Ecological Modelling 263 (2013) 174–186

Contents lists available at SciVerse ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel

Review

Evaluating ecological resilience with global sensitivity and uncertainty analysis

Stephen G. Perz[a,*], Rafael Muñoz-Carpena[b], Gregory Kiker[b], Robert D. Holt[c]

[a] Department of Sociology and Criminology & Law, University of Florida, Gainesville, FL, USA
[b] Department of Agricultural and Biological Engineering, University of Florida, Gainesville, FL, USA
[c] Department of Biology, University of Florida, Gainesville, FL, USA

ARTICLE INFO

Article history:
Received 7 February 2013
Received in revised form 24 April 2013
Accepted 26 April 2013
Available online 10 June 2013

Keywords:
Resilience
Complexity
Uncertainty
Tipping points
Ecosystems
Sensitivity analysis

ABSTRACT

Concern about catastrophic tipping points has motivated inquiry to better understand ecosystem dynamics in the presence of human action. This requires that we confront multiple challenges in the evaluation of complex systems. One challenge is that resilience has proven difficult to quantify; another issue is that the value of model complexity relative to system complexity is disputed; and finally, local methods for assessing uncertainty are inadequate for more complex models. We address these three challenges simultaneously by proposing a means of evaluating ecological resilience via employment of global sensitivity and uncertainty analysis and comparing models of varying complexity. We suggest that probability distribution functions in output from global sensitivity and uncertainty analysis can be interpreted in terms of ball-and-cup diagrams used in systems theory to visualize ecological resilience. This permits quantification of ecological resilience in terms of the probability of whether a system will remain in a pre-existing state or shift to a different state. We outline the methods for using global sensitivity and uncertainty analysis to evaluate ecological resilience and provide examples from recent research. We highlight applications of these methods to assessment of ecosystem management options in terms of their ramifications for ecological resilience.

Contents

* Corresponding author at: 3219 Turlington Hall, University of Florida, PO Box 117330, Gainesville, FL 32611-7330, USA. Tel.: +1 352 294 7186; fax: +1 352 392 6568.
E-mail address: sperz@ufl.edu (S.G. Perz).

0304-3800/$ – see front matter © 2013 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.ecolmodel.2013.04.024

1. Introduction

Human action increasingly affects global ecosystems (Millennium Ecosystem Assessment, 2005; Intergovernmental Panel on Climate Change, 2007), pushing them toward potentially catastrophic “tipping points” (Scheffer, 2009; Scheffer et al., 2009), beyond which systems are unable to return to their initial states. This concern has prompted calls for greater attention to research and education concerning tipping points and broader issues of resilience in complex dynamic systems (AC-ERE, 2009; Stafford et al., 2010). Key to such efforts is the analysis of social–ecological interactions (Pickett et al., 2005), particularly through applications of dynamic simulation models (Liu et al., 2007) which capture key processes that can shift social–ecological systems from one state to another.

Three lines of inquiry have sought to understand complex systems for the sake of anticipating and avoiding radical changes in socio-ecological systems. First, there is a growing literature on the measurement and evaluation of resilience. A priority in the resilience literature has been to develop methods to identify the conditions under which complex systems remain in a pre-existing state or surpass a tipping point and thereby shift to a different state, as opposed to exhibiting non-catastrophic dynamics (e.g., Holling, 1996; Gunderson and Pritchard, 2002; Cumming et al., 2005; Scheffer, 2009). Second, increasing computing power has stimulated interest in the relationship between model complexity and system behavior (e.g., Nihoul, 1994; Snowling and Kramer, 2001; Ascough et al., 2008). There, inquiry has focused on the significance of model complexity for model output, due to debate over the question of whether more complex models are more likely to reveal the potential for transitions among multiple system states (e.g., Waldrop, 1992; Scheffer, 2009). And third, there is growing concern among modelers about how best to evaluate the implications of interacting sources of uncertainty in models, a concern that has prompted development of new methods to evaluate model uncertainty for its effects on model output (Saltelli et al., 2000, 2004, 2008). Parallel to concerns among modelers are similar preoccupations among ecosystem managers who must make decisions under conditions of uncertainty about system dynamics and tipping points. These three areas of research are in fact interrelated, and each highlights challenges to the assessment of complex systems for ecosystem management.

Section 2 of this paper therefore reviews the literatures on these lines of inquiry. In the process, we combine contributions from engineering and ecology (Gattie et al., 2007; Schulze, 1996). From engineering, we draw insights concerning complexity in model design and the evaluation of uncertainty in model predictions; and from ecology, we employ the concept of ecological resilience applied to understanding complex dynamics in social–ecological systems. We begin by reviewing relevant literature on three topics: (1) the evaluation of ecological resilience, (2) the relationship of model and system complexity, and (3) the relationship of model complexity and uncertainty. We then propose a means of unifying these literatures using global sensitivity and uncertainty analysis (Saltelli et al., 2000, 2004) to evaluate ecological resilience. This review motivates the first of our three main arguments: analysis of model uncertainty permits assessment of ecological resilience, including the identification of different system states. In particular, we suggest that changes in model inputs map onto changes in model outputs, which can be interpreted in light of ecological resilience. This argument integrates work on resilience and uncertainty; however, implementation requires a concrete methodology to put this integration into practice.

Section 3 therefore outlines the methods of global sensitivity and uncertainty analysis (GSA/UA) as a means for evaluating ecological resilience. Sensitivity and uncertainty analyses are complementary and usefully implemented together, so we refer to their joint operation as GSA/UA. We show how output from GSA/UA for a given model indicates in probabilistic terms the range of possible values for an indicator of system states, which in turn provides quantitative information about uncertainties in important simulated system components as well as insights into the ecological resilience of the system.

For “proof of concept,” Section 4 of the paper illustrates the implementation of GSA/UA by reviewing three previously published mechanistic dynamic models of ecosystems. To each, we apply GSA/UA in order to highlight its utility for quantitatively assessing model uncertainty and ecological resilience, and to show its value in applied contexts such as ecosystem management. Our first example models the effects of climate change and sea level rise on coastal habitats for shorebird populations; in this example, the application of GSA/UA reveals high probabilities of observing multiple possible system states. Furthermore, as climate change occurs, the relative probabilities associated with different system states change over time, which suggests dynamic shifts in the system and its ecological resilience. This substantiates our first argument and permits conclusions about model uncertainty and ecological resilience in terms of the probability of observing different system states. The second example focuses on phosphorus concentrations and vegetation dominance in a wetland ecosystem and compares models of varying complexity. This provides an illustration of our second central argument: increasing model complexity can raise the probability of observing multiple and quite distinct system states. The third example takes up the question of how GSA/UA of ecosystem models can be applied as a practical tool in ecosystem management for ecological resilience. We present a population model for an endangered species and evaluate management decisions using a Monte Carlo filtering procedure in GSA/UA to reflect management strategies in order to see if the resulting model output indicates reduced probabilities of observing undesirable system states. This provides an illustration of our third main argument, that GSA/UA has applications to ecosystem management for ecological resilience by permitting observation of the probabilities of different system states under specific management regimes defined by subsets of distributions in uncertain model inputs.

Given this review of case studies of GSA/UA applied to ecosystem models, we conclude in Section 5 by suggesting that GSA/UA provides a basis for the quantitative evaluation of ecological resilience. In particular, we discuss the use of GSA/UA to support ecosystem management, notably as a tool to respond to concerns about uncertainty in adaptive management (Gregory et al., 2006).

2. Literature review: resilience, complexity and uncertainty

2.1. Resilience in social–ecological systems

In systems theory, resilience is typically depicted in terms of “system states” subject to “disturbances” that can cause shifts among states (Carpenter and Brock, 2004; Holling, 1996; Gunderson and Pritchard, 2002; Ludwig et al., 1997; Scheffer, 2009). Complex systems are often characterized as having multiple possible system states, and encompassing processes that push the system toward one state or another, called “system attractors.” Resilience thought often invokes a “ball-and-cup” analogy that allows visualization of the behavior of complex systems, where system state (the position of the ball) is defined by the shape of a “basin of attraction” (the cup) in which the system may move. Fig. 1 (top panel) illustrates the ball-and-cup analogy. Basins of attraction reflect the tendencies of system attractors and define the possible states of a system.

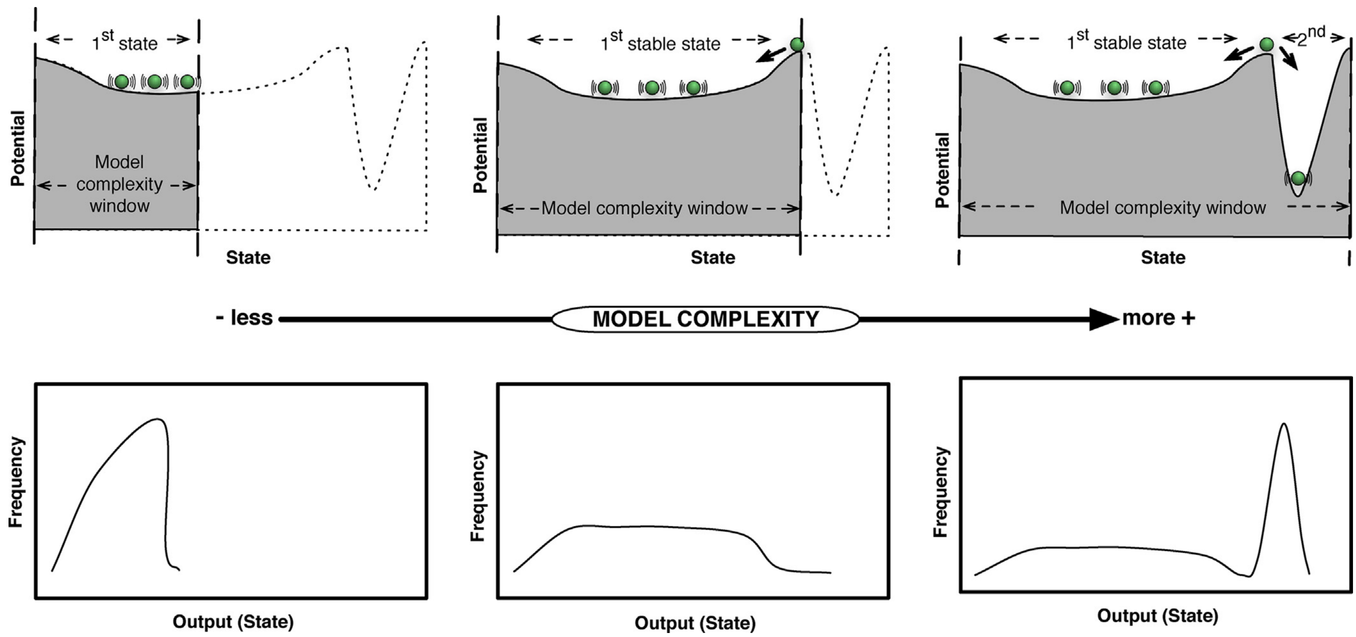

Fig. 1. Ball-and-cup diagrams to illustrate resilience in terms of system state (top) as mirrored by probability distribution functions from global sensitivity/uncertainty analysis (bottom) for an indicator of system state, from low model complexity (left) to high complexity (right).

Disturbances may prompt a system to shift from one state to another by moving from one basin of attraction to another (Gunderson and Pritchard, 2002; Cumming et al., 2005; Scheffer, 2009). This occurs at "tipping points," where a system stands between two attractors and with slight changes in initial conditions will move into either one basin or the other, resulting in different system states. Scheffer (2009) also notes that disturbances can shift the shape and distribution of basins of attraction; in other words, the "stability landscape" itself can be altered. Such shifts in landscapes themselves may prompt systems to move and thus change dramatically from one state to another. Hence in the context of Fig. 1, one could imagine the shapes of basins of attraction moving over time as a system incurs disturbances, thus also shifting the system state one is likely to observe.

Disturbances and shifts in system states have focused attention on "critical transitions," where a disturbance creates the possibility of pushing a system into an undesirable state (Scheffer, 2009; Scheffer et al., 2009). A critical transition may yield an undesirable system state due to the loss of key functions, or because the corresponding basin exhibits a strong alternative attractor that makes it difficult for the system to return to its previous state. The potential existence of critical transitions has driven a desire to articulate an analytical strategy for the quantitative evaluation of system resilience.

There are many different definitions of resilience (Strunz, 2012). For our purposes, it is useful to distinguish between "engineering resilience" and "ecological resilience." Whereas engineering resilience refers to the speed with which a system returns to its initial state after a disturbance (Holling, 1996; Rodriguez-Iturbe et al., 1991a; Scheffer, 2009, pp. 101–103), ecological resilience is defined as the degree of disturbance a system can incur and still remain in its pre-existing state (Gunderson and Pritchard, 2002, pp. 5–7; Scheffer, 2009, pp. 101–103). We focus on ecological resilience, while noting that this definition of resilience can be regarded as pertaining not only to ecosystems, but to complex systems in general.

Systems are more ecologically resilient if they can move around more in a given basin of attraction in the presence of a disturbance without falling into other basins. The cup-and-ball metaphor permits one to visualize multiple dimensions of resilience. Visually, ecological resilience refers to the size – both width and depth – of a basin of attraction (Fig. 1, top panel). Within a given basin, the sides of the surface may be steep – so that a ball, if moved a short distance, rapidly returns to its initial position – or shallow, being flat within a given domain. In the latter case, a ball when moved does not tend to return to its precise former position, but stays where it is put. Crucial to ecological resilience is that a system stays within a given basin of attraction, despite the existence of other basins with attractors and disturbances that cause systems to move around.

Concern about human perturbations leading to undesirable ecosystem states has stimulated interest in the resilience of social–ecological systems (Adger et al., 2005; Folke, 2006). Resilience has proven to be a difficult concept to define operationally for empirical evaluation, so concerns about social–ecological systems have driven efforts to move "from metaphor to measurement" of resilience (Carpenter et al., 2001; Folke et al., 2003; Cumming et al., 2005). These efforts highlight the importance of identifying social and ecological indicators of system state and using these indicators to monitor the persistence or pattern of change in a system after a disturbance. This agenda necessitates identification of "critical thresholds" for key system indicators, which are values of the indicators that can constitute system tipping points, the crossing of which catalyzes a shift in system state. The analysis of ecological resilience thus becomes at least in part an exercise in determining whether a disturbance causes an indicator of system state to cross a critical threshold between two different states.

2.2. Model complexity and system complexity

A key tool for evaluating system resilience involves simulation models (Anderies et al., 2002; Mumby et al., 2006; Schlüter and Pahl-Wostl, 2007; Scheffer et al., 2009). Increasing computer speed and power allow increasingly complex models to be explored. While definitions of complexity vary (Mitchell, 2009), we focus on "engineering complexity" in terms of attributes of model design. Increasing model complexity involves modifying model structure through the addition of model components, parameters, boundary conditions, feedbacks and interactions. In principle, greater model complexity allows researchers to more closely approximate the processes in complex systems.

This drive toward increasing model complexity, however, has stimulated debate over the criteria for selecting models that best represent a given system (Snowling and Kramer, 2001; Muñoz-Carpena and Muller, 2009; Muller et al., 2011).[1] On the one hand, simple models may fail to adequately represent the system due to structural limitations stemming from their inability to capture key processes that govern system behavior (Nihoul, 1994). On the other hand, more complex models with greater information about the system may not necessarily be better than simpler models, due to the heavier (and more costly) requirements for estimation of parameters and state variables, which constitute additional sources of errors and biases (Ascough et al., 2008).

Debate about model selection is related to discussions of model complexity and the dynamics actually observed in systems. While simple models may produce complex dynamics for some systems (May, 1974; Waldrop, 1992; Mitchell, 2009; Rodriguez-Iturbe et al., 1991a; Scheffer, 2009), in other systems, additional variables or nonlinear relationships may be necessary to shift model output from stable to cyclical or chaotic dynamics (Rogers, 1981; Scheffer, 1991; Rodriguez-Iturbe et al., 1991b).

Given concerns about ecosystem tipping points, a crucial issue is whether a model can capture critical transitions from one system state to a radically different state. If simpler models yield findings suggestive of a single stable state when in fact two or more are possible, it is necessary to increase model complexity to encompass this broader range of possibilities. In particular, it is useful to systematically increase model complexity in order to compare model output regarding changes in system behavior and system states. We suggest that the strategy for model development should be to (1) begin with relatively simple models, (2) systematically add complexity as a means of comparing model output, (3) select the model that most closely approximates the system using statistical protocols, and (4) evaluate key system indicators in model output to evaluate possible system states.

To this end, we suggest the concept of the "model complexity window" to visualize model output across levels of model complexity in terms of systems theory. Moving from left to right in Fig. 1, we schematically increase model complexity, and the model complexity window becomes wider, allowing observation of multiple system states. In our illustration, a second system state becomes evident at a relatively high level of model complexity. Fig. 1 is based on an actual ecosystem model that we describe later in this paper (Section 4.2). We recognize that the system states revealed by widening the complexity window depend on the system and the models at hand. The shape(s) of the basin(s) of attraction may differ markedly among systems, such that more complex models of a given system may or may not reveal multiple possible system states.

2.3. Model complexity and model uncertainty

Increasing model complexity has directed attention to the related issue of model uncertainty (Snowling and Kramer, 2001). Many researchers have focused on model uncertainty as a means of appraising model value for applications such as ecosystem management (Bammer and Smithson, 2009; Gregory et al., 2006). There are numerous sources of uncertainty in models, as well as different typologies of such sources (Bammer and Smithson, 2009; Draper, 1995; Osenberg et al., 1999; Pascual et al., 2003). Distinct typologies of sources of uncertainty in models come from engineering (Saltelli et al., 2000; Shirmohammadi et al., 2006) and ecology (Osenberg et al., 1999; Clark and Bjornstad, 2004; Gregory et al., 2006; Ogle, 2009; Turley and Ford, 2009). For present purposes, we emphasize three sources of uncertainty in dynamic models: (1) errors in input data defining state variables (e.g., initial conditions); (2) uncertainty in parameter values; and (3) structural uncertainty, i.e., whether a model includes all necessary components, relationships and feedbacks of a system.[2] Data, parameter and structural uncertainties reflect limitations in knowledge about a system, and to the extent that a system is not well-understood, models of complex systems may yield unrealistic or misleading output. Recognition of multiple sources of uncertainty has prompted modelers to express unease about the value of model output for guiding management applications (Manson, 2007; Messina et al., 2008).

A common intuition is that adding model complexity reflects greater knowledge about the system of interest and thus reduces model uncertainty. However, some have suggested that complexity and uncertainty actually have a U-shaped relationship (e.g., Fisher et al., 2002; Hanna, 1993; Snowling and Kramer, 2001). Models of low complexity may have high uncertainty due to structural limitations in model design, and increased complexity reduces uncertainty by incorporating more processes and other information. However, each new parameter or variable also constitutes a new source of empirical uncertainty, since measurement error is inevitable. Thus at high levels of model complexity, uncertainty may rise because of the addition of system components and feedbacks. In particular, at high levels of model complexity, individual sources of uncertainty are more likely to exhibit interactions that can greatly increase overall model uncertainty (Lindenschmidt, 2006). In models with many interactions among sources of uncertainty, overall uncertainty may thus be amplified.

2.4. Model complexity, sensitivity/uncertainty analysis, and evaluating system resilience

The foregoing review offers three observations: (1) resilience can be evaluated schematically in terms of ball-and-cup diagrams that characterize possible system states among basins of attraction; (2) selection of simulation models must account for model complexity relative to system complexity, if system dynamics and attractors are to be adequately represented; however, (3) model uncertainty may exhibit a U-shaped relationship with model complexity, such that increasing model complexity can reduce the overall uncertainty of the model by spanning a larger array of possible outcomes, but highly complex models may also yield more uncertain output due to interactions among sources of uncertainty. We suggest that the apparent dilemma in observations 2 and 3 actually offers an important opportunity for the analysis of ecological resilience via identification of different system states. This opportunity arises from a critical review of established methods of sensitivity and uncertainty analysis (Saltelli et al., 2000).

With sensitivity and uncertainty analysis, one starts with a model with defined state variables and parameter values. Given these, a deterministic model will generate a single time-dependent trajectory describing system states over time (whereas a stochastic model will generally produce a range of potential outcomes).

[1] Beyond model complexity as related to system complexity, model selection is driven by the goals of the model in question, which in turn also affect model output. The citations here address this broader issue.

[2] We are aware that other typologies have identified other sources of uncertainty (e.g., Osenberg et al., 1999). For example, process uncertainty may involve changes in parameter values over time; stochastic uncertainty may arise in a system due to external forcing functions; and uncertainty may exist regarding the functional form of algorithms. GSA/UA may also handle these sources of uncertainty, though this question deserves further inquiry.

However, different initial choices for the state variables and parameters, as well as measurement errors, will lead to different trajectories of change, and possibly different system states. What is needed is a systematic protocol for describing how variation in model input factors (including their interactions) is related to variation in model output, and a means of evaluating which input factors exert the strongest influence on model output.

Sources of uncertainty and their effects on model output have not been studied exhaustively across a wide range of systems and models (Grimm and Railsback, 2005; Shirmohammadi et al., 2006; Muñoz-Carpena et al., 2007). There remain important limitations in established approaches to evaluating model sensitivity to sources of uncertainty. First, common methods of uncertainty analysis do not quantify the probability that a system will move toward one state or another. For example, scenario analysis addresses uncertainty by articulating different futures (Peterson et al., 2003; Soares-Filho et al., 2004; Alcamo et al., 2006), but it cannot quantify the probability of observing those futures. Second, traditional sensitivity analysis employs "local" or "one at a time" techniques, which assume that sources of uncertainty have linear effects on model outcomes and are independent of one another (Saltelli et al., 2000, 2004). In complex models with many components and feedbacks, this is unlikely to be the case.

To overcome these limitations, "global" sensitivity and uncertainty analysis (GSA/UA) is required (Saltelli et al., 2004, 2008). GSA/UA provides a systematic protocol for describing how variation in multiple model input factors (including their interactions) is related to variation in model output, as well as a means of evaluating which input factors exert the strongest influence on model output. GSA/UA systematically evaluates multiple sources of uncertainty. This is crucial because different sources of uncertainty may interact, generating non-linear effects on the uncertainty of model output. Output from GSA/UA reflects multiple sources of uncertainty going into a model, including interactions among sources. In the next section, we discuss the complementary roles of GSA and UA and outline implementation of GSA/UA.

For purposes of this section, a key issue concerns the utility of GSA/UA output for evaluating ecological resilience. GSA/UA generates probability distribution functions (PDFs) of key system indicators, which in turn allow visualizations of uncertainty (Morgan and Henrion, 1990), as shown in Fig. 1 (bottom panel). A PDF permits observation of the frequencies (or relative probabilities) of observing a modeled system in a specific state in terms of the value of an indicator of system state. A PDF quantifies the uncertainty in model output because it permits calculation of measures of dispersion in model output values. This quantification opens possibilities for comparing output uncertainty across models, indicators, locations and time points.

This brings us to the first of our three central arguments: a PDF of an indicator of system state can be interpreted as visualizing possible system states (Fig. 1, bottom panel). Because GSA/UA yields a PDF that shows the range of modeled values for an indicator of system state, we suggest that those values are related to possible system states at a given point in time. In effect, a PDF estimates the probability that a system in the presence of a disturbance will remain in a pre-existing state or shift to another as of a specific moment. By extension, if the basins of attraction of a system shift over time, then we can produce a time series of PDFs in order to observe consequent shifts in probabilities of seeing the system in different states. This provides a probabilistic basis for evaluating ecological resilience.

In particular, we suggest that the shape of a PDF permits appraisal of ecological resilience in terms of basins of attraction. PDFs from GSA/UA of dynamic simulation models reflect basins of attraction which in turn result from system attractors that make certain system states more likely to be observed. Specifically, the

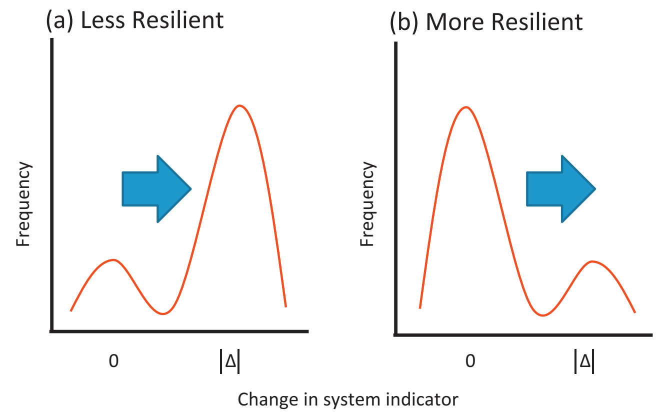

Fig. 2. Evaluating ecological resilience in multimodal probability distribution functions from global sensitivity and uncertainty analysis. GSA/UA generates a PDF that permits observation of probabilities that the system will remain in its initial state (0), or shift to another state (|Δ|). The larger the area of the PDF around |Δ|, the more likely the system is to shift to another state, thus indicating a lack of ecological resilience (panel A, left); the larger the area of the PDF around 0, the more likely the system will remain in its initial state, an indication of ecological resilience (panel B, right).

peaks in a PDF indicate the lowest or midpoint of basins of attraction in ball-and-cup diagrams (Fig. 1, top and bottom panels). Similarly, valleys in PDFs correspond to transition or tipping points between basins where attractors make it less likely to observe the system. Thus, we can relate the probability of observing a system in a given state (in terms of the values of a key system indicator) to the system's basins of attraction at a given point in time. Further, if basins of attraction themselves shift over time, we can evaluate a time series of PDFs to look for changes in probabilities of observing different system states.

Relating PDFs to system states gives an indication of where the lowest or midpoints of basins of attraction for a system are located. A system with one strong attractor will yield a tall and thin unimodal PDF with high probabilities centered on a single value for an indicator of system state (Fig. 1, left). By contrast, a system without a strong attractor will yield a flat and wide PDF with lower probabilities of observation spread over a range of indicator values within a basin of attraction (Fig. 1, middle). Further, a system with multiple attractors will yield a multimodal PDF that exhibits multiple peaks with troughs in between, indicative of multiple possible system states separated by a tipping point (Fig. 1, right). Finally, a system with shifting attractors will exhibit changing shapes in a time series of PDFs.

Analysis of PDFs in light of ecological resilience also provides a quantitative basis for assessing the probabilities that a system will shift from one system state to another. The cases of tall as well as wide unimodal PDFs suggest ecological resilience, since such PDFs imply that a system is able to move around in a basin of attraction without falling into another basin. This conclusion is reinforced to the extent that basins of attraction themselves remain stationary, resulting in a time series of similar unimodal PDFs. The case of a multimodal PDF is of particular interest, as it indicates multiple peaks in the output distribution which suggest different possible system states. For a multimodal PDF, we can not only observe the ranges of values in an output indicator that delineate basins of attraction and shifts in such basins over time, we also can calculate the proportional areas of the PDF within each basin of attraction, which corresponds to the probability of observing the system in each state. This allows determination of the probability of whether a model indicates that a system is more likely to remain in its present state or shift to a different state, and thus whether a system is ecologically resilient.

Fig. 2 illustrates two cases of PDFs with regard to ecological resilience. Here the horizontal axis indicates potential departures ($|\Delta|$) from an initial system state (0), and the areas under curves reflect the probability of observing the system in the initial state or another state. Whereas a larger area of the PDF corresponding to a basin indicative of a substantial change would imply low ecological resilience (Fig. 2a, left panel), a larger area corresponding to a basin indicative of limited change would suggest greater resilience (Fig. 2b, right panel). By extension, in systems with shifting attractors, the appearance of multimodal PDFs may indicate a point in time where it is becoming less probable that the system will stay in one state and thus more probable to shift to another. A time series of PDFs may thus reveal unimodal PDFs for a time, followed by a multimodal PDF, followed by a unimodal PDF with a mode of a very different value than before. Thus, GSA/UA not only evaluates multiple sources of model uncertainty, it also provides the basis for a probabilistic analysis of resilience that corresponds to systems theory concerning different system states.

3. Implementation of global sensitivity and uncertainty analysis

In practice, GSA and UA complement each other and operate in tandem. Whereas the role of UA is to propagate various input uncertainties onto model outputs, GSA determines how uncertainty in model output can be apportioned among different inputs. Thus, UA indicates the extent of uncertainty in a model, and GSA decomposes that uncertainty in order to identify its most important sources (Saltelli et al., 2000, 2008).

The logic of GSA/UA runs as follows. For a given model, one defines a range of possible values for each input factor (initial conditions, boundary conditions, parameters, model structure control factors, etc.). Ranges take distributions either based on empirical observations when available, or assumed standard distributions (normal, exponential, uniform, etc.). GSA/UA randomly samples from those distributions to select values for each input factor and creates input sets consisting of various combinations of input factor values. Iteration of this procedure with repeated random sampling permits systematic evaluation of the modeled system over many simulations (from hundreds to thousands) in order to observe whether different input sets yield variation in model output. One then performs UA to determine the degree of uncertainty in model predictions, along with GSA to identify the input factors and interactions most responsible for the uncertainty.[3] The many simulations involved together yield a PDF for each output indicator of system state. Where the output indicator is more sensitive to input factor values, the result will be wider PDFs indicating greater model uncertainty; and where many simulations yield similar output values, clustering in PDFs indicates system attractors.

We propose a GSA/UA framework as a systematic approach for characterizing ecological resilience. The framework uses two techniques (Muñoz-Carpena et al., 2007): a screening method (Morris, 1991), and a quantitative variance-based method (Saltelli et al., 2004). We combine these two techniques because evaluation of numerous input factors in complex models with many parameters and feedbacks is inefficient unless a screening method is applied first. For present purposes, we provide an outline of the procedures for implementation; a formal presentation appears in Appendix A.

A screening method provides a ranking of inputs in terms of their effects on output variation. This allows the user to focus on the most important inputs, i.e., those inputs to which the output indicator is most sensitive. We employ the screening method proposed by Morris (1991) and later modified by Campolongo et al. (2007) because its results are easily interpreted and it requires relatively few simulations. The Morris method calculates two sensitivity measures for each input factor: (1) the mean absolute value of the elementary effects, which estimates the overall effect of each individual input factor on the output; and (2) the standard deviation of the elementary effects, which estimates the higher-order contributions of the input factors (i.e., interactions) to model uncertainty (see Appendix A for additional details).

Next, GSA/UA generates a quantitative measure of sensitivity for each important input factor (Saltelli et al., 2000, 2004). This involves decomposing the total variance of the model output among the input factors, including first-order terms (denoting the proportion of total output variance due to individual input factors) and higher-order terms (denoting the proportion of variance due to interactions among input factors). From this decomposition we can calculate the first-order sensitivity index, defined as the proportion of the total variance attributed to single factors (see Appendix A for additional details). For a perfectly additive model with no interactions, the sum of the first-order sensitivity indexes equals the total variance of model output (Saltelli et al., 2008).

More complex models are generally not perfectly additive, and the first-order sensitivity indexes sum to less than the total variance. In this case, the quantitative variance-based technique is appropriate (Saltelli et al., 2000, 2004). Here the most commonly employed methods are the extended Fourier Analysis Sensitivity Test, or FAST, and the method of Sobol (Saltelli et al., 2000, 2004). To calculate the sensitivity index, variance-based techniques randomly sample the multi-dimensional sampling space defined by combinations of values for input factors. This allows identification of important higher-order terms but requires more simulations than does GSA/UA without interactions (see Appendix A for additional details).

GSA/UA procedures are model-independent. This means that they can be integrated with various dynamic simulation environments for immediate analysis of sources of uncertainty in model output, shown in Fig. 3. The basic procedure follows six main steps: (1) construct distributions of values for uncertain input factors; (2) generate input sets by sampling values from distributions for input factors, using either empirically generated or plausible distributions for those factors; (3) execute model simulations for the input sets; (4) perform GSA to obtain the sensitivity index; (5) employ a screening method to generate a subset of important inputs, and repeat steps 2 through 4 for those inputs; and (6) assess uncertainty based on PDFs of key output indicators of system state. This procedure can be repeated for each of a series of models that differ in terms of their complexity (see Appendix A for additional details). Integration of simulation models and GSA/UA for models of varying complexity thus permits evaluation of the effect of complexity on uncertainty by comparing PDFs for each model. In the next section, we outline three examples that illustrate the value of the proposed framework.

4. Case study review: examples of global sensitivity/uncertainty analysis of ecosystems

In this section we review examples of implementation of GSA/UA, not only for assessing ecological resilience, but also for evaluating options for managing ecosystems to avoid shifts to undesirable system states. Our examples are established ecosystem models previously developed and calibrated for specific

[3] Grimm and Railsback (2005) in their discussion of individual-based models of ecosystems suggest that one conduct a "robustness analysis", a kind of inverse of sensitivity analysis characterizing which output features of a model are robust to changes in assumptions and inputs. We suggest that recent advances in GSA/UA provide a powerful tool for carrying out such robustness analyses.

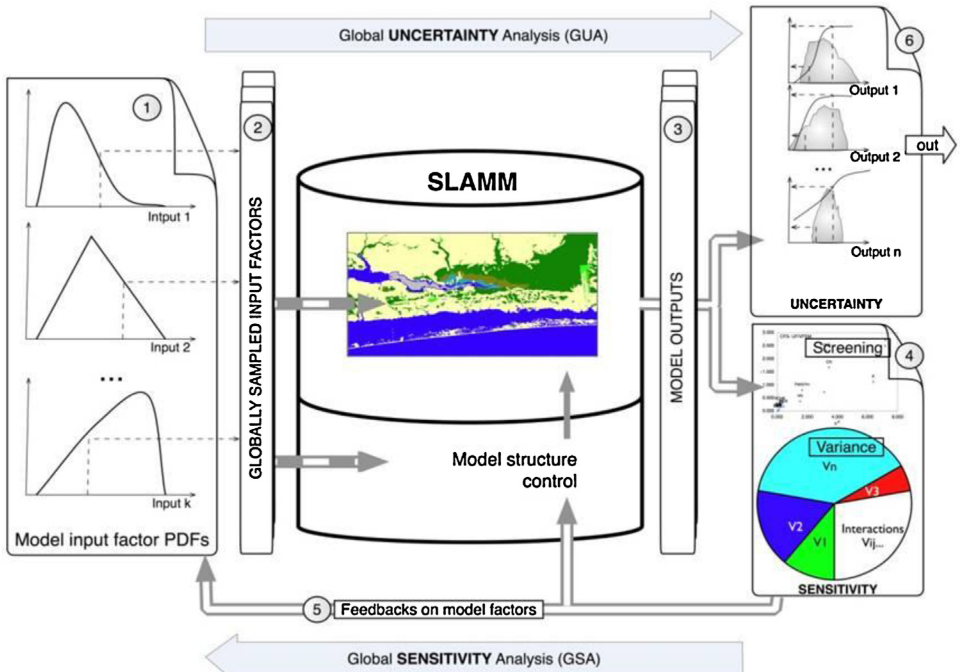

Fig. 3. A dynamic simulation modeling platform of a habitat model (SLAMM) coupled with global sensitivity and uncertainty analysis for integrated model development and resilience assessment. Numbers denote six steps in the model evaluation procedure: (1) construct ranges of values for uncertain input factors; (2) generate input sets by sampling values from ranges for input factors; (3) execute model simulations for the input sets; (4) perform GSA to obtain the sensitivity index; (5) employ a screening method to generate a subset of important inputs, and repeat steps 2 through 4 for those inputs; and (6) assess uncertainty based on PDFs of key output indicators of system state.

ecological systems, with the details contained in prior publications. The examples were also chosen because they involve mechanistic models that incorporate feedbacks which permit observation of nonlinearities and thus potentially complex dynamics, including possible shifts in system states germane to evaluation of ecological resilience. Finally, we chose our examples because they address our main arguments concerning (1) uncertainty and resilience, (2) complexity and resilience, and (3) resilience analysis and ecosystem management.

Specifically, we consider three recent case studies. Our first example (Chu-Agor et al., 2011) provides an illustration of a multimodal PDF with implications for ecological resilience in terms of probabilities of a shift from one system state to another. The second example (Muller et al., 2011) presents models of varying complexity, which yield PDFs of varying shapes. The third example (Chu-Agor et al., 2012) incorporates Monte Carlo filtering in GSA/UA to illustrate applications to ecosystem management for ecological resilience. In discussing each case, we focus on our key arguments, which relate uncertainty and complexity to ecological resilience, thus unifying the literatures on those three topics. Further details on each model can be found in the cited publications.

4.1. Vulnerability of coastal habitats to sea level rise

The first example illustrates the application of GSA/UA to an ecosystem model which yields PDFs that indicate multiple possible system states, as well as shifts in basins of attraction over time. Climate change stands to yield shifts in the extent and composition of coastal habitats, especially along shorelines. The Sea Level Affecting Marshes Model, or SLAMM (Clough, 2008) has been widely used to simulate wetland conversion and shoreline modification for the purpose of vulnerability assessment and decision making for coastal habitats (Park et al., 1993; Galbraith et al., 2002; McLeod et al., 2010). However, doubts remain concerning the suitability of SLAMM for management, due to uncertainties involved in selecting many of the model's input parameters (Craft et al., 2009).

Chu-Agor et al. (2011) therefore employed GSA/UA with SLAMM to evaluate uncertainties in climate change models for coastal habitat loss. They simulated changes in the land areas of both salt marsh and beach shorebird habitats on Santa Rosa, a barrier island in Eglin Air Force Base, Florida. GSA/UA generated PDFs for the two types of coastal habitat in order to explore their potential fates in the context of climate change and sea level rise during 21st century. Fig. 4 presents the resulting output PDFs for salt marsh and beach habitats in the study area for two points in time, the years 2060 and 2100. PDFs exhibit multimodal distributions for both habitats in 2060, and salt marsh in 2100. Beaches exhibit a multimodal PDF with three peaks in 2060, but by 2100, the PDF is unimodal with a large variance and indicates a likely decline in beach area. This study not only reveals multimodal PDFs, it also shows that GSA/UA can be used to observe PDFs at multiple points in time for evaluation of dynamics in probabilities of observing different system states. In this case, while both PDFs indicate multimodality, their shapes indicate changes in the relative land areas in salt marshes and beaches, which suggests shifts in underlying basins of attraction for the two key habitats.

These findings suggest a system in danger of being destabilized in 2060, with three possible system states corresponding to a rise, stasis or decline in beach area, followed by a reduction in beach area by 2100. The PDF for salt marsh is bimodal in both 2060 and 2100, and the peaks indicate either slight rises or larger declines in salt marsh. These findings indicate two very different but probable system states as regards salt marsh. Interestingly, the probability of maintaining salt marsh area is higher in 2060, but the probability of salt marsh decline is higher in 2100. GSA/UA with SLAMM suggests that via sea level rise, climate change poses a threat to coastal habitats in the form of changes in system states as key habitats appear likely to exhibit reductions in their land areas. This case thus illustrates our first main argument, that output from GSA/UA

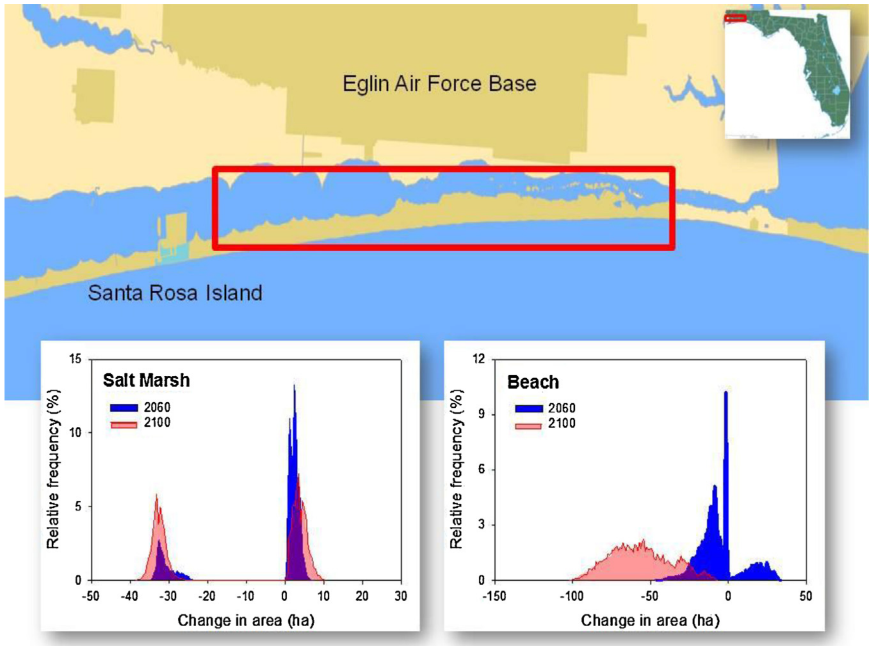

Fig. 4. Global sensitivity and uncertainty analysis applied to the SLAMM habitat model. The top panel shows the study region of Santa Rosa Island in Eglin Air Force Base, and the bottom panel shows PDFs for salt marsh and beach habitats in 2060 and 2100. Note that the salt marsh PDF is bimodal, indicating the existence of different system states. PDFs for both habitats indicate likely shifts over time due to sea level rise.
Adapted from Chu-Agor et al. (2011).

can be applied to the evaluation of ecological resilience, including for ecosystems with shifting basins of attraction over time.

4.2. Phytoplankton and macrophytes in a wetland ecosystem

In our second example, we focus on comparisons of system states across models of varying complexity. This affords an evaluation of the effect of model complexity not only on the shape of PDFs in general but specifically on the likelihood of observing multimodal PDFs. This example addresses our second main argument in this paper, namely that model complexity affects the shape of PDFs and observation of multimodality in system states, which is important for evaluating ecological resilience.

The second example comes from Muñoz-Carpena and Muller (2009) and Muller et al. (2011), who model phosphorus concentrations in surface water in the Everglades wetland of south Florida. The Comprehensive Everglades Restoration Plan (CERP) is a multi-billion-dollar, multi-decadal effort seeking to restore water flows and phosphorus concentrations to historical levels in south Florida wetlands. Phosphorus concentrations are linked to the dominant vegetation, which in turn influences other components of the Everglades ecosystem. To support CERP, the TaRSE (Transport and Reactions Simulation Engine) framework was designed to model water quality with particular attention to phosphorus levels (Jawitz et al., 2008).

Muñoz-Carpena and Muller (2009) and Muller et al. (2011) apply GSA/UA to TaRSE in order to evaluate the possibility of observing different system states in terms of dominant vegetation by accounting for uncertainties in the input factors affecting phosphorus levels. In particular, they constructed three models of differing complexity and used them as inputs into GSA/UA, performed for each model. Whereas the "low complexity" model had only eight input factors to GSA/UA, the "medium complexity" model had 12 input factors and the "high complexity" model had 16. The rise in the number of input factors reflects additions of new parameters and feedbacks to the model, which modified model structure.

Fig. 5 summarizes the findings from Muñoz-Carpena and Muller (2009) and Muller et al. (2011), showing the model parameters and feedbacks (top panel), with model complexity increasing from left to right, and the corresponding PDF outputs (bottom panel). The "low complexity" model (bottom panel, at left) yields a tall unimodal PDF suggestive of a single, strong system attractor. By contrast, the "medium complexity" model (bottom panel, middle) produces a flat and wide PDF, indicative of a single weak system attractor. The "high complexity" model generates a bimodal PDF, which suggests two possible system states, where vegetation is either phytoplankton-dominated or macrophyte-dominated. The two basins of attraction are very different in shape, with a flat high variance shape for the phytoplankton-dominated state and a tall low variance shape for the macrophyte-dominated state. The wide area represents conditions for which macrophytes are suppressed and mimics that of the "medium complexity" model, where phytoplankton dominates the surface water system dynamics. The sharp end-point corresponds to conditions when die-off of macrophytes is caused by their explosive growth, which results in draining of porewater phosphorus at a rate faster than diffusion or oxidation can supply it back to the system (Muller et al., 2011).

Importantly, the two system states observed in the high complexity model correspond to empirically observed stable states in wetland ecosystems (Beisner et al., 2003; Scheffer, 1990; Scheffer et al., 1993). Given the wide range of conditions explored, as captured by GSA/UA in the many possible combinations of input factors considered, it was expected that the models would capture both states of the system. However, this was only achieved with the high complexity model. At least in the case of Everglades vegetation, additional model complexity is required to observe multimodality; lower levels of model complexity are not sufficient to capture the known tipping point. Model complexity is therefore important for observation of multiple system states, and is thus eminently relevant to observing multiple system states and assessing ecological resilience.

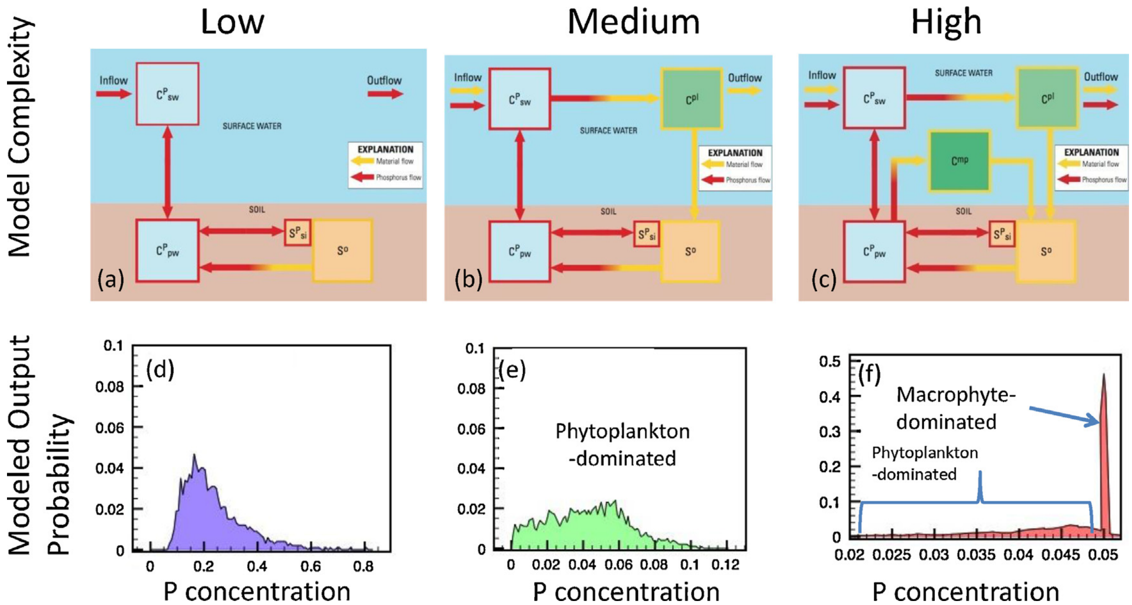

Fig. 5. Global sensitivity and uncertainty analysis applied to a biogeochemical wetland model of the Everglades, with three models of differing levels of complexity. Increasing complexity by adding parameters and feedbacks, and therefore input factors in GSA/UA, changes the shape of the model output PDFs. Increasing complexity via the addition of phytoplankton (center model) and then macrophytes (right-hand model) causes the most complex model to exhibit two different system states represented by a bimodal output PDF, i.e., phytoplankton-dominated vs. macrophyte-dominated wetlands.

Adapted from Muller et al. (2011).

4.3. GSA/UA and management planning for snowy plovers

In our third and final example, we illustrate the relevance of GSA/UA to ecosystem management by integrating Monte Carlo filtering into UA (Chu-Agor et al., 2012; Linhoss et al., 2013). Whereas UA requires definition of input distributions and generates output PDFs, and GSA identifies the inputs most responsible for the PDFs, Monte Carlo filtering can be used to create subset ranges of selected input factors that correspond to ecosystem parameters which managers can potentially control.[4] GSA/UA then generates PDFs associated with those input subsets in order to observe whether the corresponding management decisions affect the probabilities of observing "desirable" and "undesirable" system states in light of management goals.[5] To the extent that it yields PDFs with different shapes and ranges, subsetting can indicate the extent to which management decisions can affect probabilities of observing different system states in terms of their desirability. In the same stroke, subsetting can reveal "parameter breakpoints" such that subsetting below the breakpoint yields model output centered on one system state whereas subsetting above the breakpoint yields output centered on a different system state. Monte Carlo filtering with GSA/UA thus permits evaluation of management decisions for their implications for ecological resilience in terms of reducing the probability of ecosystems shifting toward undesirable states.

Chu-Agor et al. (2012) employ these methods by revisiting the SLAMM model discussed above (Section 4.1). They focus on populations of Snowy Plovers (*Charadrius alexandrinus*), a species vulnerable to sea level rise. The authors integrated the coastal habitat model SLAMM with a maximum entropy (MaxEnt) habitat suitability model (Phillips et al., 2006) and the RAMAS-GIS Snowy Plover population dynamics model (Akçakaya, 2005). This permits integrated modeling of habitat availability and change as well as population size, structure, and growth. The integrated plover model included 21 uncertain input factors which were used to evaluate PDFs for outputs including final average population, expected minimum abundance, risk of extinction, and interval risk with a threshold set at 90 individuals.

Chu-Agor et al. (2012) then subjected the integrated model to GSA/UA with Monte Carlo filtering on the population outputs indicating bimodal PDFs (Fig. 6a). In each case, an undesirable (1st mode) outcome indicated population decline or higher extinction probability (non-viable population, left of Fig. 6a), whereas a desirable (2nd mode) outcome indicated plover population growth or lower risk of extinction (viable population, right of Fig. 6a). GSA then identified the important input factors accounting for the distinct outcomes: final population maximum growth rate (*Rmax*) and population dispersion along the north Florida coast (*dbn*).

Chu-Agor et al. (2012) identified subsets of the distributions of these two important input factors using Monte Carlo filtering (Fig. 6b and c). Statistical tests (Smirnov comparisons) indicated significant differences in these distributions. However, observation of the input distributions for desirable and undesirable outputs indicated that although no distinct input distributions could be separated in the prior distribution of *dbn* (Fig. 6c), *Rmax* contained two sub-distributions (Fig. 6b) with large differences. This implies that management actions based on *dbn* will not necessarily lead to different system states, but that *Rmax* has an important parameter breakpoint, and managers should instead focus on maintaining *Rmax* values above the breakpoint. This can be fostered by management actions that enhance the habitats of Snowy Plovers, control plover predators, and provide restrictions on human activities in plover breeding areas. This illustrates our third key argument, that GSA/UA with Monte Carlo filtering provides a basis for evaluating ecosystem management options in terms of ecological resilience via avoidance of undesirable system states.

5. Discussion and conclusions

GSA/UA permits the quantitative evaluation of ecological resilience by relating values of indicators of system states in PDFs

[4] One caveat with Monte Carlo filtering in the context of GSA/UA is that testing of subsets is only performed for first-order input factors and not interactions (Chu-Agor et al., 2012).

[5] Statistical tests such as the two-sided Smirnov comparison of distributions test permit confirmation of differences in PDFs for the subsets of a given input factor.

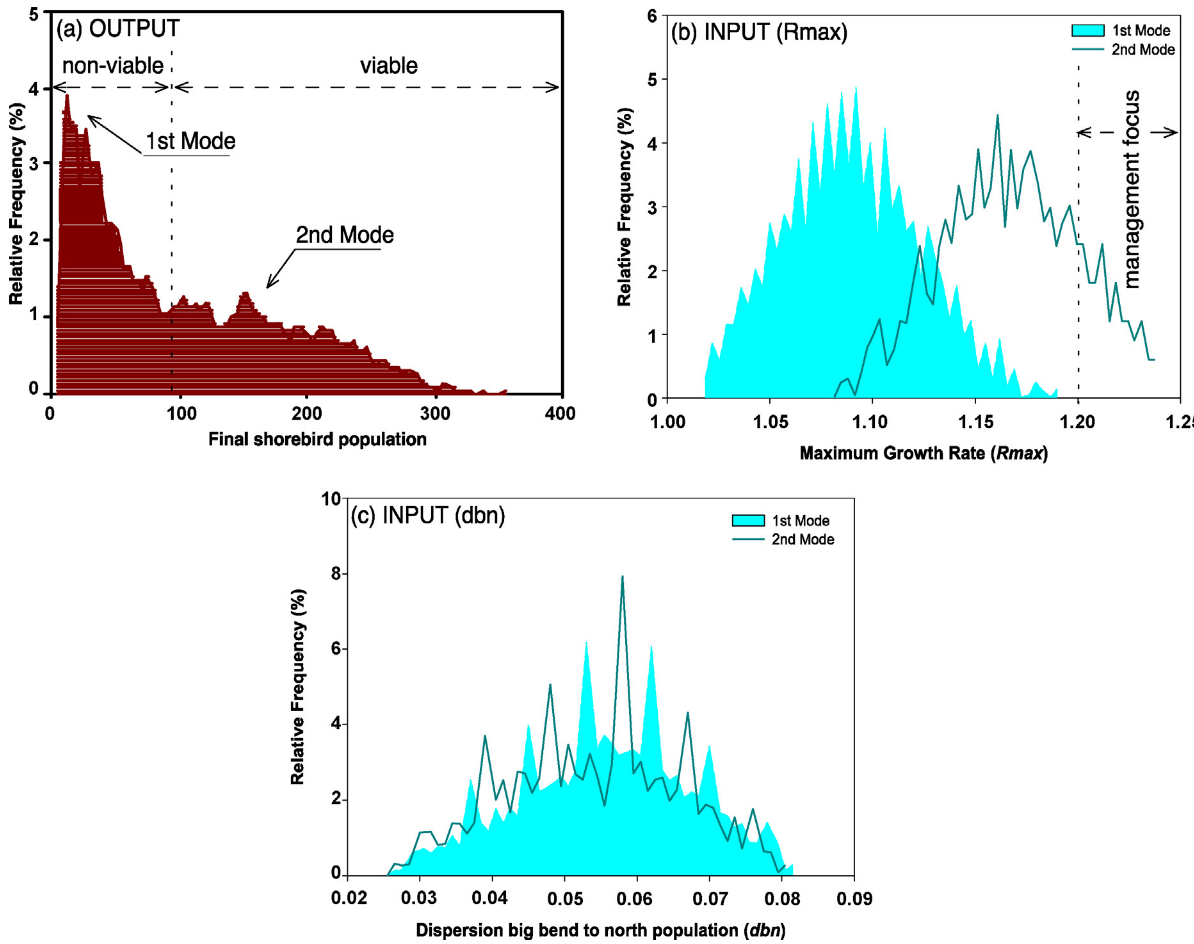

Fig. 6. Shorebird final population projections by year 2100 (a) where two different states are identified represented by the two modes of the distribution. The two most important input factors controlling the final population maximum growth rate (*Rmax*) (b) and population dispersion along the north Florida coast (*dbn*) (c) are shown with partial input distributions obtained through Monte Carlo filtering to correspond to the different states (1st and 2nd modes) presented in (a).
Adapted from Chu-Agor et al. (2012).

to basins of attraction. To recap: (1) select an empirical indicator of system state with a known range of possible values related to different system states; (2) identify initial and desired system states as distinct from undesirable states in terms of values of the indicator of system state; (3) identify critical thresholds in quantitative terms as low probability values of the indicator which fall between the different system states; (4) use calibrated models of actual ecosystems (rather than simplified theoretical models) in order to evaluate system dynamics; (5) apply GSA/UA to identify relevant input factor distributions in order to generate model output PDFs for indicators of system states; and (6) quantify resilience by calculating the relative probabilities of observing the modeled system in one state or another based on the value of the critical threshold of the output indicator of system state. Further, (7) identify combinations of important model inputs that contribute most to system variability and thus output sensitivity; and (8) use Monte Carlo filtering of those important input factors to subset their values as a means of testing for parameter breakpoints, that is, whether different subsets yield significantly different output PDFs, for which we can also calculate relative probabilities of observing the system in different states.

GSA/UA thus not only provides tools for the systematic evaluation of multiple sources of uncertainties in complex models (Saltelli et al., 2000, 2008), it also yields output that indicates probabilities of observing multiple system states relevant to evaluating ecological resilience (Holling, 1996; Gunderson and Pritchard, 2002; Scheffer, 2009). Depending on distributions of simulated values for key indicators of system states, we can quantify the probability of observing different system states and the likely characteristics of those states; further, if the system has shifting basins of attraction, we can compare model output for different time points to look for changes in probabilities of observing different system states (Chu-Agor et al., 2011). To that end, it is crucial to evaluate uncertainties in models of varying complexity for a given system, in order to systematically test for the possibility of multiple system states (Muñoz-Carpena and Muller, 2009; Muller et al., 2011). With Monte Carlo filtering, one can specify ranges for uncertain input factors that correspond to management decisions to see whether different input subsets affect the probabilities of observing desirable and undesirable system states, thus guiding ecosystem management for ecological resilience (Chu-Agor et al., 2012; Linhoss et al., 2013).

Our examples included applications of GSA/UA to different kinds of ecological models, ranging from climate-habitat (SLAMM) and shorebird population (RAMAS-GIS) models to a biogeochemical model (TaRSE). Because GSA/UA is model-independent, it can be integrated with a variety of other dynamic simulation models. Of particular interest is application of GSA/UA to social–ecological models in order to evaluate the possibilities of human action bringing about critical transitions in ecosystems. For such models, GSA/UA offers not only the possibility of observing different system states but also the ability to identify the most important input factors to which outputs are most sensitive. Since by definition social–ecological models incorporate human action as well as ecological processes, it becomes possible to assess whether the human or biological components of a system yield the largest variation in output PDFs and thus the more important impacts on system states.

Additional work is required with GSA/UA for the assessment of ecological resilience. First, there remains a need for systematic evaluation of model complexity for output uncertainty. While GSA/UA can identify key sources of uncertainty and provide PDFs indicating system attractors and tipping points, it does not directly relate sources to the shape of PDFs. This is especially relevant to the evaluation of models of varying complexity for a given system. If models of increasing complexity yield PDFs with differing shapes, it is not immediately obvious which of the newly added input factors account for the differences. One way to address this problem is to add one input factor at a time and analyze PDFs for changes at each step, but that implies many different model renderings and requires considerable computing time.

A second issue concerns the management of complexity and uncertainty as they may both affect the shape of PDFs. While model complexity may be required to observe multiple system states, that may also be possible in simple models with considerable uncertainty in the input factors. Rodriguez-Iturbe et al. (1991a,b) showed that errors of greater magnitude and multiplicative effects of errors in stochastic model inputs may give rise to multimodal output suggestive of multiple system states. Conversely, van Nes and Scheffer (2003) found that in systems with known alternative stable states, parameter noise can greatly magnify uncertainty in output. Alternatively, a seemingly complex model might not exhibit different states in the output distribution when inputs have relatively small errors, or when feedbacks in the model buffer sources of variation. Regardless of model complexity, GSA/UA demands care in the specification of distributions for values of uncertain input factors. Larger ranges, especially among strongly interacting sources of uncertainty, may yield multimodal PDFs.

A third issue concerns the incorporation of stochastic processes in models. This is very similar to what GSA/UA does when it randomly samples distributions of possible values for data and parameters. Models including stochastic processes thus add a layer of uncertainty to that which is evaluated in GSA/UA. It is possible that the “layered stochasticity” may be more likely to produce flat and wide unimodal distributions, whereas deterministic models may be more likely to yield tall and narrow or multimodal PDFs. This remains an open question in need of more systematic comparisons.

Our third example showed that GSA/UA bears implications for ecosystem management. Adaptive management has been critiqued for highlighting the issue of uncertainty in theory but for failing in practice to explicitly address sensitivity and uncertainty in iterated management experiments (Gregory et al., 2006). Efforts to incorporate sensitivity analysis in adaptive management are recent and limited to traditional “local” techniques (Pahl-Wostl et al., 2008; Howes et al., 2010). GSA/UA provides a framework for systematically assessing uncertainty in adaptive management and thereby provides a probabilistic basis for ecosystem management via the use of Monte Carlo filtering (Chu-Agor et al., 2012). Managers and user groups can define management regimes by subsetting distributions for input factors and then observing the resulting output PDFs in light of management objectives. This permits evaluation of management effectiveness for ecological resilience in terms of increased probabilities of desirable system states as management outcomes. Conversely, Monte Carlo filtering with GSA/UA can also reveal instances in which a given management option does not greatly reduce probabilities of undesirable outcomes. GSA/UA thus provides a means of evaluating uncertainties in complex systems with ramifications for ecological resilience, whether via research seeking to identify or confirm multiple system states, or via management applications involving the appraisal of different subsets of input distributions to see if they change the probability of observing desirable or undesirable system states.

Acknowledgements

The ideas behind this manuscript were developed for National Science Foundation Coupled Natural and Human Systems grant #1114924. RDH and RMC acknowledge the University of Florida Foundation for its support.

Appendix A. Global sensitivity methods

A.1. The Morris method

Morris (1991) proposed conducting individually randomized experiments that evaluate the elementary effects (in terms of relative output differences) of changing one parameter at a time, and aggregating the elementary effects into a global measure. Each input factor is defined by a probability distribution that is sampled at discrete numerical values, called levels. Each sample set for a model run is allowed to vary only the value of one input factor along a search trajectory. For each parameter, one employs two sensitivity measures: (1) the mean of the elementary effects (μ), which estimates the overall effect of the parameter on a given output; and (2) the standard deviation of the effects (σ), which estimates the higher-order characteristics of the parameter (such as curvatures and interactions). Since model output is sometimes non-monotonic, Campolongo et al. (2007) also suggest considering the distribution of absolute values of the elementary effects (μ^*) to avoid the canceling of effects of opposing signs. The number of simulations (N) required in the Morris screening method is:

$$N = r(k+1) \tag{1}$$

where r is the number of search trajectories (r = 10 produces satisfactory results), and k is the number of input factors.

Although elementary effects are local measures, the method is considered global because the final measure μ^* is obtained by averaging the elementary effects; this eliminates the need to evaluate the specific values at which they are calculated (Saltelli et al., 2004). Morris (1991) recommended applying μ (or μ^* thereof) to rank parameters in order of importance and when examining the effects of interactions. To interpret the results in a manner that accounts for both the parameter ranks and possible interactions, Morris (1991) suggested plotting the points on a (μ,σ) Cartesian plane, later extended to (μ^*,σ). Because the Morris method is qualitative in nature, it should only be used to assess relative parameter rankings.

A.2. Variance decomposition methods: extended FAST and Sobol

Having identified the most important sources of uncertainty in terms of rankings, a variance-based method like the Fourier Amplitude Sensitivity Test (FAST) and the method of Sobol can be used to obtain a quantitative measure of sensitivity (Cukier et al., 1978; Koda et al., 1979; Saltelli et al., 2000). These methods decompose the total variance ($V=\sigma_Y^2$) of the model output $Y=f(X_1, X_2, \ldots, X_k)$ in terms of the individual factors X_i, using spectral analysis, so that:

$$V = \sigma_Y^2 = V_1 + V_2 + V_3 + \ldots + V_k + R \tag{2}$$

where V_i is the part of the variance that can be attributed to a given input factor X_i alone (direct effects), k is the number of uncertain factors, and R is a residual corresponding to higher-order terms. The first-order sensitivity index, S_i, is defined as the proportion of the total output variance attributed to a single factor. S_i can be interpreted as a measure of global sensitivity of Y with respect to X_i, i.e.:

$$S_i = \frac{V_i}{V} \tag{3}$$

For a perfectly additive model, $\Sigma S_i = 1$, that is, no interactions are present and the total output variance is explained as a summation of the individual variances introduced by varying each input factor individually. In general, models are not perfectly additive, and $\Sigma S_i < 1$.

FAST (Cukier et al., 1978) was extended by Saltelli et al. (2000) to non-additive models. This is done by incorporating the calculation of the higher order effects through the total sensitivity index S_{Ti}. This is calculated as the sum of the first and all higher order indices for a given parameter X_i. For example, for X_1:

$$S_{T1} = S_1 + S_{1i} + S_{1jk}, + \ldots + S_{1\ldots n} \tag{4}$$

For a given parameter X_i, interactions with other parameters can be isolated by calculating $S_{Ti} - S_i$:

$$S_{T1} - S_1 = S_{1i} + S_{1jk}, + \ldots + S_{1\ldots n}, \tag{5}$$

which makes the extended FAST a powerful method for quantifying the individual effect of each parameter alone (S_i) or through interactions with others ($S_{Ti} - S_i$). To calculate S_i, extended FAST randomly samples the kth-dimensional space of the input factors based on a complex algorithm that explores the space through sinusoidal waves of increasing harmonics (frequencies of ω_i, $2\omega_i$, ..., $M\omega_i$), the Fourier spectrum (Cukier et al., 1978). This requires a number of model evaluations expressed as:

$$N = Mk \tag{6}$$

where M is a number between 500 and 1000.

The method of Sobol utilizes Sobol's pseudo-random numerical sequences to improve the kth-dimensional space sampling (Saltelli et al., 2000, 2008) with a number of simulations equal to

$$N = M(2k + 2). \tag{7}$$

Although the method requires more simulations than FAST, its refined sampling scheme allows a better treatment of highly non-linear models, or those with discrete or difficult output. In addition, Sobol allows for the higher order decomposition of interactions, such as by quantifying the variance assigned to 2-way interactions (S_{ij}), 3-way interactions (S_{ijk}), etc.

A.3. Uncertainty analysis

An additional benefit of the variance decomposition analysis is that since the results are derived from a randomized sampling procedure, they can be used as the basis for the uncertainty analysis by constructing cumulative distribution functions (CDFs) for each of the selected outputs. This leads to efficient Monte Carlo type of uncertainty analysis, since only the sensitive parameters are considered as the source of uncertainty.

Appendix B. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolmodel.2013.04.024.

References

Adger, W.N., Hughes, T.P., Folke, C., Carpenter, S.R., Rockström, J., 2005. Social–ecological resilience to coastal disasters. Science 309, 1036–1039.

Advisory Committee for Environmental Research and Education (AC-ERE), 2009. Transitions and Tipping Points in Complex Environmental Systems. National Science Foundation, Washington, DC.

Akçakaya, H.R., 2005. RAMAS GIS: Linking Spatial Data with Population Viability Analysis (Version 5). Applied Biomathematics, Setauket, NY.

Alcamo, J., Kok, K., Busch, G., 2006. Searching for the future of land: scenarios from the local to the global scale. In: Lambin, E.F., Geist, H. (Eds.), Land-use and Land-Cover Change: Local Processes and Global Impacts. Springer-Verlag, Berlin.

Anderies, J.M., Janssen, M.A., Walker, B.H., 2002. Grazing management, resilience, and the dynamics of a fire-driven rangeland system. Ecosystems 5, 23–44.

Ascough, J.C., Maier, H.R., Ravalico, J.K., Strudley, M.W., 2008. Future research challenges for incorporation of uncertainty in environmental and ecological decision-making. Ecological Modelling 219, 383–399.

Bammer, G., Smithson, M. (Eds.), 2009. Uncertainty and Risk: Multidisciplinary Perspectives. Earthscan, London.

Beisner, B.E., Haydon, D.T., Cuddington, K., 2003. Alternative stable states in ecology. Frontiers in Ecology and Environment 1, 376–382.

Campolongo, F., Cariboni, J., Saltelli, A., 2007. An effective screening design for sensitivity analysis of large models. Environmental Modeling & Software 22, 1509–1518.

Carpenter, S.R., Walker, B., Anderies, M.J., Abel, N., 2001. From metaphor to measurement: resilience of what to what? Ecosystems 4, 765–781.

Carpenter, S.R., Brock, W.A., 2004. Spatial complexity, resilience and policy diversity: fishing on lake-rich landscapes. Ecology and Society 9 (1), 8 (online) http://www.ecologyandsociety.org/vol9/iss1/art8/

Chu-Agor, M.L., Muñoz-Carpena, R., Kiker, G., Emanuelsson, E., Linkov, I., 2011. Exploring sea level rise vulnerability of coastal habitats through global sensitivity and uncertainty analysis. Environmental Modeling & Software 26, 593–604.

Chu-Agor, M.L., Muñoz-Carpena, R., Kiker, G., Aiello-Lammens, M.E., Akçakaya, H.R., Convertino, M., Linkov, I., 2012. Simulating the fate of Florida Snowy Plovers with sea level rise: exploring research and management priorities with a global sensitivity and uncertainty analysis perspective. Ecological Modelling 224, 33–47.

Clark, J.S., Bjornstad, O.N., 2004. Population time series: process variability, observation errors, missing values, lags, and hidden states. Ecology 85, 3140–3150.

Clough, J.S., 2008. SLAMM 5.02. Technical Documentation. Warren Pinnacle Consulting Inc., Warren, VT.

Craft, C., Clough, J., Ehman, J., Joye, S., Park, R., Pennings, S., Guo, H., MachMuller, M., 2009. Forecasting the effects of accelerated sea-level rise on tidal marsh ecosystem services. Frontiers in Ecology and Environment 7, 73–78.

Cukier, R.I., Levine, H.B., Schuler, K.E., 1978. Nonlinear sensitivity analysis of multiparameter model systems. Journal of Computational Physics 26, 1–42.

Cumming, G.S., Barnes, G., Perz, S.G., Schmink, M., Seiving, K.E., Southworth, J., Binford, M., Holt, R.D., Stickler, C., Van Holt, T., 2005. An exploratory framework for the empirical measurement of resilience. Ecosystems 8, 975–987.

Draper, D., 1995. Assessment and propagation of model uncertainty. Journal of the Royal Statistical Society Series B (Methodological) 57, 45–97.

Fisher, B.E.A., Ireland, M.P., Boyland, D.T., Critten, S.P., 2002. Why use one model? An approach for encompassing model uncertainty and improving best practice. Environmental Modeling and Assessment 7, 291–299.

Folke, C., 2006. Resilience: the emergence of a perspective for social–ecological systems analysis. Global Environmental Change 16, 253–267.

Folke, C., Colding, J., Berkes, F., 2003. Building resilience and adaptive capacity in social–ecological systems. In: Berkes, F., Colding, J., Folke, C. (Eds.), Navigating Social–Ecological Systems: Building Resilience for Complexity and Change. Cambridge University Press, Cambridge, pp. 352–387.

Galbraith, H., Jones, R., Park, R., Clough, J., Herrod-Julius, S., Harrington, B., Page, G., 2002. Global climate change and sea level rise: potential losses of intertidal habitat for shorebirds. Waterbirds 25 (2), 173–183.

Gattie, D.K., Kellam, N.N., Turk, H.J., 2007. Informing ecological engineering through ecological network analysis, ecological modeling, and concepts of systems and ecological engineering. Ecological Modelling 208, 25–40.

Gregory, R., Ohlson, D., Arvai, J., 2006. Deconstructing adaptive management: criteria for applications to environmental management. Ecological Applications 16, 2411–2525.

Grimm, V., Railsback, S.F., 2005. Individual-based Modeling and Ecology. Princeton University Press, Princeton, NJ.

Gunderson, L.H., Pritchard, L. (Eds.), 2002. Resilience and the Behavior of Large-scale Systems. Island Press, Washington, DC.

Hanna, S.R., 1993. Uncertainties in air quality model predictions. Boundary-Layer Meteorology 62, 3–20.

Holling, C.S., 1996. Engineering resilience versus ecological resilience. In: Schulze, P.C. (Ed.), Engineering within Ecological Constraints. National Academy Press, Washington, DC, pp. 31–44.

Howes, A.L., Maron, M., McAlpine, C.A., 2010. Bayesian networks and adaptive management of wildlife habitat. Conservation Biology 24, 974–983.

Intergovernmental Panel on Climate Change (IPCC), 2007. Climate Change 2007: Synthesis Report, Available at www.ipcc.ch/

Jawitz, J.W., Muñoz-Carpena, R., Muller, S., Grace, K.A., James, A.I., 2008. Development, testing, and sensitivity and uncertainty analyses of a transport and reaction simulation engine (TaRSE) for spatially distributed modeling of phosphorus in south Florida peat marsh wetlands. U.S. Geological Survey, Scientific Investigations Report 2008-5029.

Koda, M., McRae, G.J., Seinfeld, J.H., 1979. Automatic sensitivity analysis of kinetic mechanisms. International Journal of Chemical Kinetics 11 (4), 427–444.

Lindenschmidt, K., 2006. The effect of complexity on parameter sensitivity and model uncertainty in river water quality modeling. Ecological Modeling 190 (1–2), 72–86.

Linhoss, A.C., Muñoz-Carpena, R., Kiker, G., Hughes, D., 2013. Hydrologic modeling, uncertainty, and sensitivity in the Okavango basin: insights for scenario assessment. Journal of Hydrologic Engineering, http://dx.doi.org/10.1061/(ASCE)HE.1943-5584.0000755.

Liu, J., Dietz, T., Carpenter, S.R., Alberti, M., Folke, C., Moran, E., Pell, A.N., Deadman, P., Kratz, T., Lubchenco, J., Ostrom, E., Ouyang, Z., Provencher, W., Redman, C.L., Schneider, S., Taylor, W., 2007. Complexity of coupled human and natural systems. Science 317, 1513–1516.

Ludwig, D., Walker, B., Holling, C.S., 1997. Sustainability, stability, and resilience. Conservation Ecology 1 (7), 7 http://www.consecol.org/vol1/iss1/art7

Manson, S.M., 2007. Challenges in evaluating models of geographic uncertainty. Environment and Planning B: Planning and Design 34, 245–260.

May, R.D., 1974. Biological populations with nonoverlapping generations: stable points, stable cycles, and chaos. Science 186, 645–647.

McLeod, E., Poulter, B., Hinkel, J., Reyes, E., Salm, R., 2010. Sea-level rise impact models and environmental conservation: a review of models and their applications. Ocean and Coastal Management 53 (9), 507–517.

Messina, J.P., Evans, T.P., Manson, S.M., Shortridge, A.M., Deadman, P.J., Verburg, P.H., 2008. Complex systems models and the management of error and uncertainty. Journal of Land Use Science 3, 11–25.

Millennium Ecosystem Assessment, 2005. www.millenniumassessment.org

Mitchell, M., 2009. Complexity: A Guided Tour. Oxford University Press, Oxford.

Morgan, M.G., Henrion, M., 1990. Uncertainty: A Guide to Dealing with Uncertainty in Quantitative Risk and Policy Analysis. Cambridge University Press, Cambridge.

Morris, M.D., 1991. Factorial sampling plans for preliminary computational experiments. Technometric 33, 161–174.

Muller, S., Muñoz-Carpena, R., Kiker, G., 2011. Model relevance: frameworks for exploring the complexity–sensitivity–uncertainty trilemma. In: Linkov, I., Bridges, T.S.S. (Eds.), Climate: Global Change and Local Adaptation. NATO Science for Peace and Security Series C: Environmental Security. Springer, Boston, pp. 35–65.

Mumby, P.J., Hedly, J.D., Zychaluk, K., Harborne, A.R., Blackwell, P., 2006. Revisiting the catastrophic die-off of the urchin *Diadema antillarum* on Caribbean coral reefs: fresh insights on resilience from a simulation model. Ecological Modelling 196, 131–148.

Muñoz-Carpena, R., Muller, S.J., 2009. Formal exploration of the complexity and relevance of biogeochemical models through global sensitivity and uncertainty analysis: opportunities and challenges. In: Silva Rojas, O., Carrera Ramírez, J. (Eds.), Estudios en la Zona no Saturada del Suelo IX. CIMNE, Barcelona, pp. 27–40.

Muñoz-Carpena, R., Zajac, Z., Kuo, Y.M., 2007. Evaluation of water quality models through global sensitivity and uncertainty analyses techniques: application to the vegetative filter strip model VFSMOD-W. Transactions of ASABE 50, 1719–1732.

Nihoul, J.C.J., 1994. Do not use a simple model when a complex one will do. Journal of Marine Systems 5, 401–410.

Ogle, K., 2009. Hierarchical Bayesian statistics: merging experimental and modeling approaches in ecology. Ecological Applications 19, 577–581.

Osenberg, C.W., Sarnelle, O., Cooper, S.D., Holt, R.D., 1999. Resolving ecological questions through meta-analysis: goals, metrics and models. Ecology 80, 1105–1117.

Pahl-Wostl, C., Kabat, P., Möltgen, J. (Eds.), 2008. Adaptive and Integrated Water Management: Coping with Complexity and Uncertainty. Springer, Berlin.

Park, R.A., Lee, J.K., Canning, D., 1993. Potential effects of sea level rise on Puget Sound wetlands. Geocarto International 8, 99–110.

Pascual, P., Stiber, N., Sunderland, E., et al., 2003. Draft Guidance on the Development, Evaluation and Application of Environmental Models. Council for Regulatory Environmental Models and Environmental Protection Agency, Washington, DC.

Peterson, G.D., Cumming, G.S., Carpenter, S.R., 2003. Scenario planning: a tool for conservation in an uncertain future. Conservation Biology 17, 358–366.

Phillips, S., Anderson, R., Schapire, R., 2006. Maximum entropy modeling of species geographic distributions. Ecological Modelling 190, 231–259.

Pickett, S.T.A., Cadenasso, M.L., Grove, J.M., 2005. Biocomplexity in coupled natural-human systems: a multidimensional framework. Ecosystems 8, 225–232.

Rodriguez-Iturbe, I., Entekhabi, D., Bras, R.L., 1991a. Non-linear dynamics of soil moisture at climate scales. 1. Stochastic analysis. Water Resources Research 27 (8), 1899–1906.

Rodriguez-Iturbe, I., Entekhabi, D., Bras, R.L., 1991b. Non-linear dynamics of soil moisture at climate scales. 1. Chaotic analysis. Water Resources Research 27 (8), 1907–1915.

Rogers, T.D., 1981. Chaos in systems in population biology. Progress in Theoretical Biology 6, 91–146.

Saltelli, A., Chan, K., Scott, E.M. (Eds.), 2000. Sensitivity Analysis. Wiley, Chichester.

Saltelli, A., Tarantola, S., Campolongo, F., Ratto, M., 2004. Sensitivity Analysis in Practice: A Guide to Assessing Scientific Models. Wiley, Chichester.

Saltelli, A., Ratto, M., Andres, T., Campolongo, F., Cariboni, J., Gatelli, D., Saisana, M., Tarantola, S., 2008. Global Sensitivity Analysis: The Primer. Wiley Interscience, Chichester.

Scheffer, M., 1990. Multiplicity of stable states in freshwater systems. Hydrobiologia 200, 475–486.

Scheffer, M., 1991. Should we expect strange attractors behind plankton dynamics—and if so, should we bother? Journal of Plankton Research 13, 1291–1305.

Scheffer, M., Hosper, S.H., Meijer, M.L., Moss, S., Jeppeson, E., 1993. Alternative equilibria in shallow lakes. Trends in Ecology and Evolution 8, 275–279.

Scheffer, M., 2009. Critical Transitions in Nature and Society. Princeton University Press, Princeton.

Scheffer, M., Bascompte, J., Brock, W.A., Brovkin, V., Carpenter, S.R., Dakos, V., Held, H., van Nes, E.H., Rietkerk, M., Sugihara, G., 2009. Early-warning signals for critical transitions. Nature 461, 53–59.

Schlüter, M., Pahl-Wostl, C., 2007. Mechanisms of resilience in common-pool resource management systems: an agent-based model of water use in a river basin. Ecology & Society 12, 1–23.

Schulze, P.C. (Ed.), 1996. Engineering within Ecological Constraints. National Academy Press, Washington, DC.

Shirmohammadi, A., Chaubey, I., Harmel, R.D., Bosch, D.D., Muñoz-Carpena, R., Dharmasri, C., Sexton, A., Arabi, M., Wolfe, M.L., Frankenburger, J., Graff, C., Sohrabi, T.M., 2006. Uncertainty in TDML models. Transactions of ASABE 49, 1033–1049.

Snowling, S., Kramer, J., 2001. Evaluating modeling uncertainty for model selection. Ecological Modelling 138, 17–30.

Soares-Filho, B., Alencar, A., Nepstad, D., Cerqueira, G., del Carmen Vera Diaz, M., Rivero, S., Solorzano, L., Voll, E., 2004. Simulating the response of land cover changes to road paving and governance along a major Amazon highway: the Santarém-Cuiabá corridor. Global Change Biology 10, 745–764.

Stafford, S.G., Bartels, D.M., Begay-Campbell, S., Bubier, J.L., Crittenden, J., Cutter, S.L., Delaney, J.R., Jordan, T.E., Kay, A.C., Libecap, G.D., Moore, J.C., Rabalais, N.N., Rejeski, D., Sala, O.E., Shepherd, J.M., Travis, J., 2010. Now is the time for action: transitions and tipping points in complex environmental systems. Environment 52, 38–45.

Strunz, S., 2012. Is conceptual vagueness an asset? Arguments from philosophy of science applied to the concept of resilience. Ecological Economics 76, 112–118.

Turley, M.C., Ford, E.D., 2009. Definition and calculation of uncertainty in ecological process models. Ecological Modelling 220, 1968–1983.

van Nes, E.H., Scheffer, M., 2003. Alternative attractors may boost uncertainty and sensitivity in ecological models. Ecological Modelling 159, 117–124.

Waldrop, M.M., 1992. Complexity: The Emerging Science at the Edge of Order and Chaos. Simon & Schuster, New York.