenge: changes to relevant scales and processes, additional sources of uncertainty, legacy effects, threshold dynamics, and socio-economic impacts.

Key words: climate change; expert opinion; extrapolation; simulation model.

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† **E-mail:** kcudding@uwaterloo.ca

Introduction

Decisions about the management of a natural resource necessarily make use of predictive models that are based on some theory of future conditions. In this era of rapid change in climate and other physical processes, the models we use to inform management in all areas of application require careful consideration. In this contribution, we offer an overview of the relationships among theory, models and ecological system management. We focus on the problem of management at local and regional scales given global change, as opposed to the problem of slowing this change. Global change will lead to changes in abiotic and biotic conditions that will affect population and community dynamics on time scales and spatial scales that are challenging for management. Therefore, global change creates a set of novel problems for both modelers and managers.

Although there are several approaches to modeling natural systems, since the late 1980s there has been some consensus amongst ecologists that management decisions are best guided by models which are grounded in ecological theory, and which strike a balance between too much or too little detail describing the relevant processes (e.g., DeAngelis 1988, Starfield 1997, Jackson et al. 2000, Carpenter 2003, Nelson et al. 2008). We argue that such process-based models (sometimes called mechanistic models) are the most appropriate approach for the majority of management questions, and indeed are essential given global change. We outline four categories of models that can be used to inform management decisions, and highlight the relevance of process-based models. We then provide guidelines for evaluating and constructing process-based models to be used for guiding management in the face of ubiquitous and rapid anthropogenic change.

From Theory to Management: The Process of Modelling Natural Systems

We define management as the process of deciding on the desired future states of ecological systems, and the selection and implementation of actions predicted to achieve these states, given constraints. When formulating a decision, a manager typically has in mind some conceptual framework that guides her decision. The conceptual framework guides expectations for the future, and relates the proposed management action to the desired future states of the system. In almost every situation, a manager uses some form of ecological theory regarding current and future states of the system to project or model the probable response of the system to management actions.

The word 'theory' may seem grandiose and inappropriate in the context of routine management decisions. In ecology we often reserve the word theory to refer to broad, unifying structures such as island biogeography (MacArthur and Wilson 1967) or neutral theory (Hubbell 2001). Indeed, some managers may argue that they rely on data, not theory, to guide decisions. However, data in and of themselves are not predictive. At a bare minimum the move from data to management decision requires a theory of future conditions in the natural system. For example, the theory of island biogeography has been used to guide the design of natural reserves (e.g., Williams et al. 2007), based on the projection that future biodiversity would be related to the number, size and connectivity of reserves. Some theories underlying proposed management actions are less complete or not fully articulated, such as: "with climate change, there will be poleward movement of species ranges". Even the statement "future conditions will be similar to the conditions under which the data were collected", refers to a statistical theory describing the natural system.

Given a theory of natural processes, one can construct a model to produce predictions for a particular system. When constructing a model, one is constantly trading off the degree of precision, generality and realism (Levins 1966). It is not possible to include all details of a system and still have a useful predictive tool. For example, a one-to-one scale map of a city may include all details, but ceases to be useful as a guide for finding the nearest hotel. As a result, models are always false in some aspects of their representation of a system, and there is no one correct model that links a theory to a particular system (Fig. 1).

Furthermore, different model formulations of a given theory can lead to different management conclusions. A striking example is the contribution of demographically structured population models to the development of conservation strategies for turtle populations suffering by-catch pressure. Prior to 1987, most turtle conservation efforts were directed at eggs on nesting beaches. Stage-structured models that divided a single turtle population into relevant life-history stages such as eggs, juveniles and adults (Crouse et al. 1987), predicted the same low population growth as unstructured models that did not include the development stage of individuals. However, the stage-structured models also indicated that population growth was relatively insensitive to egg mortality, but quite sensitive to the mortality of older and larger stages. The new model structure and analysis provided key insights for developing appropriate management strategies which targeted survival enhancement of adult sea turtles (i.e., turtle excluder devices to

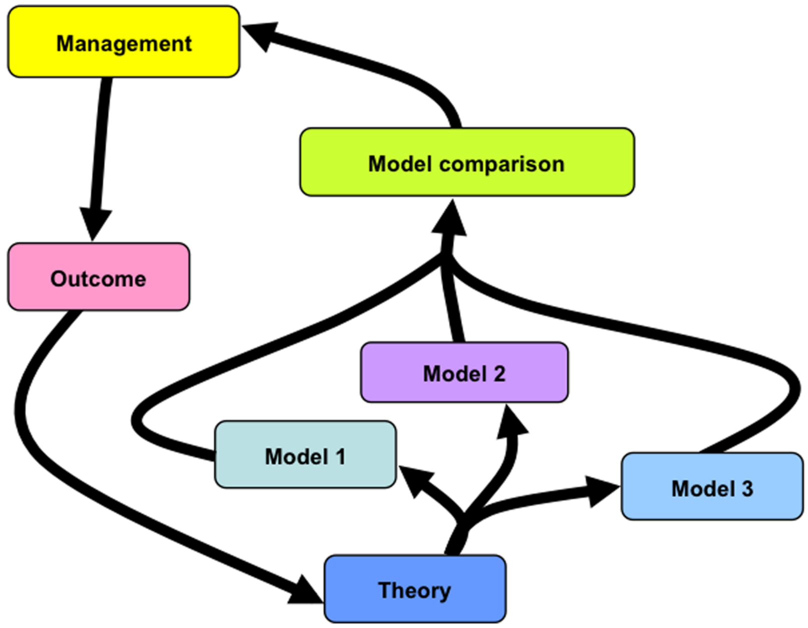

Fig. 1. Schematic depiction of the relationships between ecological theory, models and management. Note that more than one model can correspond to a given theory, multi-model comparison informs management decisions, and management outcomes may feed back to theory.

reduce by-catch losses).

Identifying Models that are Relevant to Management Decisions

While there are merits and drawbacks of different modelling approaches, some frameworks may be better able to support management decisions under conditions of global change (Table 1). There are four classes of models commonly used to guide management decisions: expert opinion or rule-based models, statistical extrapolation, process-based models and detailed simulation models.

Traditionally, the most common approach to management has involved expert opinion or rules of thumb (Possingham 1996, Sutherland 2006). This approach is most appropriate where there is a need for repeated response to management problems that remain similar over time. It works well within a hierarchical institution, and facilitates integration of institutional constraints and legacy information from a history of management applications. While the development of a rule may take some time, expert opinion can be accessed rapidly in most cases, and in some cases is the only information available (O'Neill et al. 2008). However, the role of theory and the assumptions behind expert opinion and rules of thumb are rarely transparent, so there may be little potential for evaluating the assumptions that support models of this sort. Expert opinions inevitably are divergent (e.g., Czembor et al. 2011), although there may be techniques for building consensus among a group of experts (e.g., Delphi technique, Rowe and Wright 1999). It is also possible that the rules of thumb or expert opinion do not include adequate concepts of scale and uncertainty (e.g., Burgman 2005) that are a requirement for appropriate management under global change (see Box 1). However, when the main requirement is that a decision be made extremely quickly with very limited data, expert opinion or rule-based models have a clear time advantage over other types of models.

Another common approach to management decisions is extrapolation based on observed statistical relationships. A benefit as well as a potential drawback of these models is that they are based on data from past conditions of the system. When these data have been previously collected, rapid decisions based on statistical

Table 1. Potential benefits of different modeling approaches in a changing world (see text for more explanation) on a 1–3 scale where 3 is best.

Opinion or rule	Extrapolation	Process model	Complex simulation	Potential benefit
•••	••	•	•	Allows rapid response
•••	•	••	••	Integrates institutional requirements
•	•••	•••	•	Transparent assumptions
•	•••	•••	•••	Integrates and distributes uncertainty
•••	••	•	•	Lower data requirements
•	•	••	•••	Explicit scaling
•••	••	•	•	Ease of development
•	•	•••	••	Appropriate for projection

relationships may be possible. However, under conditions of global change, models based on the past behaviour of a system may not be suitable for projection forward (Williams et al. 2007, Lawler et al. 2010). For example, changes in climate are predicted to change the geographic range of many species (e.g., Elith and Leathwick 2009). Niche-based models such as MaxEnt (Phillips et al. 2006) use species occurrence data, and climatic conditions at those locations, to create correlations that are used to extrapolate the future range of species under climate change (e.g., Rodder and Lotters 2010). These models, however, do not explicitly include important ecological processes such as demographic relationships or interspecific interactions that may also limit geographic range. If these ecological relationships are also sensitive to climatic conditions, (e.g., perhaps the outcome of competition is a nonlinear function of temperature), their effects may not be incorporated in predictions based on extrapolation from current conditions. Because of this limitation, practitioners are increasingly recommending hybrid models that include both ecological mechanisms and correlational components (e.g., Thuiller et al. 2008, Cabral and Schurr 2010), where extrapolated changes in climate are linked directly to processes known to shape species' ranges such as abiotic and demographic constraints, species interactions and dispersal limitation (Davis et al. 1998, Buckley 2008).

When making decisions about the future, we must consider which approach is most robust to changing conditions that may be outside the scope of past conditions (Williams et al. 2007). For solely data-driven or statistical models, extrapolation beyond known data is particularly problematic, and sometimes impossible. On the other hand, the underlying assumptions of extrapolation models are often quite transparent, being based in statistical theory. In addition, statistical models do allow the sophisticated partitioning of uncertainty among fixed model elements. However, the correlative rather than causal nature of these models may limit our ability to determine the sensitivity of model predictions to alternative management strategies.

In contrast to expert opinion or rule-based models, but like extrapolation models, process-based models are built on explicit assumptions about how a system works. This transparency of assumptions is further enhanced by the mathematical formulation of process models. Whereas the assumptions of extrapolation models are based on statistical theory, the assumptions of process models are grounded in ecological theory. Like extrapolation models, process-based models also allow for the partitioning of uncertainty in model predictions. As a result, managers may target any part of the ecological process for evaluation of assumptions and updating of parameter estimates. Because these models are based on causal mechanisms rather than correlation, our confidence in extrapolating beyond known data is enhanced. Of course, there is always uncertainty about how an ecological process will interact with novel global change conditions. This uncertainty about which model is appropriate should always be acknowledged, and can be incorporated into our predictions using multi-model inference (e.g., averaging predictions across alternative models). In fact, comparing models with alternate process formulations can inform management regarding the range and probability of given outcomes (Fig. 1). One less avoidable drawback of this approach is that the development and comparison of process-

Box 1

"Are we lost in parameter space?" and other questions to ask when developing a process-based model

The advantages of process-based models cannot be taken for granted. Some vigilance is required to ensure that the model aligns with management needs in a changing world. We suggest that the following questions should be addressed during model development.

Tactical or strategic? Management needs that are more immediate may require tactical models that include details specific to one or a limited number of systems, locations and periods of time. Long-range planning requires more strategic models that generalize across conditions encountered at different times and places. With increasing uncertainty about future conditions, the relative importance and utility of tactical models may appear to rise. However, managers faced with increasing uncertainty also require a robust understanding of the process being modeled, which is more likely to be derived from a more general model. There is often utility in the combined use of separate tactical and strategic models, to simultaneously address different management needs (Holling 1966).

Is the scale of the process in flux? Global change includes changes in climate, habitat connectivity and nutrient dynamics at various spatial and temporal scales. If key scales of a process are likely to be in flux over the period targeted for management, the model should allow an exploration of how these changes affect outcomes. Changing the scale of a process can alter the relative importance of key drivers, or disrupt the process altogether.

What are the other scales to consider? When modeling processes at the scale of interest (e.g., the forest stand), the conditions at this scale may depend on linked processes at scales above (landscape, region, continent) and below (local, microsite, seedbed). In some cases this linkage can be safely incorporated into constant or trended parameter values (e.g., increasing CO_2) leading to a simpler and easier to interpret model formulation, but in other cases the dynamics of the linkage must be included in the model.

Are drivers in flux? If global change is expected to alter the relative importance of key drivers, it is especially important to consider alternative process models. A model-averaging approach can be used to account for shifting drivers. It may be advisable to lower the bar for inclusion of alternative models during the model averaging process when we suspect fundamental changes in the focal ecological process over time.

Can we tune the frequency and magnitude of extreme events? Because the frequency and magnitude of extreme events are in flux with global change, models must allow for an exploration of how this variation affects dynamics.

Are we lost in parameter space? Complex simulation models can be process-based, but a highly dimensional model will be difficult to analyze. As the number of estimated parameters increases, the size of the parameter space (i.e., the number of possible combinations of parameter values) increases, and the potential for an informative sensitivity analysis declines.

based models requires more resources (information, time and ability) than rule-based models and extrapolation models.

Detailed simulations of specific systems are a heterogeneous category of models that may range from very detailed, but purely process-based, descriptions to mixtures of rule-based, statistical and process-based components. While complex simulation models often include descriptions of ecological systems that are based on theory, the explicit mathematical formulation that corresponds to the simulation rules may not be provided, clouding transparency. In addition, the use of statistical relationships may be problematic for projection. Even when purely process-based, these complex simulation models include a larger number of parameters and functions than is typical for process-based models. Simulating a specific system in such detail can facilitate the investigation of management interventions at multiple spatio-temporal scales, and makes full use of available information. However, the complexity of a detailed simulation model can obscure even the most explicit assumptions. Further, some assumptions may be violated inadvertently because of programming structure.

These simulation models are also data intensive. In most cases, limited resources will prevent the parameterization of more than one detailed model, limiting opportunities for multi-model inference (Carpenter 2003). Such analysis is essential to produce meaningful predictions. Valle et al. (2009) found that alternate modeling assumptions in the forest stand simulation model SYMFOR can account for 66–97% of the variance in predicted stand dynamics. While the authors were able to complete this comparison of differing models formulations for SYMFOR, they note that it may be very difficult to do the same for exceedingly complex models.

Given a simulation model based on many interacting functions, searching or sampling the large parameter and function space sufficiently to support reliable insights may be an extraordinarily lengthy process. In the situation where there are many resources (e.g., time, data, money), and in the hands of an expert modeler who can clarify assumptions for managers, this can be an excellent approach for decision-making at a particular location. Generalizing from these results to another system, location or future global change condition, however, is more difficult than with similar process-based models because of the data requirements, and the analytical difficulties generic to complex simulations.

Modelling and Managing for Global Change: Challenges for Prediction

Of the four major classes of models we have identified, process-based models offer some clear advantages over other approaches for managing ecological systems in a time of global change. Process-based models provide transparent assumptions, the ability to extrapolate beyond known conditions, and the potential for easy analysis of multiple management scenarios. Greater use of these models, however, also presents significant challenges for managers and researchers alike. Here, we describe the challenges of using process-based models, and the emerging research needs required to model the responses of ecological systems to global change.

Appropriate scales and complexity

Successful modeling implies a series of compromises regarding the resolution, scale and complexity of the included spatial, temporal and ecological processes, where simplification is achieved using our understanding of the system. However, our intuitions about what spatial and temporal scales are relevant, and what degree of model complexity is appropriate, may be unreliable when modeling for global change predictions.

In addition, some authors have argued that one of the reasons for the gap between ecological theory and management policy is that the spatial and temporal scales of much experiment and modeling are not matched with management scales (Stevens et al. 2007). Just considering the spatial axis, models constructed to guide local decisions will require decisions about: the size of the area described, the spatial features within that area which will be included, the local, regional and global spatial processes that affect these features, and the connection to both temporal and ecological processes.

Decisions about the relevant spatial and temporal scales and ecological processes that influence a response of interest (e.g., a population growth) can be guided by theory. For example, Rayfield et al. (2009) considered the connectivity of habitat patches for American marten (*Martes americana*) and its two primary prey species to determine the optimal area and arrangement to achieve management objectives. This kind of process-based approach to reserve design also allows for modification of the relevant mechanisms of under future climate scenarios.

Global change may alter the relevant spatial or temporal scales of our local management model. Forest stand growth models are typically parameterized for specific species and regions (Porté and Bartelink 2002). These models traditionally focus on change in forest stand characteristics (e.g., basal area), since foresters typically make decisions (e.g., harvesting) at the stand level. It seems clear that models of forest stand dynamics should be related to the scale at which management decisions are made. However, in light of climate change, processes operating at scales different from the scale of decision-making may be critical to description and prediction (Sturtevant et al. 2007), forcing us to reconsider the scale and scope of models required to answer management questions. In the case of forest dynamics, global atmospheric trends in carbon may be important for making predictions about stand growth (Purves and Pacala 2008). In some cases, metamodels that integrate two or more spatial scales and the corresponding processes (Papaik et al. 2010) may be a useful approach.

In addition to reconsidering the relevant spatial or temporal scales for our predictions, we may also need to reconsider which ecological processes may be relevant. For example, initial projections of future fish productivity and fishing yields in a global warming scenario were developed by scaling up the food web using temperature-dependent primary productivity (Sarmiento et al. 2004, Cheung et al. 2010). Cheung et al. (2009, 2010) predicted northern range shifts, and northern increases in fisheries catch potentials. The focus on the effects of temperature on a basal trophic level seems a reasonable and process-based approach to predicting climate change impacts on fisheries. However, it was soon discovered that other, perhaps less obvious, climate change factors, such as ocean acidification and decreased oxygen levels, resulted in decreases in predicted fisheries catch by 20–30% (Cheung et al. 2011). Moreover, even this more sophisticated approach to global change does not consider the direct effect of temperature on secondary productivity, which could also significantly reduce fish production (Lopez-Urrutia et al. 2006, O'Connor et al. 2011). Identifying which processes are relevant and how they change with climate conditions is no simple task.

Additional sources of uncertainty related to global change

While process-based models may be superior for extrapolation to novel conditions, it is clear that global change will reduce our confidence in these predictions, even when we are reasonably certain that we have identified the appropriate spatial and temporal scales and the relevant ecological processes. Most practitioners are aware that models based on observational data have two sources of uncertainty in their predictions: data measurement error, and process approximation error. These uncertainties can be differentiated using hierarchical models including (Bayesian) state-space modeling approaches (Clark 2007). One major impact of global change on our ability to model ecological systems is the requirement that we consider additional types of uncertainty stemming from the fact that there are no observational data available.

Additional sources of uncertainty arise when the model of local ecological processes requires inputs describing larger scale land use or climate change. For example, there are many General Circulation Models which have various algorithms, parameterizations and scenarios of future production of greenhouse gases that all contribute to differences in the predictions of climate. When creating an ecological management model it may be unclear which of these approaches are the most appropriate (see Beaumont et al. 2008), which is troubling since the predictions of these models may vary widely for some aspects of climate (e.g., precipitation). Climate predictions may also focus on mean conditions when extreme events or variance are most important for the organisms under study. Moreover, circulation models are generally created to make predictions over large geographical regions and will require downscaling to produce predictions for local and regional scales (see discussion in Littell et al. 2011).

Uncertainty in the rate and magnitude of changing climate factors at the local or regional scale is compounded by uncertainty in the responses of ecological processes to these changes. In many cases, it is not yet clear if a process (e.g., predation) changes linearly with temperature, hyperbolically with precipitation, or whether the response depends on another factor entirely. Some uncertainty is inherent in the process, as in larval dispersal of coastal marine species (Siegel et al. 2008), while other uncertainty may represent a research gap in relating a process to climate factors. For example, a simple conceptual model assumes that temperate and polar regions will experience the greatest impact from climate change because the expected changes in temperature are greatest in these regions. However, recent work on biogeographic variation in thermotolerance indicates that tropical insects have less tolerance for temperature variability than those of temperate regions. Therefore, the number of species extinctions may be greater in tropical areas (Deutsch et al. 2008). The assumption that tropical and temperate insects will respond in the same way to climate change clearly leads to a different conclusion than a model based on varying responses. It is possible that new ecological research can better characterize and perhaps reduce this uncertainty in the ecological response. But in the absence of such information, management scenarios should consider the range of possible uncertainties in ecological responses.

Legacy effects

While global change may focus our modeling effort forward towards uncertain future conditions which alter ecological processes, we also need to look backwards, since historical, temporal and spatial patterns of natural systems also can influence our ability to predict the results of future change. Past abiotic events, spatial configuration and species assemblages are known to constrain subsequent ecological processes (known as legacy effects; Peterson 2002, James et al. 2007, Cuddington 2012).

While standard statistical techniques routinely use past conditions to predict future states, legacy effects can be particularly long-lasting, far beyond durations that are typically used as a frame of reference. Plow horizons in soils can last hundreds of years (McLauchlan 2006), and such changes in abiotic conditions can alter population and community dynamics for long periods, sometimes even more so than current land uses. In addition, the history of populations also can constrain genetic or culturally transmitted information to a subset of its past breadth, so that, for example, a population no longer contains the genetic variability that would have enabled it to respond to novel conditions. When attempting to extrapolate forward into novel conditions, past events, even past management activities, often need to be considered.

Combinations of legacy effects and accelerated change may have unprecedented impacts. Species introductions are escalating with increasing trade (Ewel et al. 1999), and some invasive species produce long-lasting changes to the ecosystem that persist after their removal (e.g., elevated nitrogen levels in the soil following invasions by nitrogen-fixing plants; Liao et al. 2008). Such legacy effects are important contributors to the success of subsequent invaders and native species and can cause problems for restoration following invasion. Currently, legacy effects have been modeled using statistical or simulation approaches (e.g., Gimmi et al. 2012), however, these types of relationships call for process-based models that explicitly include mechanisms which incorporate time-dependent responses in the form of time lags or irreversible changes in land use that constrain future ecological responses.

Threshold dynamics

In some systems, nonlinear responses to changes in environmental conditions or species densities make the system more likely to abruptly cross a threshold from one ecosystem state to another (i.e., alternative stable states, see Beisner et al. 2003). Such threshold effects are a particular challenge for both management and modeling, even if we were working in the absence of global change. Nonlinear responses can lead to a small change in conditions resulting in a large change the system, and in some cases a similar small change in the reverse direction will not produce a reversal of state (e.g., when clear lakes become dominated by algae or when vegetated regions in arid landscapes become barren). Lengthy data series are required to confirm the presence of such dynamics (e.g., Bestelmeyer et al. 2011), but such data are unlikely to exist given the current rates of rapid global change. Moreover, Suding and Hobbs (2009) note that human impacts may increase the range of systems where such threshold dynamics are likely to occur.

Under rapid global change, communities and ecosystems may also have new quasi-equilibrium states (Polasky et al. 2011). For example, Hughes et al. (2007) found that coral reassembly after bleaching depended on whether herbivorous fish where present in high density or were absent.

Overfished areas had different, novel, community states. Global change events clearly present novel combinations of external drivers that in turn can create novel system states from which it is difficult to recover to more desirable states. While rapid global change may preclude strong evidence that a system can undergo threshold dynamics, scenario imaging and multiple model formulations can be used to explore the management option space.

Socio-economic impacts

In light of global change, management strategies that mitigate both economic and ecological impact will have great value. Moreover, there has been great success in the use of models that integrate both economic and ecological factors to evaluate management strategies (Epanchin-Niell and Hastings 2010). Management decisions may alter when financial, sociological and biological factors are all included in the evaluation process. For example, the removal of coastal vegetation for development (i.e., mangrove swamps and salt marshes), can expose the shoreline to greater flood surge. At the same time, greater flooding from storm surge is predicted with global climate change due to rising sea levels and increased storm intensity caused by rising water temperatures (IPCC 2007, FitzGerald et al. 2008). The protection and restoration of coastal wetlands can be more cost effective than barrier construction as a means to reduce storm damage (Halpern et al. 2007, Costanza et al. 2008, although see Francis et al. 2011).

One framework for jointly modeling ecological and socio-economic systems is that of ecosystem services. Ecosystem service models that integrate ecological and climatic processes with management constraints will be most useful, although it is anticipated that financial and sociological factors will be subject to the same rapid change and uncertainty which is associated with ecological processes in a time of global change.

Moreover, the dynamics of the cost and effectiveness of management strategies may exhibit some of the same kinds of nonlinear responses that we find in ecological systems. Wintle et al. (2011) modelled optimal management strategies for the South African fynbos. This habitat boasts a high percentage of endemic plant species, but climate change predictions suggest that this region will be subject to more frequent fire events, which could lead to the destruction of plants before they reach reproductive maturity. The authors find that the optimal management strategy depends non-linearly on the available budget. At low budget, fire management is the most effective strategy because every dollar results in a larger increase in population persistence. At high budget, an initial investment in habitat management is most important, followed by fire management as diminishing returns are realized from habitat protection. Process-based models that describe both the cost and effectiveness of proposed management strategies therefore have an important role to play in determining optimal solutions.

Conclusions

Global change is altering the context of management decisions (e.g., climatic, economic and land-use conditions), and therefore altering the ability of different predictive tools to inform these decisions. Process-based models are particularly appropriate to guide management decisions under conditions of ubiquitous and rapid global change. Such process-based modeling may guide management decisions, but global change requires that we pay particular attention to the appropriate spatial and temporal scales describing a relevant ecological process, the types of uncertainty involved, effects of past conditions, the possibility of threshold dynamics, and the importance of socio-economic feedbacks. Unfortunately, knowledge of the relevant processes that may determine a system's response to future conditions is extremely limited, and basic models of these processes may be nonexistent. These challenges necessitate a clear line of communication between scientists and managers in developing models for management, and a willingness to alter strategies as models are improved, with particular emphasis on the underlying ecological theory, assumptions, and appropriate level of complexity.

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