

UC Berkeley

UC Berkeley Previously Published Works

Title

Appropriate complexity landscape modeling

Permalink

<https://escholarship.org/uc/item/5kf6w015>

Authors

Larsen, Laurel G
Eppinga, Maarten B
Passalacqua, Paola
[et al.](#)

Publication Date

2016-09-01

DOI

10.1016/j.earscirev.2016.06.016

Peer reviewed



Invited review

Appropriate complexity landscape modeling



Laurel G. Larsen ^{a,*}, Maarten B. Eppinga ^b, Paola Passalacqua ^c, Wayne M. Getz ^{d,e}, Kenneth A. Rose ^f, Man Liang ^c

^a University of California, Berkeley, Department of Geography, United States

^b Utrecht University, Department of Environmental Sciences, Netherlands

^c University of Texas, Austin, Department of Civil, Architectural and Environmental Engineering, United States

^d University of California, Berkeley, Department of Environmental Science, Policy and Management, United States

^e University of KwaZulu-Natal, School of Mathematical Sciences, South Africa

^f Louisiana State University, Department of Oceanography and Coastal Sciences, United States

ARTICLE INFO

Article history:

Received 9 February 2016

Received in revised form 25 June 2016

Accepted 29 June 2016

Available online 09 July 2016

Keywords:

Modeling

Forecasting

Landscapes

Complex systems

Emergent properties

ABSTRACT

Advances in computing technology, new and ongoing restoration initiatives, concerns about climate change's effects, and the increasing interdisciplinarity of research have encouraged the development of landscape-scale mechanistic models of coupled ecological-geophysical systems. However, communication barriers and uneven infiltration of new strategies for data-driven induction persist in the context of simulation model development across disciplines. One challenge is that ecology and the geosciences have embraced different modeling epistemologies, with ecologists historically favoring inductive inference from generalized, phenomenological models and geoscientists favoring deductive inference from detailed first-principles models. Today, many models used for environmental management, particularly for aquatic ecosystems, tend to be highly detailed, with ecological and geophysical components represented in different modules that are linked but often not closely integrated. These observations highlight a need for cross-disciplinary dialogue about landscape-scale modeling objectives and approaches. The philosophies of pattern-oriented modeling in ecology and exploratory modeling in geophysics have yielded advances in theoretical and applied knowledge in both of those disciplines, but they are not comprehensive across all aspects of landscape-scale modeling. Here we define and synthesize the "Appropriate-Complexity Method" (ACME), which builds upon these two philosophies to guide the development of process-oriented models across a spectrum of scientific and management objectives. ACME helps modelers efficiently converge upon an optimal modeling structure through: i) systematic evaluation of the attributes that comprise computational and representational detail, for which we have developed an operational decision tree; ii) iterative adjustment of models based on pattern-oriented model evaluation strategies; and iii) the use of appropriate datasets (where applicable) to build conceptual models and formulate predictions. Decisions about aspects of computational and representational detail are based on the landscape's emergent properties. They are also based on a hierarchy of classes of questions governing model objectives that represent a multi-attribute tradeoff among validation potential, interpretability, tractability, and generality as functions of computational and representational detail. Tradeoff curves, together with model objectives, provide further guidance for determining the "appropriate" level of complexity for representation of processes in models. Once deemed adequate for addressing the original research question of interest, models may be used for projection and scenario testing. They may next undergo expansion that moves them down the hierarchy, where they can then be used to address research questions of higher specificity, detail, and validation potential, though at a cost of lower tractability and interpretability on the tradeoff curves. This practical, systematic procedure provides clear guidance for the design and improvement of landscape models that may be used to address a wide variety of questions relevant to restoration, over a spectrum of scales.

© 2016 The Author(s). Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

Contents

1. Introduction	112
2. ACME within a spectrum of approaches to modeling	113

* Corresponding author.

E-mail address: laurel@berkeley.edu (L.G. Larsen).

2.1.	The concept of “detail” in models	113
2.2.	Basic approaches to modeling in ecology and geosciences: A brief history	113
2.3.	Modeling frameworks that ACME builds upon: Pattern-oriented modeling (ecology) and exploratory modeling (geosciences)	113
3.	The “appropriate-complexity” tradeoff	114
4.	ACME as a practical guide for developing numerical models	117
4.1.	Case studies	117
4.2.	Step I: Identify appropriate question class governing model objectives	117
4.2.1.	Questions well suited to exploratory models.	117
4.2.2.	Questions well suited to models with intermediate or high level of detail.	117
4.3.	Step II: Identify relevant emergent patterns/properties and their critical scales	118
4.4.	Step III: Develop conceptual model(s) of processes and identify their critical scales	119
4.5.	Step IV: Systematically evaluate the model's attributes that constitute “detail”	119
4.5.1.	State variables	120
4.5.2.	Spatial/temporal dimension	121
4.5.3.	Extent and boundary conditions	121
4.5.4.	Resolution	121
4.5.5.	Representation of coupling	122
4.6.	Step VI: Model evaluation—How to tell when the level of detail in a model is good enough?	124
4.7.	Step VIIa: Projection and scenario modeling.	125
4.8.	Step VIIb. Progression of model objectives.	125
5.	A look ahead: Opportunities for ACME to advance environmental science and management	125
	Acknowledgements	126
	Appendix A. Decision tree for honing attributes of model “detail”.	126
	References.	126

1. Introduction

How will marsh habitat distribution and the abundance of submersed aquatic vegetation change when proposed diversions to the Mississippi River are enacted? What are the primary drivers regulating landscape structure in the Florida Everglades? These types of questions have prompted the development of models that couple ecological and geophysical processes at the landscape scale so that the processes driving complex environmental systems can be better understood and/or predicted. Aided by the increasing propensity to work across disciplinary boundaries and by the panoply of modeling tools, approaches (e.g., agent-based, cellular automata, finite element, finite difference, GIS-based modeling), and resources (e.g., supercomputer time), modelers face fewer barriers than ever before. However, development of guiding theory has lagged behind emergence of computational tools. Compounding the challenge, approaches to modeling in ecology and geophysics have been divergent, and preexisting ecological and geophysical models that are simply coupled together commonly fail to adequately represent the bidirectional feedbacks crucial in the emergence of landscape structure (Jackisch et al., 2014).

A legacy of the International Biological Program of the 1960s and 1970s and its reductionist emphasis on measuring and modeling everything is that models used by regulatory agencies for management of landscapes attempt to represent many state variables and require immense computational resources to simulate just a few scenarios (SFWMD, 2005; USEPA, 2010; Cloern et al., 2011; Groves et al., 2012). Despite attempts to make the models as representative as possible, these complex models may suffer from accumulation of error (Hajek and Wolinsky, 2012) and may not provide insight into why phenomena that they can predict, such as toxic cyanobacteria blooms, occur (Li et al., 2014). Less visible in the environmental management scene are models with reduced scope, scale, or representational detail (e.g., Seybold et al., 2007; Larsen and Harvey, 2011; Liang et al., 2015b), often formulated by individual researchers or groups of researchers, as opposed to agencies. Compared to more detailed models, these types of models may be more appropriate for providing process-level insight into dominant driving processes or system sensitivity to perturbation (Murray, 2003). In fisheries management, Collie et al. (2014) describe a “sweet spot” for models at intermediate levels of complexity, for which model fit is reasonably good but excess parameter uncertainty has not accumulated.

Here we describe how models along the full spectrum of complexity could fulfill different roles in environmental management, and provide guidance to help modelers select an appropriate formulation. We use the term “complexity,” in a loose sense, to refer to the level of detail in models, as explicated further in Section 2.1. However, when we refer to complex systems, we refer to collections of entities that exhibit emergence (i.e., phenomena that arise non-additively from interactions between the components).

The Appropriate-Complexity Method (ACME) is a comprehensive guide for developing and implementing models of complex environmental systems for purposes of understanding the dominant factors responsible for their emergence and predicting how they will respond to changes in those drivers, including alternate management scenarios. Its focus is on mechanistic models, as many correlative statistical models, even models constructed using advanced machine learning techniques, are not robust to violations of stationarity (Milly et al., 2008). In a non-stationary regime, drivers may shift outside the envelope of variability for which these statistical models were constructed. However, certain types of emerging data-driven modeling techniques have roles in this framework for resolving complex networks of interactions or forecasting the future behavior of certain types of systems understood to behave deterministically, in a manner that is robust to nonstationarity.

ACME emerges from modeling traditions in ecology and geosciences, building on extant frameworks. Model objectives are first broken down into intermediate objectives classified within a hierarchy. This classification sets the coarse-scale level of “appropriate” detail. Next the modeler identifies the emergent properties of the system that the model should reproduce and develops a conceptual model of the sets of processes and variables hypothesized to be responsible for the development of those emergent properties. From this starting point the modeler systematically evaluates and fine-tunes distinct components of the model's “detail,” making decisions that will ultimately regulate the balance among the model's ability to reproduce emergent phenomena, its interpretability, tractability, and specificity. The next step is model evaluation, which determines whether the model adequately reproduces the system's key emergent behavior(s). The final step is iteration, whereby the model is expanded to tackle questions that become progressively detailed or location-specific. New data-driven inference strategies can aid in structuring models by identifying dominant variables and the strength and nature of their couplings. When forecasting

is the strict objective, some of these data-driven strategies make it possible to use an equation-free approach to develop predictions that are robust to nonstationarity, but this alternative may be appropriate only for a subset of low-dimensional systems.

2. ACME within a spectrum of approaches to modeling

2.1. The concept of “detail” in models

A clear definition of “detail” with respect to model formulation is critical in developing a concept of “appropriate complexity.” Here, we differentiate between “representational detail” and “computational detail.” Briefly, **representational detail** refers to the number of state variables, processes, and interactions that a model simulates, directly or indirectly, and their spatiotemporal extent. **Computational detail** refers to *how* processes are simulated and includes factors such as spatio-temporal resolution and whether processes are directly simulated (mechanistic descriptions converted to equations) or implicitly considered (phenomenological descriptions represented by parameterized functions, as discussed in Getz, 1998). Though correlated, the two types of detail are not identical, as modelers can employ techniques that reduce computational detail while not sacrificing representational detail. Examples include implicit representation of processes or variables within a spatial dimension not contained within the governing equations (e.g., stress or turbulence arising from flow gradients in a vertical dimension that is not simulated), referred to as a “quasi” 2D or 3D simulation, and parameterization of certain processes. Henceforth, when we look across the set of models that are used to compute a specific process (e.g., population growth), we refer to models at the low end of the “computational detail spectrum” as “simple” and those at the high end as “complex.”

2.2. Basic approaches to modeling in ecology and geosciences: A brief history

Traditional approaches to modeling in ecology and the geosciences diverge with respect to representational detail, which translates into epistemological differences in how models have been used in each field. Geoscientists traditionally used models grounded in first principles in a deductive manner, to derive predictions for specific systems. In contrast, ecologists traditionally used phenomenological models to induct common system behavior from observations. Recent changes in approaches to modeling have expanded the ways in which models are used for inquiry in both disciplines.

In geophysics the primary drivers can often be represented as systems of partial differential equations originating from classical mechanical theory (e.g., describing heat flow, fluid flow, sediment transport, or rock mechanics). Models with strictest adherence to first principles are computationally intensive and thus typically limited to a small spatial scale (e.g., usually centimeters to tens of centimeters for models of the Navier-Stokes equations for fluid flow, but also see Khosronejad et al., 2014). However, geophysicists are increasingly tackling problems at the landscape scale, with greater numbers of coupled state variables, using a variety of approaches. Modern landscape evolution models couple hillslope, channel, tectonic, and even vegetation processes by linking physically-grounded equations that are simplifications relative to first principles (e.g., gradient-flux equations, geomorphic transport laws) and/or semi-empirical (e.g., organic accumulation equations). These models may combine stochastic (e.g., probabilities of sediment detachment) and deterministic (e.g., water flow velocities) dynamics (Willgoose, 2005; Tucker and Hancock, 2010; Fagherazzi et al., 2012).

Although many of the leading landscape evolution (reviewed in Willgoose, 2005 and Tucker and Hancock, 2010) and ecogeomorphic (reviewed in Fagherazzi et al., 2012 and Saco and Rodríguez, 2013) simulation models are typically run over large domains and are computationally intensive, geoscientists have also been leading the charge to

reduce computational and representational detail in models to a minimal level. Stark and Passalacqua (2014) developed a highly simplified landscape evolution model as a set of low-dimensional, coupled dynamical systems to explore the coevolution of biomass and regolith under mass wasting and runoff erosion. The popular, alternative strategy of cellular automata modeling involves abstracting the physics governing fluid flow or sediment transport to discrete rules that route parcels of water, air, or sediment based on information from surrounding model grid cells (Willgoose et al., 1991; Murray and Paola, 1994, 1997). Cellular automata strategies have made it possible to simulate the development of braided streams (Thomas and Nicholas, 2002; Coulthard and Van De Wiel, 2006), floodplains (Murray and Paola, 2003), sand dunes (Zhang et al., 2010, 2012), wetland landscape pattern (Larsen and Harvey, 2010, 2011), and river deltas (Liang et al., 2015a, 2015b, 2016), and evaluate their sensitivity to global change and human drivers.

In contrast to the geosciences, ecological modeling approaches were originally phenomenological or analytical, with later increases in detail as data and computing resources improved. Phenomenological representations—termed “demonstration models” (Evans et al., 2013)—were first used to describe predator-prey dynamics (Volterra, 1928; Holling, 1959; Arditi and Ginzburg, 1989), fisheries (Ricker, 1952), logistic growth of microbes to a carrying capacity (Monod, 1949), and ultimately competition (MacArthur and Levins, 1967; Tilman, 1982). One advantage of these models was that, despite their simplicity, they could reproduce complex dynamics, including the transition between regular and chaotic population dynamics (May, 1974; Wilson et al., 1994; Bascompte and Solé, 1995). However, a shortcoming was their implicit inclusion of complicated dynamics through parameters difficult to quantify in reality (Eppstein and Molofsky, 2007). As a result, a tradition of working with theoretical analytical models emerged, with a focus on general equilibrium solutions. Because the parameters are difficult to quantify, modelers would examine how different parameter combinations influence ecosystem properties, thus emphasizing a general understanding of the consequences of ecological dynamics rather than a specific understanding of how those dynamics affect a particular site.

In answer to increasing calls to focus on transients and variability rather than equilibrium dynamics (Hastings, 2004), ecologists have gravitated toward more representational models, particularly as computing resources improve. Lagrangian (particle-tracking) methods such as agent-based modeling have been revolutionizing ecological modeling by providing a means to account for spatial and functional heterogeneities, deal with abruptly changing boundary conditions, and represent animal dispersal (Mooij and DeAngelis, 2003; Barraquand and Benhamou, 2008; Avgar et al., 2013). Other models incorporate detail hierarchically, such as stage- or age-structured models (Tuljapurkar and Caswell, 2012; de Roos and Persson, 2013; Massie et al., 2013; Harsch et al., 2014; de Valpine et al., 2014) or employ conditional parameters (Bowler and Benton, 2005).

2.3. Modeling frameworks that ACME builds upon: Pattern-oriented modeling (ecology) and exploratory modeling (geosciences)

ACME targets model detail based on underlying scientific questions and the nature of the system being studied, building upon two transformative frameworks in ecology and the geosciences: pattern-oriented modeling (Grimm and Railsback, 2012) and exploratory modeling (Murray, 2007; Larsen et al., 2014), respectively. These frameworks serve as philosophies of how to use models and improve them in an iterative way. Pattern-oriented modeling is an approach to model development and assessment based on the extent to which the output mimics patterns. Strong patterns are the dominant emergent features a model should reproduce: population cycles or a spatial distribution of vegetation patches, for example. Weak patterns are typically loose qualitative relationships, like a positive association between one

variable and another, or the existence of a population over a particular span in time. Generally, ecological modelers will tune parameters to determine the range of values that produce a match to either type of pattern. It is likewise important in model assessment that models reproduce broad spatiotemporal averages of interest such as an ecosystem organic carbon content (Belyea and Baird, 2006; Voroney et al., 2011), but for models of complex systems, this ability is often not sufficient (Grimm and Railsback, 2012). Even the ability to match a pattern may not be sufficient in the assessment of models of complex systems, as it is common for multiple mechanisms to produce similar patterns at a particular spatiotemporal scale (Levin, 1992; van de Koppel and Crain, 2006; Eppinga et al., 2009). Rather, Grimm and Railsback (2012) argue that multiple weak patterns at different scales or levels of organization typically have more power in model validation and selection than a single strong pattern or bulk average.

Exploratory modeling refers to the use of simplified models to provide insight into the core processes responsible for the development of emergent features. As in pattern-oriented modeling, models representing alternative conceptualizations of the system are evaluated and discarded when they are unable to replicate key patterns. However, whereas pattern-oriented modeling typically compares effects of alternate parameter values, exploratory modeling usually compares models with fundamentally different structures, representing different sets of driving mechanisms. In pattern-oriented modeling the emphasis is on output and validation so that the model can eventually be used for prediction or scenario testing. In contrast, in exploratory modeling the emphasis is on the processes: what are the dominant governing mechanisms and sensitivities? Often this approach leads to exclusion of processes or variables not because they are thought to be unimportant but because their effect

may confound the interpretation of results needed to address the specific research questions.

In ACME, exploratory and pattern-oriented modeling frameworks become influential once the research question is classified within a hierarchical scheme (Fig. 1). The most elementary type of motivating question warrants an exploratory modeling approach focused primarily on elucidating the system's dominant driving mechanisms. If that basic behavior is well understood, the next step is a more detailed simulation model. ACME guides decisions about the appropriate level of detail for the model, including whether to use a cellular or differential equation-based algorithm, Eulerian or Lagrangian framework, and the number and type of dimensions, variables, and boundary conditions. Throughout, a pattern-oriented approach guides interactions between model development and evaluation.

3. The “appropriate-complexity” tradeoff

Inarguably, models are imperfect representations of systems that balance constraints on computing capabilities, expert knowledge, and desired level of detail. The particular balance of factors in this tradeoff determines whether a model is useful for an application. Early in the history of ecological modeling, Levins (1966) stated that models needed to sacrifice generality, realism, or precision; they could not possess all three qualities. Despite advances in computing technology, the general idea of tradeoffs in modeling persists (Odenbaugh, 2006). As a first step in developing a practical guide for the establishment of useful models, we expand on Levins (1966), detailing the nature of contemporary modeling tradeoffs. Namely, increases or decreases in computational and/or representational detail affect the tractability, specificity,

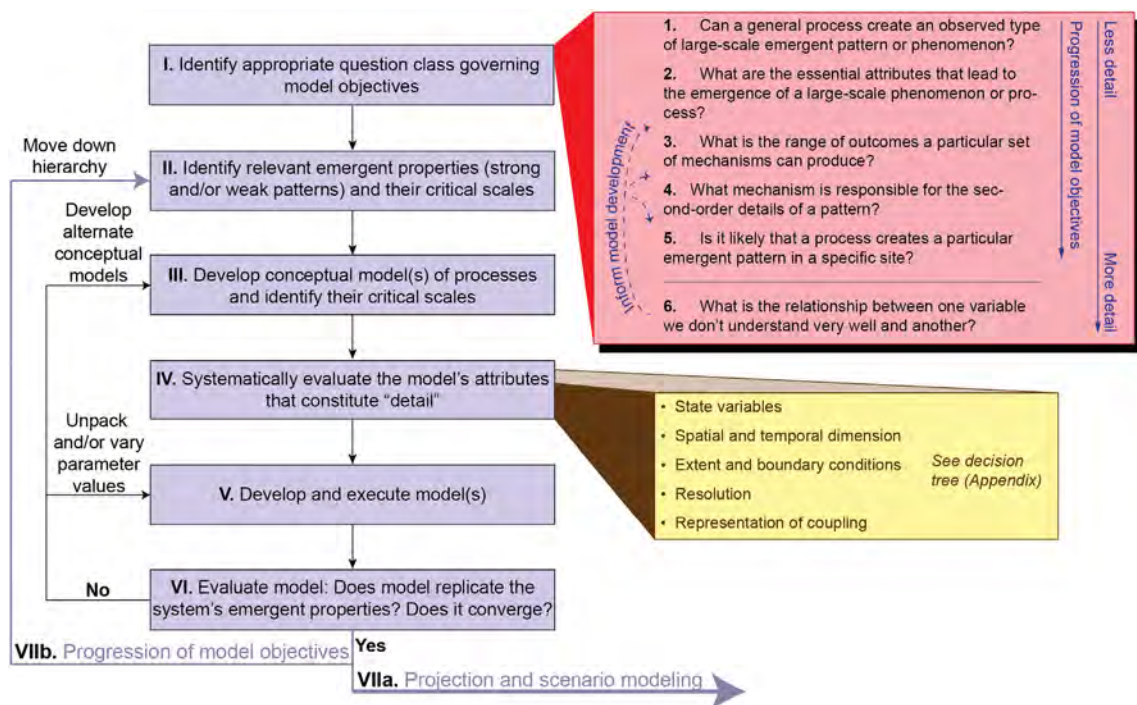


Fig. 1. Overview of the Appropriate-Complexity Method (ACME) for developing process-based models for understanding mechanisms at the interface of geophysics and ecology. Coarse-tuning the appropriate level of detail for a model begins with identification of the class of questions motivating the model and proceeds with identification of the relevant emergent patterns and properties. Questions 1–3 within the hierarchy of motivating questions tend to be suitable for exploratory models, whereas the higher numbers are suitable for models with higher levels of detail. The most detailed models (Question 6) are often applicable only over small scales but may inform the development of larger-scale models by establishing an empirical form for relationships between variables that interact in complex ways (Section 4.2.2). Part IV describes the process of fine-tuning model detail systematically by making strategic decisions regarding each of the critical attributes of detail (yellow box). In part VI, the model is executed, evaluated, and adjusted using a pattern-oriented modeling strategy. Mismatches between modeled and observed patterns trigger refinement of the conceptual and/or numerical models (Section 4.6), whereas a match indicates that the model is ready to be used for projection and scenario testing (VIIa) or expansion/extension to questions further down the hierarchy (numbers 1–5). Note also how ACME interfaces with emerging data-driven approaches for understanding and predicting system behavior as depicted in Fig. 4. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

interpretability, and validation potential of the model (Fig. 2). The optimal balance is constrained by the available resources, which establish acceptable ranges in tractability, and on the application (i.e., the system and questions addressed), which sets acceptable ranges in the other entities.

Tractability refers primarily to the computational resources (i.e., number of processors, time per processor) demanded for the execution of a single run, together with the number of runs needed to address the motivating questions. In Fig. 2, we have conveniently represented tractability as a negative power-law function of representational detail. In reality, tractability is related most directly to computational detail. Although computational detail encompasses more than just resolution and spatial dimension, it was these aspects of detail that motivated the depiction of tractability using a negative power-law functional relationship. In an N -dimensional computational domain divided into x cells per dimension, the total number of von Neumann adjacencies (i.e., shared hyperfaces) in the domain is equal to $2Nx^N$. Assuming that each of these adjacencies requires a flux computation, the total time required to compute fluxes would scale with Nx^N .

Specificity is the opposite of generality or universality; it refers to the extent to which a model applies to a single site or community rather than a general type. It has a minimum at moderately low levels of representational detail (Fig. 2), below which so many simplifying assumptions have been employed that the model represents only special cases. Evans et al. (2013) argue that increasing model complexity often increases generality, in the sense that a linear equation (simple) is a special case of a nonlinear equation (more complex but more general). In our conceptual model, this increase in generality with increasing model complexity contributes to the minimum in specificity when approached from the left. To the right of that minimum, specific details included in the model restrict the number of sites to which it applies. Modeling “tricks” that reduce the computational detail associated with a particular level of representational detail typically do so by increasing specificity. Often, these tricks involve parameterization or statistical (empirical) representation of dynamic processes, both of which require calibration to site-specific conditions.

Building on the pattern-oriented modeling concept, **validation potential** may be quantified as the number of patterns (strong and

weak) a model can be expected to replicate, assuming its parameters are set reasonably. One model, for instance, may produce a river, whereas the next produces a river with mean meander curvature that matches that of an actual river, whereas the next replicates the mean and variance of meander curvature. Because validation potential refers to the patterns and processes represented, it should scale directly and linearly with representational detail, to a point. Beyond that point, increasing representational detail will have diminishing returns. As we will discuss later in this paper, determining whether the model produces a robust “match” to a specified pattern remains research territory that is largely undeveloped.

Last, **interpretability** refers to the extent to which a signal in the model's output is traceable to specific processes or inputs. Generally, models that are more interpretable provide greater mechanistic insight. We assume that interpretability is most directly a function of computational detail, with an approximated inverse linear relationship. Further, for a given level of representational detail, in the absence of extensive post-processing of output, we assume that lower computational detail results in a more interpretable model.

Levins argued that because of the tradeoff in the desirable attributes of models, suites of models weak in different areas were needed to advance ecological theory; in other words, that “our truth is the intersection of independent lies” (1966; p. 423). One example of this tactic in contemporary times is the use of ensemble models to predict global climate change and its effects. Here we argue that models with different positions on the tradeoff continuum (Fig. 2) may be individually sufficient to provide answers to individual questions, but a spectrum of questions (addressed optimally with a corresponding spectrum of models of varying levels of detail) lies behind most theoretical and management challenges. Articulating the motivating questions clearly enables identification of the key strong and weak emergent properties that each model must reproduce. Then, in general, the model with the minimum representational detail that replicates these properties will strike the best balance between resource requirements and ability to address scientific and management questions meaningfully. Further increases in detail will incur strict penalties in the form of diminished interpretability, generality, and resource use.

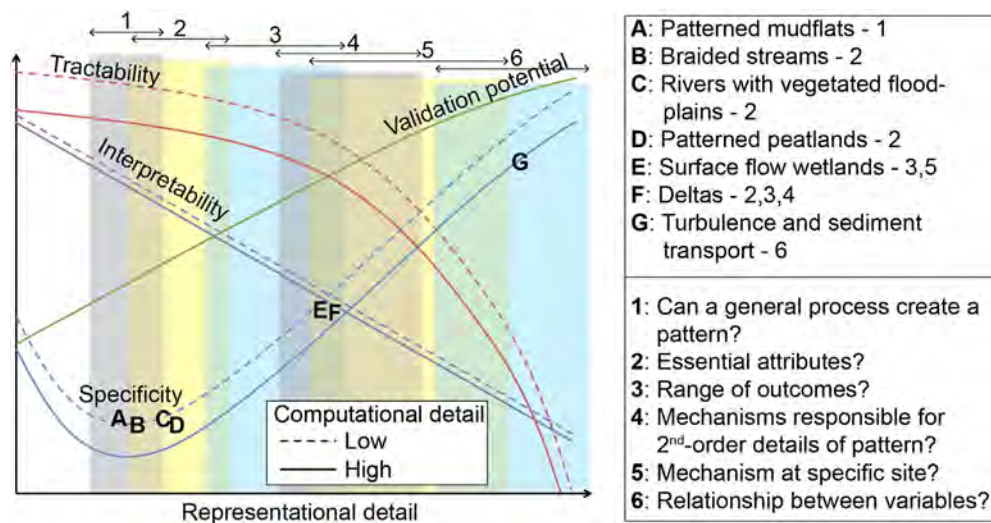


Fig. 2. Proposed tradeoffs between specificity, interpretability, tractability, and validation potential of models as a function of their representational and computational detail. Note that computational and representational detail typically scale together, and that “low” and “high” computational detail, as used here, are relative to a particular level of representational detail. (In other words, for both the dashed and solid curve, computational detail increases from left to right.) Approximate locations of the case-studies (A–G, as depicted in Fig. 3) are depicted on the specificity family of curves. The position of each case study on the other sets of curves will have the same x-coordinate, with the same relative positioning between the “low” and “high” computational detail curves. Semi-transparent shaded regions depict putative optimal regions for models that address the six classes of governing questions listed in Fig. 1 and paraphrased on the right panel. The top portion of the right panel indicates the types of questions that the case-study models have been used to address. Note: Figure also available online without annotations for teaching purposes.

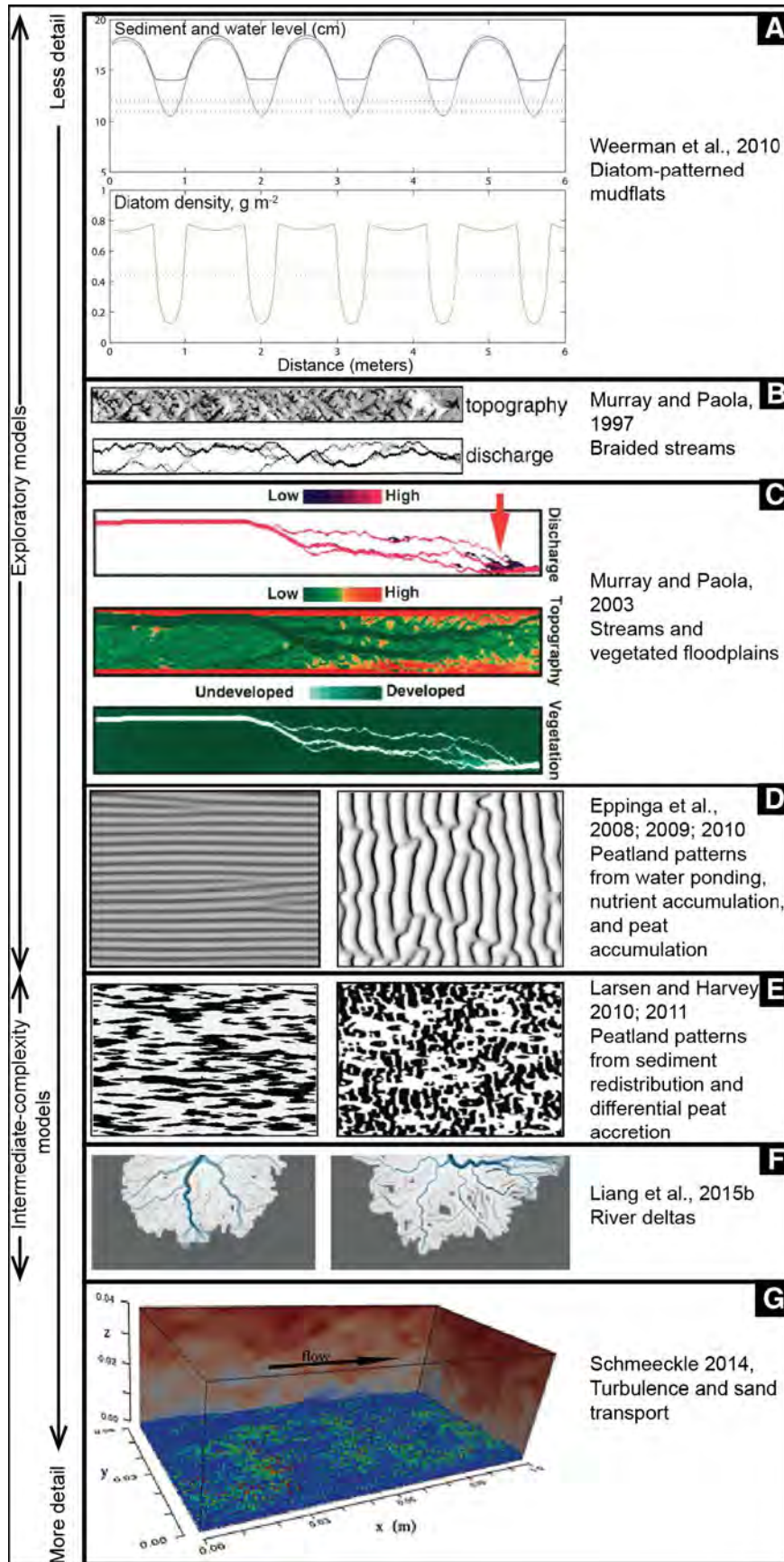


Fig. 3. Case-study models of landscapes sculpted by water, formulated across a gradient of complexity. Except for A, where flow is into the page, and F, where flow is from top to bottom, the flow vector is from left to right.

4. ACME as a practical guide for developing numerical models

4.1. Case studies

Throughout this paper we illustrate major concepts and decisions with a set of key case studies that have emerged within or at the interface of ecology and the geosciences (Fig. 3). Although the influence of human activities in the systems we focus on is typically restricted to boundary conditions and/or input-output fluxes, we hope that this synthesis also represents a step forward in the conversation about appropriate strategies for modeling coupled natural-human systems in which feedbacks between human decision making and environmental phenomena are explicitly simulated.

4.2. Step I: Identify appropriate question class governing model objectives

At the coarsest scale, the levels of computational and representational detail included in models should be set by the nature of the motivating scientific question. Under the ACME framework (Fig. 1), studies ideally evolve from the most basic sets of questions (low numbers in the figure) to more complicated questions that require a progressive increase in the model's detail. Establishing the "ultimate" or "end-point" question often follows from consideration of how the results will be used and who the audience is.

4.2.1. Questions well suited to exploratory models.

1. Can a general process create an observed type of large-scale emergent pattern or phenomenon? This question seeks to evaluate the feasibility of first-order drivers or mechanisms for explaining observations. Exploratory models are often well suited to this type of question. For example, Weerman et al. (2010; Fig. 3A) used a highly simplified model to evaluate whether stress divergence could explain the occurrence of regularly spaced ridges on mudflats. Key simplifications included erosion rates that depended on diatom biomass but not water depth, constant maximum erosion rates in hollows, use of just a single spatial dimension, and diatom growth rates that depended only on diatom abundance and water level. Murray and Paola (1997; Fig. 3B), meanwhile, asked whether simple sediment transport rules (lateral erosion, limited uphill transport by flow, downstream transport by flow) were sufficient to explain the development of braided streams. Their key simplifications involved representing flow and sediment as discrete parcels that were exchanged between neighboring cells based on their elevation differences.

Though exploratory models may show that a particular process is a feasible mechanism through which an emergent phenomenon can arise, they cannot confirm that the mechanism is responsible. Instead, they are often useful for ruling out hypothesized mechanisms. Sometimes exploratory models will show that several mechanisms can produce the same emergent phenomenon, termed *equifinality*. In that case, a pattern-oriented modeling approach that compares model output to one or more weak patterns may provide resolution, as in Eppinga et al. (2008, 2009, 2010, Fig. 3D), who evaluated effects of three different feedback processes on peatland development in a factorial design experiment. They showed that either a water stress feedback by itself or coupled to a nutrient accumulation feedback could reproduce the strong pattern of interest: regularly spaced ridges aligned perpendicular to peatland slopes. However, the models diverged in their ability to replicate a weak pattern: the relative difference in phosphorus concentrations between ridges and hollows (Eppinga et al., 2009). Subsequent field sampling of porewater nutrients at these locations was sufficient to resolve the combination of dominant mechanisms operative at different peatland sites worldwide (Eppinga et al., 2008, 2010).

Often, in evaluating whether particular processes can reproduce emergent properties, researchers will focus on the stable or end state of the model. However, natural systems may be responding to transient phenomena and located far from equilibrium (Hastings, 2001, 2004). It

is important to recognize that systems with the same equilibrium point may exhibit very different distributions of state variables on their way to that equilibrium, and that the appropriate pattern comparison may require consideration of the transient state(s).

2. What are the essential attributes that lead to the emergence of a large-scale phenomenon or process? As above, this question lends itself well to exploratory models. It takes the first question one step further by recognizing that, even if a proposed set of mechanisms can produce an observed pattern, it may do so only within restricted ranges of environmental variables or under certain formulations (e.g., sediment transport simulated as a threshold rather than a simple power-law process). Because of their efficiency, exploratory models facilitate sensitivity analyses, enabling exploration of the effects of many alternate rules or parameterizations. In Weerman et al. (2010; Fig. 3A), such sensitivity analyses revealed the bounds on the maximum erosion rate within which patterned mudflats could persist and probed the influence of diatom density on pattern structure. In their model of braided streams, Murray and Paola (1994) examined the influence of different sediment transport rules on channel braiding (Fig. 3B). They concluded that essential features were erodible banks and limited uphill sediment transport.

3. What is the range of outcomes a particular set of mechanisms can produce? Truly a variant of question 2, this question asks how the emergent properties of a system change as parameters are varied within their feasible range (i.e., a sensitivity analysis). Because this question is focused on the effects of generalized, first-order mechanisms, it is also well suited to the use of exploratory models that can easily be run many times. Various strategies can be employed to explore the parameter space, including regular or randomized sampling of parameters or space-filling algorithms. Larsen and Harvey (2011; Fig. 3E) used space-filling Latin hypercube sampling of a nine-parameter space to determine the range of effects arising from the combination of a flow-sediment redistribution feedback with a differential organic sediment accretion feedback. They found that these two feedback processes could produce patterns similar to a wide variety of wetland landscapes.

Bifurcation diagrams generated from simple analytical or numerical models delineate the range of parameter values within which an emergent behavior is stable. They also suggest whether a system's dynamics may be characterized by tipping points. Heffernan (2008) analytically developed a bifurcation diagram depicting equilibrium abundance of riparian vegetation. A logistic growth equation and a modified Michaelis-Menten equation representing mortality due to scour comprised the model. The diagram showed that over a range of flood frequencies, vegetated and bare riparian zones were alternate stable states, and that an increase in flood frequency beyond this range could tip the system from vegetated to bare. Larsen and Harvey (2010; Fig. 3E) derived a numerical bifurcation diagram of wetland landscape patterns emerging from feedback between flow, sediment transport, and vegetation dynamics over a range of water-surface slopes. To do so, they initiated their runs from different initial conditions and ran them to stability. As with the analytical analysis of Heffernan (2008), Larsen and Harvey's numerical analysis indicated that these flow-sediment-vegetation feedbacks produce alternate stable landscape patterns and the potential for catastrophic shifts.

4.2.2. Questions well suited to models with intermediate or high level of detail.

4. What mechanism is responsible for second-order details of a pattern? This question addresses the general (i.e., not site-specific) mechanistic drivers of second-order effects, or weak patterns. Whereas first-order questions might focus on the mechanisms producing distinct vegetation patches, second-order questions might focus on the mechanisms behind the patches' size distribution or shapes. Reproducing those features may require an increase in the model's representational detail. As an example, while Murray and Paola's simple cellular

automata model (1994) reproduced the bifurcations and channel-shifting characteristic of braided streams, the simulated streams were overly sinuous (Doeschl-Wilson and Ashmore, 2005; Nicholas and Quine, 2007). To represent meanders realistically, secondary circulation (Nicholas et al., 2012; Nicholas, 2013) or an algorithm that determined the radius of flow curvature on a cell-by-cell basis was needed (Coulthard and Van De Wiel, 2006). In an example from ecology, second-order questions about resilience of vegetation patches to disturbance were investigated with both an exploratory and individual-based model (Realpe-Gomez et al., 2013). The more detailed model realistically produced patch shapes less smooth than those of the simpler model and indicated that resilience may be underestimated if plant establishment and growth is simplified to a single state variable.

5. Is it likely that a process creates a particular emergent pattern in a specific site? A second question invoking the need for validation with “weak” patterns is that of dominant mechanisms at specific sites. Answering this question may require resolving equifinality and/or modifying the model's details specific to a site. Other conditions might also suggest the necessity of more detail in a model. Expert knowledge or preliminary investigations may suggest that emergent patterns are sensitive to boundary conditions or inputs, or exhibit path dependency. In these cases, the model would need to represent the historical inputs, perturbations, or variable distributions at the site in a more detailed simulation framework. Landscapes operating near a threshold also require more detail, usually in the representation of processes and/or resolution. For example, flows in the historic Everglades were likely near the threshold of entrainment for flocculent bed sediment. A model of that landscape (Larsen and Harvey, 2010; Fig. 3E) thus required physically governed and field validated representation of flow and sediment flux through different vegetation canopies, as well as fine spatial resolution in the transitions between vegetation communities. Such a model addresses a different question (*Could stress divergence and resulting sediment redistribution have given rise to the ridge and slough landscape in the Everglades?*) than the mechanistically similar but simpler model of Weerman et al. (2010) (*Can stress divergence trigger the development of ridges parallel to flow in a generalized mudflat?*).

6. What is the relationship between one variable we do not understand very well and another? Highly detailed models are sometimes used to delineate the functional form of the relationship between a pair of variables that interact in complex ways. Schmeckle (2014; Fig. 3G) used a large eddy simulation model together with a discrete element model that simulated the motion of individual grains of sand to elucidate the relationship between hydraulic roughness and shear velocity. With sediment transport, the model showed a multifold increase in hydraulic roughness, with an order-of-magnitude increase upon transitioning from bedload- to suspended load-dominated transport. As is typical with this type of model, spatial and temporal resolution were necessarily fine (e.g., 2×10^{-4} m vertical resolution), compensated for by limited extent ($12 \times 6 \times 4$ cm, with results compiled from 5 s simulated time).

Using highly detailed models to elucidate complex relationships may be an important first step to inform development of larger-scale or more extensively coupled models and/or to provide guidance for reducing a model's computational detail. As an example of the former, the roughness solution developed in the Schmeckle (2014) model might be a component of a larger-scale but simpler model of turbidity currents that would need to represent tight coupling between hydraulic and sediment dynamics. As an example of the latter, Larsen and Harvey's model of Everglades landscape dynamics (2010) needed to incorporate a solution for bed shear stress within different vegetation canopies over a range of water surface slopes and water levels. Solving for bed shear stress within vegetation canopies requires knowledge of vertical velocity profiles, which might have compelled three-dimensional modeling. Instead, the authors initially used a detailed fluid dynamical model to solve for velocity profiles and depth-averaged velocities in different vegetation canopies over a range of water depths and water surface

slopes. Then, in their two-dimensional, intermediate-complexity model, they incorporated a lookup table for bed shear stress as a function of water depth and depth-averaged velocity, based on the fluid dynamical modeling. In this way, they obtained a quasi-3D solution of flow conditions while incurring only the computational expense of a simplified 2D model.

4.3. Step II: Identify relevant emergent patterns/properties and their critical scales

In this step, the modeler identifies the emergent features to be compared against model output, given the question identified in step I. Early-stage identification of emergent properties aids in coarse- and fine-tuning model detail and deciding on a general algorithmic strategy. For lower-level questions in the hierarchy (Fig. 1), the relevant emergent properties are often one or two strong patterns. Widespread or universal landscape patterns (e.g., drainage networks, banded vegetation patterns) are generally well suited to simple modeling strategies because they are not sensitive to site-specific detail (Werner, 1995). In contrast, patterns with many types of patches and irregularly distributed features may require more detailed models that are able to reproduce weak patterns, such as distributions of patch sizes or patch richness or evenness (Grimm and Railsback, 2012).

While the appropriate emergent properties to choose for model evaluation are driven by the motivating mechanistic question, data availability is an important consideration. Information on coarse, landscape-scale emergent patterns is often readily available through remote sensing or other maps. Other times, identification of the relevant emergent properties may set an agenda for needed data collection before the modeling effort is worthwhile. The case study of Eppinga et al. (2008; Fig. 3D) provides a pertinent example. Those authors found that the weak pattern of phosphorus concentration under topographic features was required to discern between multiple possible mechanisms of landscape pattern formation, prompting a sample collection effort for the purpose of model evaluation.

Identification of the critical spatial scales of these strong and weak patterns is often straightforward, typically accomplished through visual observation in the field or from remote sensing. This information is necessary to inform later decisions about the spatial extent of the model and spatial meshing strategy for solution of the governing equations (Section 4.5). Critical temporal scales of pattern development and persistence should also be identified to the best of the modeler's ability based on historic records or paleoecological information.

Emergent patterns also provide some general indication of the type of algorithmic strategy that might be appropriate. If a variable's evolution is dominated by the behavior of variables in a local neighborhood (typically the surrounding one or two layers of cells in the computational grid), it may be well represented by a cellular automata modeling scheme or other simplified approach. Metrics based on weak patterns may provide an indication of the scale of the neighborhood of interaction. For example, the Froude number—the ratio of inertial to gravitational forces driving flow, which indicates whether small perturbations to the water surface will propagate upstream—has been used to determine whether a simple, gradient-based cellular automata modeling scheme (e.g., Murray and Paola; Fig. 3B) is an appropriate strategy for representing surface-water flow (Liang et al., 2015b; Fig. 3F). When, in contrast, a variable's evolution is dominated by drivers outside a small neighborhood of interaction, a differential equation-based modeling scheme will be more appropriate. Individual- or agent-based models are appropriate when emergent patterns are thought to arise from interactions of individuals (e.g., plants, animals, people) with their environment and when those individuals exhibit adaptive behavior or have relevant distinctive features (e.g., genetic markers, immunological state; Grimm and Railsback, 2013).

4.4. Step III: Develop conceptual model(s) of processes and identify their critical scales

Development of a mechanistic model that reproduces observed emergent phenomena depends in large part on the identification of a reasonable conceptual model of the system. The conceptual model is a hypothesis about the key state variables and the nature of the interactions among them. When a model is formulated explicitly to test a hypothesis or alternative hypotheses, the conceptual model(s) emerge(s) naturally. If the driving question is more-open ended (i.e., “What is the mechanism that causes x ?” as opposed to, “Could mechanism A cause x ?”), the development of the conceptual model may be based on expert knowledge about the system, knowledge of mechanisms driving similar types of systems (i.e., analogues), or an understanding of the general effects of certain processes. The conceptual model should include hypotheses about the critical spatiotemporal scales over which the key processes occur, which may differ from the spatial and temporal scales of emergence identified in step II. For example, processes that produce emergent patterning at the scale of kilometers may arise from distinct flow patterns that vary over the scale of individual vegetation patches or stems (centimeters to meters). At this stage, identification of the critical scale of processes need only be done to an order of magnitude or in a relative way (e.g., large, medium, small).

Investigators generally approach the challenge of developing a viable conceptual model deductively, progressively ruling out hypothesized conceptual models that do not produce outcomes similar to observations until left with one or more that do. This process can be time consuming, with no guarantee that a viable conceptual model or set of models will emerge. Alternatively, emerging data science tools may help investigators use inductive techniques to converge more rapidly on a viable conceptual model, through data-driven delineation of process networks. A *process network* (Fig. 4; Ruddell and Kumar, 2009), also known as a *causal network* (Sugihara et al., 2012), is a network of key variables and their interactions that is derived from data.

Resolution of process networks is most rigorously performed through causal inference of interactions between paired variables. Computations generally are performed on time-series of variables, such as those acquired from sensors. “Classic” causal inference involves computation of Granger causality statistics. When knowledge of a lagged history of variable A improves predictions of variable B beyond those generated from knowing the history of B alone, A is said to Granger-cause B (Granger, 1969). A more generalized alternative is transfer entropy (Schreiber, 2000), which determines the extent to which uncertainty in B is reduced by knowledge of A at some time in the past, relative to the reduction of uncertainty from B’s most recent time history. Transfer entropy is based on joint and marginal probability distributions, whereas Granger causality is based on regression. For Gaussian distributed variables, transfer entropy produces identical results to Granger causality, but transfer entropy is better at resolving nonlinear relationships and is hence more general (Abdul Razak and Jensen, 2014).

One restriction on Granger causality is that it requires variables to be separable—for A to contribute information independent of B’s long-term history to prediction of the current value of B. (Note that this restriction does not apply to transfer entropy that, as it has been operationally applied in the earth sciences (Ruddell and Kumar, 2009), evaluates the extent to which A reduces uncertainty in B relative to B’s single previous time step.) Thus, for systems that are fully coupled and deterministic, in which the time series of B contains all of the information about the previous time steps of A and other drivers, lagged values of A would contribute no unique information to the prediction of B (Sugihara et al., 2012). For such systems, transfer entropy or alternative approaches grounded in dynamical systems theory may be more appropriate. These approaches—convergent cross-mapping (CCM) and empirical dynamical modeling (EDM)—assume that the system can be

defined by a relatively small number of variables that interact deterministically.

EDM and CCM are grounded in Taken’s Theorem, which states that, for a closed, deterministic system, the manifolds representing trajectories in state-space (the space of all interacting state variables) over time, called the strange attractor, may be reconstructed as “shadow manifolds” using the time history of a single variable, given an appropriate embedding dimension (Takens, 1981; Fig. 4). In CCM, A and B are causally linked if data points in time that are close to each other (i.e., form an ellipse) in the shadow manifold of A are also close to each other in the shadow manifold of B, and that the size of the corresponding ellipse in B shrinks as the length of the time series from which the manifolds were constructed increases (i.e., convergence in the sense of Sugihara et al., 2012). In EDM, the shadow manifolds are used to forecast future behavior in B, using weighted regression based on vectors of nearest-neighbor points. If A improves the skill of prediction of the future behavior of B, it is considered causally linked (Ye et al., 2015).

In addition to identifying the variables that are causally linked, all of the causal inference techniques described above can also help identify critical spatiotemporal scales of interaction and the relative strength of interactions among pairs of variables. Time lags associated with the greatest transfer entropy or prediction skill are commonly taken as the critical time scale associated with variable interactions (Ruddell et al., 2013). The magnitude of statistically significant values of transfer entropy or prediction skill further provides information about the relative strength of interactions across the network. Such information can guide the formulation of the governing equations of a model simulating the system of interest and aid in the selection of resolution, extent, and other attributes of model detail (see Section 4.5 below).

Lastly, emerging data driven techniques can provide information about the number of dominant variables involved in a process network (top left of Fig. 4). For low-dimensional deterministic systems, Taken’s theorem can be invoked to determine the number of key variables in a process network. Namely, the correlation dimension is a type of fractal dimension that characterizes the number of time lags in a variable’s history that must be accounted for to reconstruct the strange attractor in the shadow manifold (Grassberger and Procaccia, 1983a, 1983b). It is interpretable as approximately equal to the number of state variables driving the behavior in the observed time series. Similar information can be obtained operationally by determining the embedding dimension that produces the most accurate predictions for hindcasted time series (Clark et al., 2015). In the framework of Granger causality or transfer entropy analyses, the number and identity of critical variables can only be surmised through identification of significant pairwise causal interactions based on available data, and there is no guarantee whether those data fully represent the system. Although data-driven determination of dimensionality has not yet been applied to conceptual model development for simulation modeling in the environmental sciences, Patil et al. (2001) showed how doing so can improve data assimilation for weather forecasting.

4.5. Step IV: Systematically evaluate the model’s attributes that constitute “detail”

The concept of model “detail” encompasses multiple attributes (state variables, spatiotemporal dimensions, extent, resolution, and representation of coupling), each of which presents important decisions that govern the model’s tractability, interpretability, specificity, and validation potential. Systematically making decisions about each of these attributes in light of the driving question(s) (Section 4.2) and emergent properties can help minimize computational detail for the selected “appropriate” level of representational detail without compromising standards for specificity. While it would be impossible to provide universal recommendations, we highlight several potential strategies in the next sections and in Table 1. Appendix A operationalizes the textual guidance as a decision tree, with a link to additional online materials that can

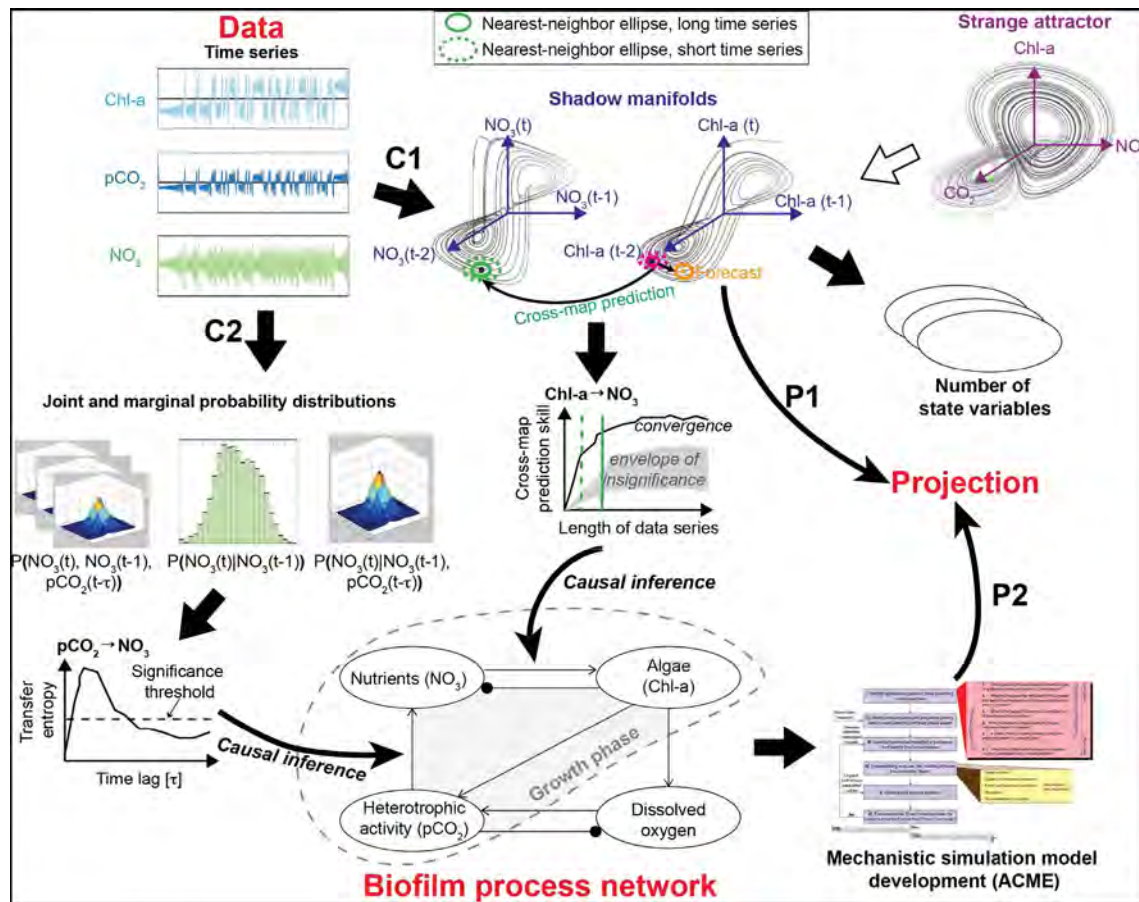


Fig. 4. Alternate strategies for data-driven causal inference (C1 for deterministic systems and C2 for a broad range of systems) to inform the development of process networks and make projections (P1 for deterministic systems and P2 for a broad range of systems). The process network is a conceptual model of a simple system, here, a biofilm, in which ellipses represent state variables (or indicators of those state variables that can be readily measured with sensors; $p\text{CO}_2$ = partial pressure of carbon dioxide; Chl-a = chlorophyll- a ; and NO_3 = nitrate), and links represent quantifiable directional causal relationships between variables. We have adopted the dynamical systems convention of representing positive relationships with arrowheads and negative relationships with circles. For convenience, we assume that the biofilm is in the growth phase, not yet limited by dissolved oxygen availability, so that the system simplifies to three state variables. If the interactions are dominantly deterministic (for example, if external nutrient concentrations are relatively steady), the system may exhibit a strange attractor (almost certainly different from the well-known Lorenz attractor depicted here). Interactions may then be resolved from data time series through the method of shadow manifold reconstruction and convergent cross-mapping (C1). Alternatively, transfer entropy can be calculated from data time series to resolve the existence and magnitude of pairwise connections (C2). Resolved process networks may be translated into numerical models, which can then be used for projection (P2). Forecasts may also be performed directly from the data, using the method of shadow manifold reconstruction (P1).

serve as a teaching tool. We also point readers to the synthesis of surface water flow modeling strategies by Liang et al. (2015b) and the overview of computational population biology by Getz (2013) for strategic modeling advice relevant to particular subdisciplines.

4.5.1. State variables

Decisions about state variables set the scope of a model. If the most parsimonious set of state variables is not known, the modeling exercise itself can identify it, based on the extent to which alternate models reproduce emergent phenomena (Larsen et al., 2014). One challenge in this type of exploratory modeling is determining whether discrepancies are primarily attributable to the limited set of processes and state variables simulated, or whether they are linked most directly to choices about the other attributes described here (Sections 4.5.2–4.5.5). Making informed decisions about the level of detail with which to represent the other attributes will minimize chances of the latter, but some trial-and-error adjustment, systematic sensitivity analyses, or tests of convergence may be necessary to achieve resolution.

Several techniques can effectively reduce the number of state variables included in models with minimal impact on the models' representativeness. When bidirectional coupling between state variables occurs over different timescales, both variables should be explicitly represented. In contrast, sometimes state variables are tightly coupled and

synchronous, making it possible to simulate just one of the correlated variables. In their patterned mudflat model, Weerman et al. (2010; Fig. 3A) modeled bed sediment fluxes not as a function of excess bed shear stress (the most directly related state variable) but of the local abundance of diatoms, which they found to be the primary driver of excess bed shear stress. In a more complex example, Larsen and Harvey (2010) avoided directly simulating phosphorus concentration as a driver of peat accumulation in the Everglades, despite its status as a highly limiting nutrient. Initial small-scale simulations by those authors (Larsen et al., 2007) revealed that within a patch, phosphorus concentrations vary predictably as a function of distance from the patch edge and local elevation. They developed empirical relations between these attributes and local rates of peat accumulation and used them to represent phosphorus indirectly in their landscape evolution model, as a spatially variable peat production parameter that was dependent on local soil elevations and distance to the patch edge.

Another option for simplification is the discretization of state variables with continuously varying attributes that influence the variables' behavior into classes or cohorts. Liang et al. (2015b; Fig. 3F) captured the different behaviors of fine and coarse sediment in river deltas using two uncoupled size classes. Meanwhile, age cohort models, which are necessarily coupled, are common in ecology (DeAngelis et al., 1993; DeAngelis and Mooij, 2005; Kendall et al., 2011).

Table 1
Strategies for reducing computational detail while maintaining high representational detail.

Aspect of detail	Potential strategies
Number of state variables	Simulate single representative variable within each synchronous group. Use proxy variables that exhibit monotonic relationships to primary drivers. Represent primary drivers indirectly through empirical relations to state variables, developed through other models or field measurement. Use classes or cohorts to represent state variables that have continuously varying quantities.
Spatial dimension	Perform spatial averaging. Develop “quasi” 2D or 3D models by parameterizing or using lookup tables to represent additional dimension in a decoupled manner. Response surface approach to decoupling: obtain multiple lower-dimension solutions to construct behavior across additional dimension.
Temporal dimension	Obtain representative solutions for periods with distinctly different behavior (seasons, storms); multiply fluxes of interest by duration of the period.
Spatial extent	Represent drivers that vary over larger scales than phenomenon of interest through specified boundary conditions, if feedback to those drivers is negligible. Use periodic boundary conditions in regularly patterned or well-mixed systems.
Resolution	Use heterogeneous and/or anisotropic grids and/or dynamic time stepping. Employ underrelaxation and/or a diffuser/smoothing.
Variable coupling	Decouple solutions for variables with different spatial/temporal scales using a hierarchical modeling scheme. Empirical representation of coupling.

4.5.2. Spatial/temporal dimension

Questions about spatial and temporal dimension typically focus on whether a model should represent vertical, lateral, and longitudinal dimensions of a problem, and whether the solution should be steady state or variable in time. For homogeneous, well-mixed systems, low-dimensional models may be appropriate. However, when the system of interest is heterogeneous, the modeler needs to decide whether processes can be represented as spatial averages, or whether fluxes need to be simulated explicitly. As an example of the former, many models of rivers are two dimensional, solving for depth-averaged flow velocities and sediment concentrations in order to compute reach-scale fluxes under different fluvial inputs. In contrast, models of habitat suitability for zebra mussels may need to represent near-bed boundary flows and concentration profiles explicitly, requiring a three-dimensional simulation (Morales et al., 2006). However, when depth-variable flow characteristics (e.g., vorticity, bed shear stress) are important, it may be possible to represent them in a way that minimally increases computational demands (e.g., “quasi” 3D or “quasi” 2D models, as described in Section 2.1). For example, in order to model sediment transport realistically, Falcini and Jerolmack (2010) represented spiral flow in river bends through parameterization. Meanwhile, the Lagrangian flow routing model of Liang et al. (2015b) solved for a two-dimensional water surface profile through the application of one-dimensional equations, applied along the streamlines of the tracked parcels of water.

Temporal solutions may compound the challenge of high spatial dimensionality, requiring a new spatial solution for each increment in time. However, temporal dimensionality is not a strict binary between steady-state and fully transient. In some circumstances, it may be possible to choose an intermediate approach, in which time is divided into coarse phases (e.g., storm vs. interstorm; summer, fall, winter, spring) over which it is reasonable to assume that use of an average flux term is appropriate. For example, Larsen and Harvey (2010) solved for the spatial distribution of flow velocities and bed shear stresses in the Everglades for mean seasonal flood conditions, and assumed that the resulting sediment fluxes were a reasonable approximation of fluxes over the whole flood period. During interflood periods, flow velocities were assumed insufficient to transport sediment and were not simulated.

4.5.3. Extent and boundary conditions

The spatial extent of a model should always be several times larger than the scale of the dominant feedback processes governing the phenomena of interest. However, extent need not be as large as the scale of controlling drivers that do not engage in bidirectional feedback with the state variables, provided boundary conditions are selected appropriately. Specified flux boundary conditions may represent input drivers governed by processes operating at much larger scales than the phenomena of interest. If natural processes would cause those

boundary conditions to vary over time and/or space, the modeler should first determine whether the model is sensitive to those variations with some test analyses. If so, the next question is whether specific sequences of inputs are relevant to the key questions being investigated (e.g., how did amphibian habitat change as a result of the July fire following the dry winter?), or whether general patterns of variation (how does amphibian habitat change seasonally and with different snowfall regimes?) are more central. If the latter, idealized patterns in the boundary conditions may be imposed (e.g., through a sinusoid). If the former, a separate model or module (e.g., a hillslope hydrology module) that covers a larger spatial extent may be needed. Extent also need not be as large as the scale of the landscape of interest. In regularly patterned or well-mixed landscapes, effectively larger areas can be simulated with use of periodic (wrap-around) boundary conditions (e.g., Thiery et al., 1995), if it can be assumed that the portion of the landscape being simulated is sufficiently far from real boundaries.

Decisions about critical temporal scale are inextricably linked to decisions about spatial scale (Werner, 2003; Murray et al., 2008; Coco et al., 2013). In most published simulations, temporal scale varies approximately linearly with spatial scale; in other words, large-scale emergent phenomena require long time scales of simulation and change at slow rates (permitting use of a large time step) relative to smaller-scale emergent phenomena. Because of the accumulation of error and the highly nonlinear nature of complex environmental systems, prediction of change for small spatial scales over long periods of time is often considered “impossible,” while prediction of change for the largest spatial scales over the smallest time scales is considered “meaningless” (Coco et al., 2013). However, hierarchical modeling strategies that simulate dynamics at different critical spatial and temporal scales, with loose coupling across scales, may expand the range of spatial/temporal scale combinations for which models generate good predictions at a reasonable computational cost (Werner, 2003; Coco et al., 2013).

4.5.4. Resolution

Spatial and temporal resolution should be selected to achieve model stability and convergence and to adequately represent phenomena over spatial and timescales of interest. With regard to the latter, fast processes will generally require high resolution (spatially and temporally), and processes affecting interfaces or patch edges generally require high spatial resolution. Meanwhile, it is the slow or large-scale processes that affect the duration/extent of the simulation. Therefore, models that simulate processes over a range of spatial and temporal scales will require long durations and short time steps and/or fine grids, resulting in a large computational burden.

Computational burdens attributable to resolution may be reduced through certain strategies. Heterogeneous grids may be used, in which cells are fine in the vicinity of interfaces but coarse elsewhere. The analogous approach for temporal resolution is to use dynamic time stepping, in which a small time step is algorithmically selected during

periods in which the state variables are changing rapidly (Salah et al., 2010). In spatially anisotropic landscapes, anisotropic discretization may be employed (Larsen and Harvey, 2010). One of the most powerful tools for reducing computational burden may be to represent variables as decoupled and simulate them on different spatial or temporal time steps. This option should only be executed under careful consideration, as detailed in the next section.

Temporal and spatial resolution choices collectively influence model stability. In gradient-flux models, the Courant number (Courant et al., 1967) specifies a necessary but not sufficient criterion for stability. Models will sometimes achieve stability through use of an underrelaxation scheme, which limits the amount by which a state variable changes in a time step (e.g., Liang et al., 2015b) by formulating its new value as a weighted average between the old value and the value that results from application of modified Gauss-Seidel iteration of the governing equations (Hoffman and Frankel, 2001). It can be an important strategy in simple models, because it may allow researchers to use spatial and temporal resolutions that would otherwise be unstable. The spatial analogy to underrelaxation is application of a spatial diffuser or smoother to ensure that variables that should vary continuously in space do not exhibit discontinuities resulting from application of simplified governing equations on a coarse grid. Relaxation and smoothing schemes are common in simulations of air and water flow but are not typically used in simulations of biotic variables.

4.5.5. Representation of coupling

Choices about spatiotemporal resolution and extent are directly related to questions about which of the model's variables should be coupled. Coupling is one of the most important aspects of "detail" in models of ecological/geophysical systems. Models of ecological-geological systems often employ the assumption that biotic-abiotic interactions are characterized by one-dimensional forcing and/or that timescales are sufficiently different that the dynamics can be simulated as decoupled, with the driver represented as a parameter or a prescribed quantity. For instance, habitat distribution may govern fish populations but not vice-versa over the time scale of interest. It is primarily with the recognition of vegetation and animals like beavers or gophers as ecosystem engineers (Jones et al., 1994; Chapin et al., 1997; Yoo et al., 2005; Corenblit et al., 2007) that bidirectional, coupled models of biotic-abiotic feedback began to proliferate. Tightly coupled models create computational challenges, but again, modelers have options for reducing computational burden based on the critical scales and emergent characteristics of the system.

First, the emergent patterns identified in step II may help indicate the extent of coupling needed. Regular patterning generally suggests strong bidirectional coupling between biotic and abiotic elements. Four classes of mechanisms generate regular patterns in landscapes (Table 2). They often involve a limited set of physical and biological entities that are in balance, requiring similar levels of representation in

models. Non-regular patterns might likewise evidence an approximate balance between physical and biological state variables. Fluvial patterns that differ from the minimum-energy configuration (such as multiple-thread or overly sinuous channels) or patchy distributions of any state variable suggest tight coupling between at least two state variables. Despite strong coupling these systems often lend themselves well to simplified models, because the driving variables are typically few and operate over similar scales. However, systems with more than two types of patches (e.g., floodplains or forests with patches composed of different vegetation communities) may be an exception, as different factors could limit the different patches.

The characteristic timescale associated with the dynamics of the coupled variables also informs the representation of coupling in models. When coupled variables operate over different time scales, models may be simplified by decoupling the dynamics at the shorter of the two timescales, such that only the cumulative or average effect of the smaller-timescale dynamics is represented at the larger scale (Fig. 5). Alternatively, if the emergent properties of interest occur over the shorter of the timescales, models may be decoupled at the longer timescale, approximating the variables that change over that longer timescale as constant.

An exploratory model of vegetation-water dynamics on dunes illustrates principles and tradeoffs of simulating interacting state variables as decoupled (Siteur et al., in press). In dunes, infiltration of water happens over very short timescales but influences the distribution of biomass on longer timescales and the buildup of hydrophobic organic compounds exuded by decomposing biomass over even longer timescales. Because of the difference in timescales, biomass and soil hydrophobic compound density may be represented as constant in a model of soil moisture dynamics. Doing so results in the emergence of two stable states: a hydrophilic wet state or a hydrophobic dry state. However, this representation does not reproduce the longer-timescale emergent phenomena that arise when biomass and hydrophobic compound buildup are simulated in a fully coupled way. Complete representation of the coupling results in cyclic dynamics, in which periods of high biomass lag periods of high soil moisture and precede periods of prolonged soil hydrophobicity.

A different approach to strategic decoupling in ecological/geophysical models is to treat the slowly changing variables not as constant through the simulation but as constant within intervals of time longer than the model's time step. As an example, consider a river, floodplain, or wetland that experiences semiannual flood pulses that redistribute sediment. Sediment redistribution changes the topography, which in turn influences the distribution of macrophytes. Establishment of macrophytes stabilizes sediment deposits and generates soil organic matter. Because of these feedbacks, state variables describing flow, topography, and vegetation growth are coupled, yet they operate over different timescales, with different spatial scales of influence. Flow may be variable throughout a year, with each flood pulse redistributing sediment.

Table 2

Strongly coupled mechanisms that lead to regular patterns in geological-ecological systems.

<p>Activator-inhibitor feedbacks: In this classic pattern-generating mechanism, patterns arise through a combination of small-scale positive feedback and larger-scale negative feedback. The larger-scale negative feedback is caused by an inhibitor produced by the activator itself. In landscapes, this mechanism typically results from biota creating conditions that are detrimental to their own</p>	<p>Turing, 1952; van de Koppel and Crain, 2006 Meinhardt, 1976; Rietkerk and Van de Koppel, 2008</p>
<p>1) growth (e.g., the production of wrack). 2) Activator-depleted substrate feedbacks: In this mechanism, patterns also arise through a combination of an activator generating a small-scale positive feedback and larger-scale negative feedback. In this case, the larger-scale negative feedback is caused by the activator depleting a more rapidly diffusing substrate. In landscapes, this mechanism typically results from biota concentrating and/or generating a resource locally, which produces a shortage in the resource outside patches that limits further expansion of the biota.</p>	<p>Weerman et al., 2010</p>
<p>3) Stress divergence feedbacks: When a stress such as wind or water flow is the primary factor influencing the spatial distribution of biota, a stress divergence feedback can produce patterning. Analogous in many respects to the activator-inhibitor feedback, it involves patches of biota deflecting the stress vectors around the patch, promoting local patch persistence but strictly limiting the width of patches.</p>	<p>Liu et al., 2013</p>
<p>4) Phase separation: Equations describing density-dependent rates of movement by animals are mathematically equivalent to the Cahn-Hilliard equation for phase separation in physics. Through differential rates of movement in organisms such as mussels (which move fastest when present at very low or very high densities and slower at intermediate densities), self-organized spatial patterns can emerge.</p>	

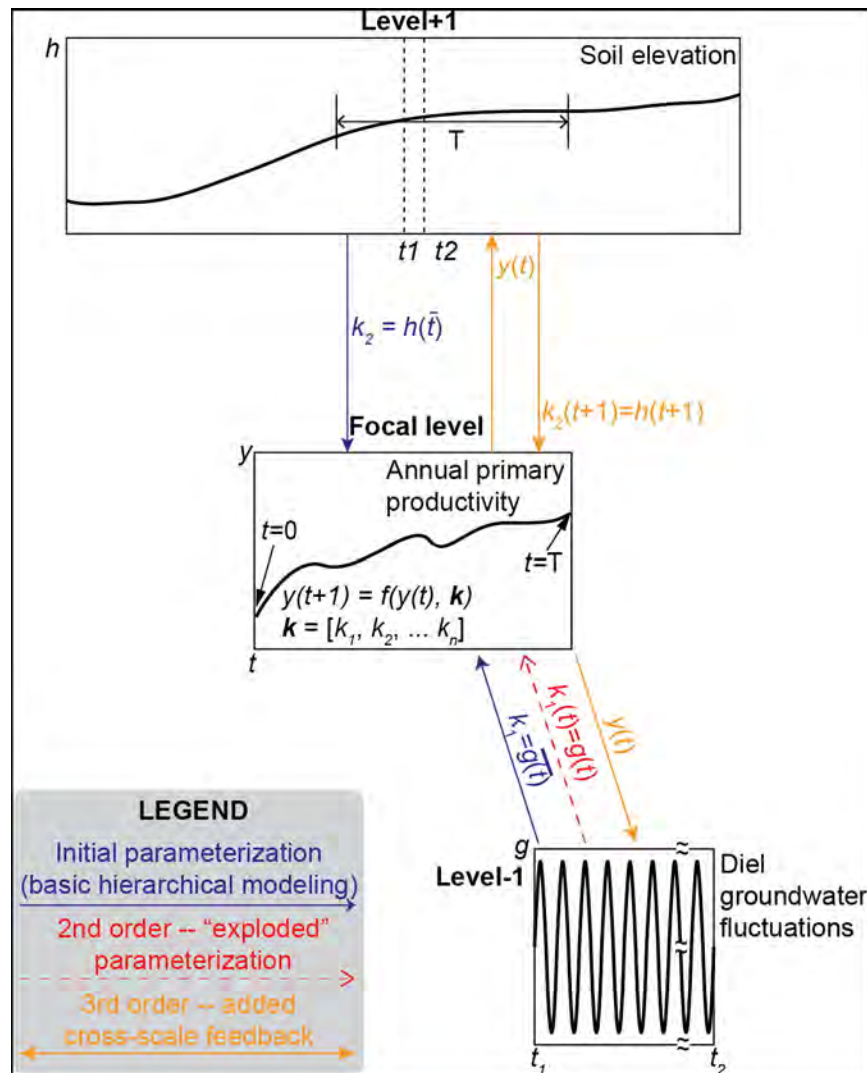


Fig. 5. Structure of a hierarchical modeling strategy and “unpacking” scheme. In basic hierarchical modeling, processes and variables (e.g., soil elevation, h) changing over scales larger or longer than the focal level (e.g., annual primary productivity, y) may be represented as constant (k_2), while those varying over smaller or shorter scales (e.g., diel groundwater fluctuations, g) may be represented as a time average (denoted with an overbar; k_1). Typically, many of these cross-scale interactions are represented as parameters at the focal level of interest; here we depict only a select few for purposes of illustration. To test for whether this simple parameterization is adequate, “unpacking” should be undertaken, whereby parameters are “exploded” into time-varying representations. If the resulting emergent features at the focal level remain the same, convergence has been achieved, and the simpler representation should be sufficient. However, if results differ, the model should continue to be unpacked by next considering cross-scale feedback, whereby changes in state variables at the focal level affect the time-varying properties of variables at other scales.

New establishment of vegetation predominantly occurs during the growing season and may be less influenced by individual storm events than by the aggregate influence of the year's storms on the topography. Thus, it may be reasonable to model vegetation and geomorphology as static over all storms within a year (e.g., D'Alpaos et al., 2007; Kirwan and Murray, 2007; Larsen and Harvey, 2010). If the storms can be approximated as steady over their duration and/or identical, the flow field from each flood pulse occurring within a year need only be simulated once, with sediment redistribution rates simply multiplied over the total storm duration or number of storms each year. At the end of the year, the vegetation dynamics would be simulated. In this way, because of loose coupling between vegetation and flow/sediment dynamics, modelers can select the longer time step of one year (compared to the subdaily time step usually used for flow) without much reduction in the model's ability to represent relevant dynamics.

An alternative strategy is to use separate time steps for coupled modules. For example, Saco and Moreno-de las Heras (2013) coupled the SIBERIA landform evolution model to a model of banded vegetation patterning but maintained separate time steps for the two. SIBERIA's

time step was set between days and years, appropriate to the erosion rates of the system, whereas the vegetation patterning model operated on a subdaily time step to capture transient infiltration and water redistribution processes.

Representation of coupling through simple parameterizations or empiricisms is often insufficient for spatiotemporal processes (e.g., animal visitation times in certain locations or disease propagation) or heterogeneities in animal behavior. In these cases, individual- or agent-based strategies are commonly used to track the movement, decisions, and/or behavior of individuals. Most agent-based models represent the “outer worlds” of animals, in which physical landscape configuration and presence of other organisms influence movement and dispersal patterns (Topping et al., 2003; Goodwin et al., 2006). One frontier lies in representing the “inner worlds” of animals through small-scale models of immunology, reproductive or metabolic processes, or even thinking processes that translate perceptual input into decisions and biological states (reviewed in Getz, 2013). These modules may operate independently of the mainframe simulation or feed back into it, computing the value of one of the mainframe simulation's parameters through the procedure illustrated in Fig. 5.

4.6. Step VI: Model evaluation—How to tell when the level of detail in a model is good enough?

Following model development as detailed above, the next step is to execute the model (step V in Fig. 1) and evaluate its performance (step VI). Many researchers will call this phase “model validation.” Although this term has been criticized when applied literally (Oreskes et al., 1994), it is often interpreted as an evaluation of suitability of the model for its intended purposes (Rykiel, 1996; Augusiak et al., 2014). Here, we view model evaluation as a judgment of the plausibility of the model and the physical processes that it represents. Depending on the objective question governing the model, model evaluation may consist of a pattern comparison phase, tests of convergence, and a ‘benchmarking’ phase.

For questions low in the hierarchy, pattern comparison should focus on the model’s reproduction of general features or processes. For questions higher in the hierarchy, pattern comparison may involve the spatiotemporal behavior of the model and/or focus on weak patterns. A prime challenge in pattern comparison is how to condense spatially and temporally variable information to a single metric that feeds into a yes/no decision about whether a pattern is matched (i.e., a so-called “rejection filter”) or statistical inference about the model’s likelihood (Hartig et al., 2011). For an exploratory model, a simple qualitative assessment may be sufficient. Quantitative pattern comparisons, however, may be necessary to automate evaluation (e.g., for sensitivity analyses), or assess the model’s ability to replicate weak or subtle patterns at later stages within the hierarchy of questions (Fig. 1). Table 3 highlights several of the most common metrics for spatial pattern comparison used in geostatistics and landscape ecology. A suitable metric should be able to distinguish between the observed pattern and randomized spatial distributions of the state variable used to compute the metric. To conduct this test, the researcher can randomly shuffle datapoints that are distributed in space to derive a probability density function of the pattern metric over randomized landscapes. The value of the pattern metric for the nonrandomized landscape should fall within the α th percentile tail; otherwise, the metric is insensitive to that particular pattern. A stricter test is that probability density functions of the

metric for different recognized classes of pattern should have minimum overlap; in other words, the variance of the metric within a class of pattern should be far less than the variance among classes, which can be tested using F-statistics or nonparametric counterparts such as the Kruskal-Wallis test.

Information that the model is unable to replicate a pattern is potentially useful, but it poses a challenge for interpretation. Mismatch between the modeled and observed pattern might arise because 1) the hypothesized mechanism is wrong, 2) the parameter values are wrong, 3) the modeled mechanisms are not represented at sufficient levels of detail, or 4) there are large errors in the observation of the pattern. If #1 or #2 is responsible for the mismatch, the modeler can rule out the hypothesized mechanism under consideration and/or delineate the parameter range within which the emergent features occur. However, if the model’s detail is insufficient to reproduce emergent properties (even if the mechanisms and parameters are “correct”), or if the pattern observations are in error (e.g., when pattern observations are themselves derived from models, such as atmospheric patterns derived from reanalysis data products; Kennedy et al., 2011), conclusions about mechanism or parameter range are suspect.

To rigorously evaluate whether a mismatch could be attributed to #3, the convergence of models could be checked through the “unpacking” strategy (Getz, 2013; Fig. 5). Most modelers are familiar with tests for convergence in spatial or temporal resolution: the modeler progressively refines the spatial grid or time step until the output ceases to change. Unpacking is similar in principle. Processes represented as a single parameter in the first-order model are “exploded” (i.e., simulated explicitly with a second-order submodel) to evaluate whether the additional detail changes the first-order emergent patterns. If not, the model has converged, and the first-order level of detail was sufficient. If the output did change, the level of detail should be exploded to third order to evaluate whether the second-order detail was sufficient. In a hierarchical modeling structure (Fig. 5), this third order expansion may involve converting the parameter submodules to a form intrinsic to the dynamical system, in which they are influenced by higher level state variables, adding feedback to the system. Although it may not be practical to undertake the test for convergence for all aspects of detail listed here, the modeler should

Table 3
Example metrics for pattern comparison and model evaluation.

Metric	Description	References
<i>Metrics for summarizing spatiotemporal pattern information</i>		
Class proportional abundances, richness, evenness, diversity, patch shape complexity, contrast, aggregation, subdivision, lacunarity, isolation	Appropriate for landscapes with categorical patches or classes of state variables.	McGarigal, 2006
Island shape factor, area, and aspect ratio	Differentiates between physiographic zones within river deltas.	Passalacqua et al., 2013
Range of spatial autocorrelation function/semivariogram	Identifies critical length scale of pattern.	Watts et al., 2010
Fractal dimension, distribution of island sizes, nearest-edge distance, distribution of shoreline sediment fluxes, nourishment/catchment area, channel-floodplain connectivity	A comprehensive suite of morphodynamic metrics applied to river deltas.	Edmonds et al., 2011 Liang et al., 2016
Shannon entropy index	Describes spatial variation in a state variable, used to classify spatially periodic patterns.	Konings et al., 2011
Connectivity-orientation curves	Directional connectivity of landscape elements over range of orientations. Curves can be compared using methods for comparing probability distributions.	Larsen et al., 2012
Spatial state-space plots	Delay-coordinate embedding of sequential river widths (applies to directional, deterministic systems). Plots are transformed into discrete probability distributions, which can be compared with the methods detailed in the following section of this table.	Sapozhnikov et al., 1998
Logarithmic correlation integral (LCI) function	Tests for self-affinity, an anisotropic form of fractal scaling.	Sapozhnikov et al., 1998
<i>Metrics for comparing vectors or distributions of summary statistics</i>		
Transportation distance	Minimum average distance elements of discretized distribution must be moved to duplicate other distribution.	Moeckel and Murray, 1997
Kolmogorov-Smirnov statistic	Maximum separation distance between cumulative probability distributions.	Smirnov, 1948
Tucker’s congruence coefficient	Index of similarity between factors, traditionally defined through factor analysis but also applicable to summary statistic vectors.	Lorenzo-Seva and Ten Berge, 2006

endeavor to do so for those variables most in question, and, as a general rule, for spatial/temporal resolution.

Tests for convergence with respect to model detail have been underutilized in the literature. One good example from ecology is the exploratory model of Scheffer et al. (2003), used to study competition between floating and submerged plants for nutrients and light. To evaluate whether the three equilibria that emerged (floating plant-dominated, submerged plant-dominated, or a stable mixed community) were artifacts of the model's simplifications, a more elaborate version of the model was also developed. This version incorporated additional mechanistic details about the seasonal life cycle of water plants, seasonal variation in solar irradiation, and light interception. Although a stable mixed state was no longer observed in the more detailed model, bistability between the floating plant-dominated and submerged plant-dominated state still occurred over a range of nutrient loading regimes, motivating subsequent empirical testing.

Last, benchmarking may also address questions of robustness or why a model fails to reproduce observed patterns. Benchmarking tests are generally performed on subcomponents of the model to ensure that they adequately represent constituent phenomena (Liang et al., 2015a). The model is applied to an idealized, simplified situation, and outputs are compared to theory or other validated models. For example, to provide the assurance that their simplified flow routing scheme for river deltas captured the relevant physics, Liang et al. (2015a) evaluated their model's outcomes against those of a computational fluid dynamics model and analytical solutions. Tests compared the shape of the water surface resulting from flow over a Gaussian bump, backwater profiles, and flow velocities and water-surface elevation in the vicinity of a channel bifurcation and over a delta with static topography. Benchmarking of modeled ecological responses may invoke comparison of output distributions of a state variable to predictions from ecological theory (e.g., plant growth should exhibit a skewed unimodal response to temperature and a "limiting factor" response to light; Austin, 2007).

4.7. Step VIIa: Projection and scenario modeling

Once a mechanistic model passes tests of convergence and exhibits agreement with observed patterns, it can be used for projection and scenario modeling. Scenario modeling typically implies the use of detailed models that address questions about how specific management alternatives or perturbation scenarios are likely to impact a system. However, in some cases the questions prompting predictive modeling may be more general and well suited to models at low or intermediate levels of detail.

Under certain circumstances, predictive models that are robust to nonstationarity and grounded in a mechanistic description of the system of interest but not explicitly process-based may be formulated. These models, derived directly from data using nonlinear forecasting techniques, completely circumvent the time-consuming steps III–IV of ACME and are free of equations and hence low-detail (arrow P1 of Fig. 4). Such models may be suitable for low-dimensional, deterministic systems for which time-series data of the critical state variable(s) are available. As with the EDM methods used for causal inference (Section 4.4), the procedure begins with shadow manifold reconstruction from the time series (Fig. 4). Based on that manifold (and potentially the shadow manifolds of other forcing variables), the variable's value at a future time can be predicted from weighted regression of vectors originating at nearest-neighbor datapoints. For chaotic systems, this method is effective only for prediction of system behavior for short times into the future, as exponential divergence of nearby trajectories is a defining feature of chaos. Nonlinear forecasting methods such as these are mechanistic in the sense that they are based on the underlying structure of the system's dynamics, even while they do not explicitly account for process-level interactions. They are robust to nonstationarity because even a nonstationary system responding to a consistent set of drivers is expected to develop a coherent strange attractor. EDMs used to

forecast fisheries yields commonly outperform more complex process-based models, due to the accumulation of error in the process-based models (Liu et al., 2012; Glaser et al., 2014; Ye et al., 2015).

Although data-driven modeling approaches described here may streamline or circumvent the standard ACME process, several key limitations restrict their widespread application in landscape modeling. Chief among them is that, whereas most processes that shape landscapes are spatiotemporal in nature, the causal inference and nonlinear forecasting strategies discussed here were developed for time series at a point. Predictions for variables that change in space may be generated by adopting a simple space-for-time substitution in the methodology outlined above (Hossain and Sivakumar, 2005), but the theoretical basis for doing so is dubious (Sivakumar, 2009). More recently, fisheries modelers have dealt with the challenge of predicting yields over space and time by performing individual phase space reconstructions for each spatial cell of interest, effectively generating as many independent models as there were predictive grid cells (Glaser et al., 2014). A similar approach is to aggregate the time series acquired at different points in space to perform a single phase space embedding, assuming the same drivers control processes at all points monitored (Clark et al., 2015). Even so, the latter two approaches do not explicitly account for the role of spatial interactions in the temporal evolution of fish yields. A second limitation is that nonlinear forecasting techniques are far more restricted in the scope of the questions they can answer than mechanistic modeling; they provide no insight into the mechanisms driving the system's behaviors and are of limited utility in sensitivity or scenario testing, as their long-term accuracy diminishes exponentially.

4.8. Step VIIb. Progression of model objectives

Once a model has been developed to address the mechanistic question for which it was originally intended, it is ready for extension or expansion, potentially to address questions further down the hierarchy of governing questions or to evaluate the role of a different set of drivers in a different environment. Typically, this progression entails moving to the right on the tradeoff diagram (Fig. 2). Practically, progression may take the form of adding new state variables or processes, or changing the way in which processes are represented. Unpacking (Fig. 5) may constitute another important part of this process. For large environmental management models, model progression may also take the form of integration of that model as a module or component of a larger model, using a coupled, hierarchical modeling scheme, as detailed in Section 5.

As an example of the progression phase, consider again the Murray and Paola (1997; Fig. 3B) model of braided streams that was originally developed to address a question of type 2 ("What are the essential attributes that lead to the emergence of a large-scale phenomenon or process?"). This model formed the basis of later models that examined the mechanisms responsible for realistic meander bend morphology (Question 4: "What mechanism is responsible for the second-order details of a pattern?") (Coulthard and Van De Wiel, 2006; Nicholas et al., 2012; Nicholas, 2013), as well as models that examined whether the same set of fluvial processes, together with the cohesive and drag effects of vegetation, could produce meandering streams in environments with vegetation (Murray and Paola, 2003; Fig. 3C).

5. A look ahead: Opportunities for ACME to advance environmental science and management

Environmental restoration projects are rife with opportunity for using, testing, and refining the principles of ACME. Many of the insights described here were derived from modeling related to restoration. Restoration projects require an understanding of how physical and biological processes interact, how those interactions cascade across scales to produce emergent features, and how those emergent features are likely to change in the future under different management scenarios and changes in external drivers such as climate.

It is generally agreed that restoration should focus on process rather than a static end state (Palmer et al., 2005; Suding and Gross, 2006), requiring an understanding of the causal interactions driving ecosystems. Hence, questions relevant to restoration and management often overlap those covered in the ACME approach. However, with the availability of off-the-shelf models for driving processes such as flow velocity distributions and sediment transport, it is easy to forget that the causal interactions sculpting particular emergent features relevant to restoration may not be well understood, and models that do not represent those interactions could lead to misleading projections. With an increasing emphasis on data-driven analyses, it is worth noting that exploratory modeling provides a robust route for testing not just the existence but the also the functional form of causal interactions, in a way that is complementary to the data-driven techniques. Resolving the main causal interactions and their simplest functional form is an important step in restoration planning, as planning models that represent many relevant interactions in high levels of detail might be too cumbersome to evaluate over a range of scenarios or determine the long-term effects of management decisions.

River delta and coastal wetland restoration projects provide apt illustrations of these points. In these dynamic and economically important environments, flow and sediment interact with vegetation to build and destroy land and habitat for fish and shellfish. Having suffered from decades of sediment starvation, subsidence, altered hydrology, and storm damage, they are targets for restoration through actions that facilitate land building. However, because of extensive feedbacks present over multiple scales, they present a challenge for forecasting and management (Kim et al., 2009). In the slow flows characteristic of deltas, vegetation distribution is governed by flow but also governs flow. Similarly, cross-scale bidirectional couplings among hydrodynamics, sediment transport, elevation, and vegetation dynamics play dominant roles in the evolution of salt marsh and mangrove environments (Fagherazzi et al., 2012; Saco and Rodríguez, 2013). Flow, sediment, and vegetation collectively affect the distribution of habitat for fish. Increasingly, principles of ACME are being applied to coastal wetlands and deltaic environments, though many opportunities remain untapped.

For example, the ACME framework can provide guidance on modeling restoration impacts over a wider range of scales than is typical today. In a review of how models guide restoration decisions relevant to fish populations of coastal Louisiana, Rose et al. (2015) stated that one of the three objective questions determined by stakeholders was ultimately discarded because of the difficulty of finding solutions at fine spatiotemporal scales. Instead of evaluating the effects of individual projects on fish populations at the local scale, models focused on long-term aggregate effects of multiple projects at the coastal scale. Moreover, some of the models were selected on the basis of their past performance rather than their ability to provide insight into the mechanisms governing fish populations, as the former was judged more relevant than the latter. The type of modeling strategies low on ACME's hierarchy of objective questions could provide novel contributions to the evaluation of effects of different management scenarios in the greater Mississippi River Delta area. Exploratory models by Seybold et al. (2007) and Liang et al. (2015b; Fig. 3F) identified the minimum set of processes essential to simulating the evolution of delta morphology, with the latter providing an algorithm that vastly simplifies hydrodynamic calculations. Use of these reduced-complexity models for the governing physics together with models representing other factors relevant to fish habitat (i.e., through the modular linking described in Section 4.8) may make it feasible to address questions about restoration's effects across scales. The focus of exploratory modeling or data-driven analyses such as CCM or transfer entropy on mechanisms, though currently deemed lower priority by managers of the coastal Louisiana restoration, may have additional benefits. These analyses identify the most critical drivers of the system, potentially leading to streamlining of models, which could then be run over a wider range of spatiotemporal scales and extent. Secondly, this process-based focus makes it relatively easy

to adjust models for major changes in drivers, such as potential effects of increased frequency of major storms interacting with changes due to management scenarios.

Importantly, converging on the appropriate level of complexity for a model composes just one step of a “best practices” approach to modeling of environmental systems (Schmolke et al., 2010; Rose et al., 2015). However, it is one of the most critical steps, and one that has not yet been approached systematically for models that combine geophysics and ecology across multiple scales. Ideally, modelers would embark on the ACME approach in coordination with other best practices for modeling: inclusion of stakeholders, and formulation of objectives with stakeholder input (Schmolke et al., 2010). Other relevant best practices include sensitivity analysis, use of multiple models (i.e., ensembles) for projection, quantification of uncertainties, peer review, and documentation for transparency. ACME is somewhat different from previously identified best modeling practices, as it considers the choice of model complexity to be inseparable from formulation of the conceptual model, parameterization and calibration, and verification, because of the iterative process inherent in the pattern-oriented evaluation of model complexity.

We emphasize that there is no single formula for the selection of the optimal level of computational and representational detail that will work for all models. However, a systematic approach to examining the different components of model detail in light of the objective questions and the emergent features of the system will doubtlessly streamline the process. In general, the simplest model that represents the dominant processes driving the emergent features of interest will be the most appropriate. Recent innovations in formulating exploratory models of physical and biological processes suggest ways to reduce the computational detail of models while retaining representational detail. Additional streamlining of the process of converging on the appropriate level of complexity may result from data-driven approaches to identifying dominant processes and, potentially, their critical timescales and length scales.

Acknowledgements

Support for this work was provided by a Gordon and Betty Moore Foundation Data-Driven Discovery Investigator Award to LGL and National Science Foundation grants EAR-1455362 and EAR-1263851. The latter grant provided support for the Art and Science of Reduced Complexity Modeling in the Environmental Sciences workshop, held in Boulder, CO March 27–29, 2013, from which the ideas of this paper emerged. Contributions of all meeting participants to the discussions were deeply influential. Meeting details, including a list of participants, are available at sites.google.com/site/rcmworkshop/home. Finally, we thank Andrea D'Alpaos, an anonymous reviewer, and the associate editor for their helpful comments on how to improve the manuscript.

Appendix A. Decision tree for honing attributes of model “detail”.

This decision tree extends and operationalizes the guidance on appropriate levels of detail with which to represent processes provided in Table 1 and the main text. An alternative, interactive format for the decision tree (potentially for use as a teaching tool) is available at http://prezi.com/ulpwhtd_1d9w/?utm_campaign=share&utm_medium=copy (screen capture below). The decision tree addresses attributes of model detail (Roman numerals) that all models share. To aid in model formulation, users should start with each Roman numeral and follow the series of questions that follows as though using a taxonomic key. For some attributes of model detail, a series of leading questions (capital letters) apply. Users are advised to “enter” the tree multiple times so that each secondary branch point (each combination of a Roman numeral and capital letter) is visited. The leaves of the tree (written in italics) constitute the relevant advice, all of which is elaborated in the main text.

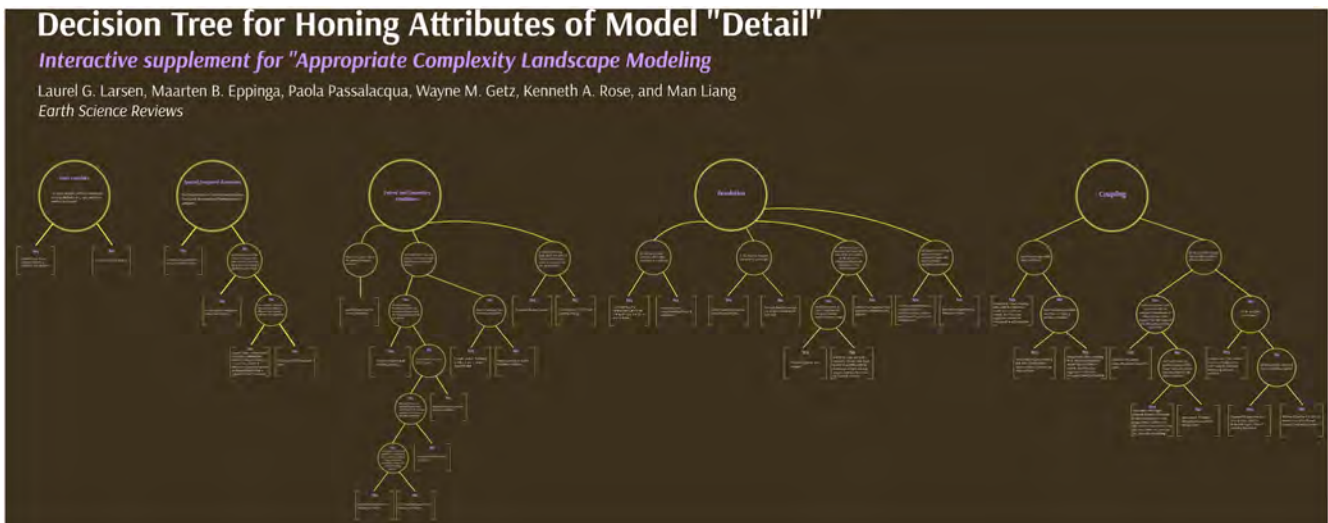


Fig. A1. Screen capture of online interactive decision tree tool.

I. State variables

- A. Do state variables exhibit continuously varying attributes (e.g., age, size) that need to be tracked?
- Yes.....Consider using discrete classes or cohorts as individual state variables.
 - No.....Proceed to the next question.

II. Spatial/temporal dimension

- A. Do the processes of interest have dynamics that could be considered homogeneous or uniform?
- Yes.....Consider using a model with low spatial dimensionality.
 - No.....Are the dynamics of the process heterogeneous over a smaller scale than the scale of the emergent phenomena of interest?
- Yes.....Consider spatial averaging to reduce dimensionality.
 - No.....Can variability along one dimension be related to a different state variable with lower dimensionality?
- a. Yes.....Consider "quasi" N-dimensional simulations: Parameterize variability along the "quasi" (i.e., not explicitly simulated) dimension or use a lookup table or empirical relation from a separate ("offline") simulation.
- b. No.....Proceed with full-dimensional model.

III. Extent and boundary conditions

- A. What is the spatial scale of the dominant feedback processes?.....Spatial extent should be several times larger.
- B. Are there drivers that vary over an extent much larger than the phenomenon of interest?
- Yes.....Do they engage in feedback with the state variables of interest over the temporal extent of the simulation?
- Yes.....Consider a hierarchical modeling strategy.
 - No.....Do the drivers vary over time or space?
- a. Yes.....Represent drivers as specified flux boundary conditions. Is the outcome sensitive to variations in the boundary conditions?
- Yes.....Can general or idealized patterns of variability in the boundary conditions (e.g., generalized seasonality) address the central modeling question?
- Yes.....Impose idealized patterns in boundary conditions.
 - No.....Use a specified sequence for boundary conditions.
- No.....Impose constant boundary conditions.

- No.....Represent drivers as constant boundary conditions.

- No.....Does the landscape have a pattern that is recurrent in space?

- Yes.....Consider periodic boundary conditions and a smaller spatial domain.
- No.....Impose constant or no-flux boundary conditions.

- C. In relative terms (e.g., large, small, fast, slow), is the intended temporal extent a close match to the spatial extent?

- Yes.....Proceed to the next question.
- No.....Consider using a hierarchical modeling strategy.

IV. Resolution

- A. Do the hypothesized processes affect edges, interfaces, or transitions?

- Yes.....Use a relatively fine computational grid in the vicinity of edges, interfaces, and transitions.
- No..... A uniformly sized computational grid may be appropriate.

- B. Is the observed emergent phenomenon anisotropic?

- Yes.....Consider spatially anisotropic computational grid cells.
- No.....Grid cells should be isotropic (i.e., all faces should be the same size).

- C. Are the simulated processes fast for at least some of the time, relative to the size of the computational grid cells and duration of the simulated period?

- Yes.....Are distinct periods of rapid change expected, interspersed among periods of slower change?

- Yes.....Consider dynamic time stepping.
 - No.....Small time steps are likely necessary. Choose time steps to achieve stability with the desired spatial grid size (e.g., using a stability criterion like the Courant criterion).
- No.....Uniform time stepping without special considerations is likely sufficient.

- D. Are requirements for high spatial or temporal resolution (if applicable) likely to diminish tractability substantially?
- Yes.....*Consider underrelaxation as a strategy to increase tractability, and/or perform spatial smoothing on a lower-resolution grid.*
 - No.....*Use standard algorithms for iterating the model.*

V. Coupling

A. Does the landscape exhibit regular patterning?

- Yes.....*Strong biotic-abiotic coupling likely. May be conducive to simple representation in models. See Table 2 for suggestions relevant to conceptual model formulation.*
 - No.....*Does the landscape exhibit more than 2–3 types of patches or features?*
- Yes.....*Model likely requires relatively high level of detail due to larger numbers of interacting state variables.*
 - No..... *Strong biotic-abiotic coupling likely. May be conducive to simple representation in models. See Table 2 for suggestions relevant to conceptual model formulation.*

B. Do the potentially coupled state variables operate at different time scales?

- Yes.....*Is the critical time scale associated with the emergent phenomenon of interest closer to the longer of the time scales of the interacting variables in question?*
- Yes.....*Represent the shorter-timescale process through its mean.*
 - No.....*Are the dynamics (i.e., gradual changes) of the longer-timescale process likely important for the shorter timescale?*
- Yes.....*Approximate the longer-timescale process as constant for discrete intervals in time, using distinct modules with different time steps for the long- and short-timescale processes (i.e., hierarchical modeling).*
 - No.....*Approximate the longer-timescale process with its average value.*
- No.....*Are variables synchronous?*
- Yes.....*Simulate one of the variables directly, and solve for the other using the empirical relationship between variables.*
 - No.....*Do the variables consist of diverse, individual agents?*
- Yes.....*Appropriate representation may be best suited for individual (agent)-based modeling framework.*
 - No.....*Represent feedback or forcing between variables through coupled governing equations.*

References

- Abdul Razak, F., Jensen, H.J., 2014. Quantifying “causality” in complex systems: understanding transfer entropy. *PLoS One* 9, e99462.
- Arditi, R., Ginzburg, L.R., 1989. Coupling in predator-prey dynamics: ratio-dependence. *J. Theor. Biol.* 139, 311–326.
- Augustiak, J., Van den Brink, P.J., Grimm, V., 2014. Merging validation and evaluation of ecological models to “evaluation”: a review of terminology and a practical approach. *Ecol. Model.* 280, 117–128.
- Austin, M., 2007. Species distribution models and ecological theory: a critical assessment and some possible new approaches. *Ecol. Model.* 200, 1–19.
- Avgar, T., Deardon, R., Fryxell, J.M., 2013. An empirically parameterized individual based model of animal movement, perception, and memory. *Ecol. Model.* 251, 158–172.
- Barraquand, F., Benhamou, S., 2008. Animal movements in heterogeneous landscapes: identifying profitable places and homogeneous movement bouts. *Ecology* 89, 3336–3348.
- Bascompte, J., Solé, R.V., 1995. Rethinking complexity: modelling spatiotemporal dynamics in ecology. *Trends Ecol. Evol.* 10, 361–366.
- Belyea, L.R., Baird, A.J., 2006. Beyond “the limits to peat bog growth”: cross-scale feedback in peatland development. *Ecol. Monogr.* 76, 299–322.
- Bowler, D.E., Benton, T.G., 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biol. Rev.* 80, 205–225.
- Chapin III, F.S., Walker, B.H., Hobbs, R.J., Hooper, D.U., Lawton, J.H., Sala, O.E., Tilman, D., 1997. Biotic control over the functioning of ecosystems. *Science* 277, 500–504.
- Clark, A.T., Ye, H., Isbell, F., Deyle, E.R., Cowles, J., Tilman, G.D., Sugihara, G., 2015. Spatial convergent cross mapping to detect causal relationships from short time series. *Ecology* 96, 1174–1181.
- Cloern, J.E., Knowles, N., Brown, L.R., Cayan, D., Dettinger, M.D., Morgan, T.L., Schoellhamer, D.H., Stacey, M.T., van der Wegen, M., Wagner, R.W., Jassby, A.D., 2011. Projected evolution of California’s San Francisco Bay-Delta-River system in a century of climate change. *PLoS One* 6, e24465.
- Coco, G., Zhou, Z., van Maanen, B., Olabarrieta, M., Tinoco, R., Townend, I., 2013. Morphodynamics of tidal networks: advances and challenges. *Mar. Geol.* 346, 1–16.
- Collie, J.S., Botsford, L.W., Hastings, A., Kaplan, I.C., Largier, J.L., Livingston, P.A., Plagányi, É., Rose, K.A., Wells, B.K., Werner, F.E., 2014. Ecosystem models for fisheries management: finding the sweet spot. *Fish Fish.*
- Corenblit, D., Tabacchi, E., Steiger, J., Gurnell, A.M., 2007. Reciprocal interactions and adjustments between fluvial landforms and vegetation dynamics in river corridors: a review of complementary approaches. *Earth Sci. Rev.* 84, 56–86.
- Coulthard, T.J., Van De Wiel, M.J., 2006. A cellular model of river meandering. *Earth Surf. Process. Landf.* 31, 123–132.
- Courant, R., Friedrichs, K., Lewy, H., 1967. On the partial difference equations of mathematical physics. *IBM J. Res. Dev.* 11, 215–234.
- D’Alpaos, A., Lanzoni, S., Marani, M., Rinaldo, A., 2007. Landscape evolution in tidal embayments: modeling the interplay of erosion, sedimentation, and vegetation dynamics. *J. Geophys. Res.* 112, F01008.
- de Roos, A.M., Persson, L., 2013. Population and Community Ecology of Ontogenetic Development. Princeton University Press.
- de Valpine, P., Scranton, K., Knape, J., Ram, K., Mills, N.J., 2014. The importance of individual developmental variation in stage-structured population models. *Ecol. Lett.* 17, 1026–1038.
- DeAngelis, D.L., Mooij, W.M., 2005. Individual-based modeling of ecological and evolutionary processes. *Annu. Rev. Ecol. Evol. Syst.* 147–168.
- DeAngelis, D.L., Rose, K.A., Crowder, L.B., Marschall, E.A., Lika, D., 1993. Fish cohort dynamics: application of complementary modeling approaches. *Am. Nat.* 142, 604–622.
- Doeschl-Wilson, A.B., Ashmore, P.E., 2005. Assessing a numerical cellular braided-stream model with a physical model. *Earth Surf. Process. Landf.* 30, 519–540.
- Edmonds, D.A., Paola, C., Hoyal, D.C.J.D., Sheets, B.A., 2011. Quantitative metrics that describe river deltas and their channel networks. *J. Geophys. Res. Earth Surf.* 116, F04022.
- Eppinga, M.B., de Ruiter, P.C., Wassen, M.J., Rietkerk, M., 2009. Nutrients and hydrology indicate the driving mechanisms of peatland surface patterning. *Am. Nat.* 173, 803–818.
- Eppinga, M.B., Rietkerk, M., Belyea, L.R., Nilsson, M.B., Ruiter, P.C.D., Wassen, M.J., 2010. Resource contrast in patterned peatlands increases along a climatic gradient. *Ecology* 91, 2344–2355.
- Eppinga, M.B., Rietkerk, M., Borren, W., Lapshina, E.D., Bleuten, W., Wassen, M.J., 2008. Regular surface patterning of peatlands: confronting theory with field data. *Ecosystems* 11, 520–536.
- Eppstein, M.J., Molofsky, J., 2007. Invasiveness in plant communities with feedbacks. *Ecol. Lett.* 10, 253–263.
- Evans, M.R., Grimm, V., Johst, K., Knuuttila, T., de Langhe, R., Lessells, C.M., Merz, M., O’Malley, M.A., Orzack, S.H., Weisberg, M., et al., 2013. Do simple models lead to generality in ecology? *Trends Ecol. Evol.* 28, 578–583.
- Fagherazzi, S., Kirwan, M.L., Mudd, S.M., Guntenspergen, G.R., Temmerman, S., D’Alpaos, A., Koppel, J., Rybczyk, J.M., Reyes, E., Craft, C., Clough, J., 2012. Numerical models of salt marsh evolution: ecological, geomorphic, and climatic factors. *Rev. Geophys.* 50.
- Falcini, F., Jerolmack, D.J., 2010. A potential vorticity theory for the formation of elongate channels in river deltas and lakes. *J. Geophys. Res. Earth Surf.* 115, F04038.
- Getz, W.M., 1998. An introspection on the art of modeling in population ecology. *Bioscience* 48, 540–552.
- Getz, W.M., 2013. Computational population biology: linking the inner and outer worlds of organisms. *Israel J. Ecol. Evol.* 59, 2–16.
- Glaser, S.M., Ye, H., Sugihara, G., 2014. A nonlinear, low data requirement model for producing spatially explicit fishery forecasts. *Fish. Oceanogr.* 23, 45–53.
- Goodwin, R.A., Nestler, J.M., Anderson, J.J., Weber, L.J., Loucks, D.P., 2006. Forecasting 3-D fish movement behavior using a Eulerian-Lagrangian-agent method (ELAM). *Ecol. Model.* 192, 197–223.
- Granger, C.W., 1969. Investigating causal relations by econometric models and cross-spectral methods. *Econometrica* 424–438.
- Grassberger, P., Procaccia, I., 1983a. Characterization of strange attractors. *Phys. Rev. Lett.* 50, 346–349.
- Grassberger, P., Procaccia, I., 1983b. Measuring the strangeness of strange attractors. *Phys. D* 9, 189–208.
- Grimm, V., Railsback, S.F., 2012. Pattern-oriented modelling: a “multi-scope” for predictive systems ecology. *Philos. Trans. R. Soc. B* 367, 298–310.
- Grimm, V., Railsback, S.F., 2013. Individual-based Modeling and Ecology. Princeton University Press.
- Groves, D.G., Sharon, C., Knopman, D., 2012. Planning Tool to Support Louisiana’s Decisionmaking on Coastal Protection and Restoration. (Product Page) http://www.rand.org/pubs/technical_reports/TR1266.html.
- Hajek, E.A., Wolinsky, M.A., 2012. Simplified process modeling of river avulsion and alluvial architecture: connecting models and field data. *Sediment. Geol.* 257, 1–30.
- Harsch, M.A., Zhou, Y., HilleRisLambers, J., Kot, M., 2014. Keeping pace with climate change: stage-structured moving-habitat models. *Am. Nat.* 184, 25–37.

- Hartig, F., Calabrese, J.M., Reineking, B., Wiegand, T., Huth, A., 2011. Statistical inference for stochastic simulation models – theory and application. *Ecol. Lett.* 14, 816–827.
- Hastings, A., 2001. Transient dynamics and persistence of ecological systems. *Ecol. Lett.* 4, 215–220.
- Hastings, A., 2004. Transients: the key to long-term ecological understanding? *Trends Ecol. Evol.* 19, 39–45.
- Heffernan, J.B., 2008. Wetlands as an alternative stable state in desert streams. *Ecology* 89, 1261–1271.
- Hoffman, J.D., Frankel, S., 2001. *Numerical Methods for Engineers and Scientists*. CRC Press, Second Edition.
- Holling, C.S., 1959. The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. *Can. Entomol.* 91, 293–320.
- Hossain, F., Sivakumar, B., 2005. Spatial pattern of arsenic contamination in shallow wells of Bangladesh: regional geology and nonlinear dynamics. *Stoch. Env. Res. Risk A* 20, 66–76.
- Jackisch, C., Zehe, E., Samaniego, L., Singh, A.K., 2014. An experiment to gauge an ungauged catchment: rapid data assessment and eco-hydrological modelling in a data-scarce rural catchment. *Hydrol. Sci. J.* 59, 2103–2125.
- Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. *Oikos* 69, 373–386.
- Kendall, B.E., Fox, G.A., Fujiwara, M., Nogueira, T.M., 2011. Demographic heterogeneity, cohort selection, and population growth. *Ecology* 92, 1985–1993.
- Kennedy, A.D., Dong, X., Xi, B., Xie, S., Zhang, Y., Chen, J., 2011. A comparison of MERRA and NARR Reanalyses with the DOE ARM SGP data. *J. Clim.* 24, 4541–4557.
- Khosronejad, A., Kozarek, J.L., Sotiropoulos, F., 2014. Simulation-based approach for stream restoration structure design: model development and validation. *J. Hydraul. Eng.* 140, 04014042.
- Kim, W., Mohrig, D., Twilley, R., Paola, C., Parker, G., 2009. Is it feasible to build new land in the Mississippi River Delta? *EOS Trans. Am. Geophys. Union* 90, 373–374.
- Kirwan, M.L., Murray, A.B., 2007. A coupled geomorphic and ecological model of tidal marsh evolution. *Proc. Natl. Acad. Sci.* 104, 6118–6122.
- Konings, A.G., Dekker, S.C., Rietkerk, M., Katul, G.G., 2011. Drought sensitivity of patterned vegetation determined by rainfall-land surface feedbacks. *J. Geophys. Res. Biogeosci.* (2005–2012), 116.
- Larsen, L.G., Harvey, J.W., 2010. How vegetation and sediment transport feedbacks drive landscape change in the Everglades and wetlands worldwide. *Am. Nat.* 176, E66–E79.
- Larsen, L.G., Harvey, J.W., 2011. Modeling of hydroecological feedbacks predicts distinct classes of landscape pattern, process, and restoration potential in shallow aquatic ecosystems. *Geomorphology* 126, 279–296.
- Larsen, L.G., Choi, J., Nungesser, M.K., Harvey, J.W., 2012. Directional connectivity in hydrology and ecology. *Ecol. Appl.* 22, 2204–2220.
- Larsen, L.G., Harvey, J.W., Crimaldi, J.P., 2007. A delicate balance: ecohydrological feedbacks governing landscape morphology in a lotic peatland. *Ecol. Monogr.* 77, 591–614.
- Larsen, L., Thomas, C., Eppinga, M., Coulthard, T., 2014. Exploratory modeling: extracting causality from complexity. *EOS Trans. Am. Geophys. Union* 95, 285–286.
- Levin, S.A., 1992. The problem of pattern and scale in ecology: the Robert H. MacArthur award lecture. *Ecology* 73, 1943–1967.
- Levins, R., 1966. The strategy of model building in population biology. *Am. Sci.* 421–431.
- Li, W., Qin, B., Zhu, G., 2014. Forecasting short-term cyanobacterial blooms in Lake Taihu, China, using a coupled hydrodynamic–algal biomass model. *Ecohydrology* 7, 794–802.
- Liang, M., Geleynse, N., Edmonds, D.A., Passalacqua, P., 2015a. A reduced-complexity model for river delta formation – part 2: assessment of the flow routing scheme. *Earth Surf. Dyn.* 3, 87–104.
- Liang, M., Van Dyk, C., Passalacqua, P., 2016. Quantifying the patterns and dynamics of river deltas under conditions of steady forcing and relative sea level rise. *J. Geophys. Res. Earth Surf.*
- Liang, M., Voller, V.R., Paola, C., 2015b. A reduced-complexity model for river delta formation – part 1: modeling deltas with channel dynamics. *Earth Surf. Dyn.* 3, 67–86.
- Liu, Q.-X., Doelman, A., Rottschäfer, V., de Jager, M., Herman, P.M.J., Rietkerk, M., van de Koppel, J., 2013. Phase separation explains a new class of self-organized spatial patterns in ecological systems. *Proc. Natl. Acad. Sci.* 110, 11905–11910.
- Liu, H., Fogarty, M.J., Glaser, S.M., Altman, I., Hsieh, C., Kaufman, L., Rosenberg, A.A., Sugihara, G., 2012. Nonlinear dynamic features and co-predictability of the Georges Bank fish community. *Mar. Ecol. Prog. Ser.* 464, 195–207.
- Lorenzo-Seva, U., Ten Berge, J.M., 2006. Tucker's congruence coefficient as a meaningful index of factor similarity. *Methodology* 2, 57–64.
- MacArthur, R., Levins, R., 1967. The limiting similarity, convergence, and divergence of coexisting species. *Am. Nat.* 377–385.
- Massie, T.M., Ryabov, A., Blasius, B., Weithoff, G., Gaedke, U., 2013. Complex transient dynamics of stage-structured populations in response to environmental changes. *Am. Nat.* 182, 103–119.
- May, R.M., 1974. Biological populations with nonoverlapping generations: stable points, stable cycles, and chaos. *Science* 186, 645–647.
- McGarigal, K., 2006. *Landscape Pattern Metrics*. John Wiley & Sons, Ltd., Encyclopedia of Environmetrics.
- Meinhardt, H., 1976. Morphogenesis of lines and nets. *Differentiation* 6, 117–123.
- Milly, P.C.D., Betancourt, J., Falkenmark, M., Hirsch, R.M., Kundzewicz, Z.W., Lettenmaier, D.P., Stouffer, R.J., 2008. Stationarity is dead: Whither water management? *Science* 319, 573–574.
- Moeckel, R., Murray, B., 1997. Measuring the distance between time series. *Phys. D* 102, 187–194.
- Monod, J., 1949. The growth of bacterial cultures. *Annu. Rev. Microbiol.* 3, 371–394.
- Moore, W.M., DeAngelis, D.L., 2003. Uncertainty in spatially explicit animal dispersal models. *Ecol. Appl.* 13, 794–805.
- Morales, Y., Weber, L.J., Mynett, A.E., Newton, T.J., 2006. Effects of substrate and hydrodynamic conditions on the formation of mussel beds in a large river. *J. N. Am. Benthol. Soc.* 25, 664–676.
- Murray, A.B., 2003. Contrasting the goals, strategies, and predictions associated with simplified numerical models and detailed simulations. *Geophys. Monogr.* 135, 151–168.
- Murray, A.B., 2007. Reducing model complexity for explanation and prediction. *Geomorphology* 90, 178–191.
- Murray, A.B., Paola, C., 1994. A cellular model of braided rivers. *Nature* 371, 54–57.
- Murray, A.B., Paola, C., 1997. Properties of a cellular braided-stream model. *Earth Surf. Process. Landf.* 22, 1001–1025.
- Murray, A.B., Paola, C., 2003. Modelling the effect of vegetation on channel pattern in bedload rivers. *Earth Surf. Process. Landf.* 28, 131–143.
- Murray, A.B., Knaapen, M.A.F., Tal, M., Kirwan, M.L., 2008. Biomorphodynamics: physical-biological feedbacks that shape landscapes. *Water Resour. Res.* 44, W11301.
- Nicholas, A.P., 2013. Modelling the continuum of river channel patterns. *Earth Surf. Process. Landf.* 38, 1187–1196.
- Nicholas, A.P., Quine, T.A., 2007. Crossing the divide: representation of channels and processes in reduced-complexity river models at reach and landscape scales. *Geomorphology* 90, 318–339.
- Nicholas, A.P., Sandbach, S.D., Ashworth, P.J., Amsler, M.L., Best, J.L., Hardy, R.J., Lane, S.N., Orfeo, O., Parsons, D.R., Reesink, A.J., 2012. Modelling hydrodynamics in the Rio Paraná, Argentina: an evaluation and inter-comparison of reduced-complexity and physics based models applied to a large sand-bed river. *Geomorphology* 169, 192–211.
- Odenbaugh, J., 2006. The strategy of “the strategy of model building in population biology.” *Biol. Philos.* 21, 607–621.
- Oreskes, N., Shrader-Frechette, K., Belitz, K., 1994. Verification, validation, and confirmation of numerical models in the earth sciences. *Science* 263, 641–646.
- Palmer, M.A., Bernhardt, E.S., Allan, J.D., Lake, P.S., Alexander, G., Brooks, S., Carr, J., Clayton, S., Dahm, C.N., Follstad Shah, J., 2005. Standards for ecologically successful river restoration. *J. Appl. Ecol.* 42, 208–217.
- Passalacqua, P., Lanzoni, S., Paola, C., Rinaldo, A., 2013. Geomorphic signatures of deltaic processes and vegetation: the Ganges-Brahmaputra-Jamuna case study. *J. Geophys. Res. Earth Surf.* 118, 1838–1849.
- Patil, D.J., Hunt, B.R., Kalnay, E., Yorke, J.A., Ott, E., 2001. Local low dimensionality of atmospheric dynamics. *Phys. Rev. Lett.* 86, 5878.
- Realpe-Gomez, J., Baudena, M., Galla, T., McKane, A.J., Rietkerk, M., 2013. Demographic noise and resilience in a semi-arid ecosystem model. *Ecol. Complex.* 15, 97–108.
- Ricker, W.E., 1952. Numerical relations between abundance of predators and survival of prey. *Can. Fish. Cult.* 13, 5–9.
- Rietkerk, M., Van de Koppel, J., 2008. Regular pattern formation in real ecosystems. *Trends Ecol. Evol.* 23, 169–175.
- Rose, K.A., Sable, S., DeAngelis, D.L., Yurek, S., Trexler, J.C., Graf, W., Reed, D.J., 2015. Proposed best modeling practices for assessing the effects of ecosystem restoration on fish. *Ecol. Model.* 300, 12–29.
- Ruddell, B.L., Kumar, P., 2009. Ecohydrologic process networks: 1. Identification. *Water Resour. Res.* 45.
- Ruddell, B.L., Brunzell, N.A., Stoy, P., 2013. Applying information theory in the geosciences to quantify process uncertainty, feedback, scale. *EOS Trans. Am. Geophys. Union* 94, 56.
- Rykiel Jr., E.J., 1996. Testing ecological models: the meaning of validation. *Ecol. Model.* 90, 229–244.
- Saco, P.M., Moreno-de las Heras, M., 2013. Ecogeomorphic coevolution of semiarid hillslopes: emergence of banded and striped vegetation patterns through interaction of biotic and abiotic processes. *Water Resour. Res.* 49, 115–126.
- Saco, P.M., Rodriguez, J.F., 2013. 2.14 Modeling Ecogeomorphic Systems A2 – Shroder, John F. Pages 201–220 Treatise on Geomorphology. Academic Press, San Diego.
- Salah, A.M., Nelson, E.J., Williams, G.P., 2010. Tools and algorithms to link horizontal hydrologic and vertical hydrodynamic models and provide a stochastic modeling framework. *J. Adv. Model. Earth Syst.* 2.
- Sapozhnikov, V.B., Murray, A.B., Paola, C., Fofoula-Georgiou, E., 1998. Validation of braided-stream models: spatial state-space plots, self-affine scaling, and island shapes. *Water Resour. Res.* 34, 2353–2364.
- Scheffer, M., Szabó, S., Gragnani, A., van Nes, E.H., Rinaldi, S., Kautsky, N., Norberg, J., Roijackers, R.M.M., Franken, R.J.M., 2003. Floating plant dominance as a stable state. *Proc. Natl. Acad. Sci. U. S. A.* 100, 4040–4045.
- Schmeckle, M.W., 2014. Numerical simulation of turbulence and sediment transport of medium sand. *J. Geophys. Res. Earth Surf.* 119, 1240–1262.
- Schmolke, A., Thorbek, P., DeAngelis, D.L., Grimm, V., 2010. Ecological models supporting environmental decision making: a strategy for the future. *Trends Ecol. Evol.* 25, 479–486.
- Schreiber, T., 2000. Measuring information transfer. *Phys. Rev. Lett.* 85, 461.
- Seybold, H., Andrade, J.S., Herrmann, H.J., 2007. Modeling river delta formation. *Proc. Natl. Acad. Sci.* 104, 16804–16809.
- SFWMD (South Florida Water Management District), 2005. Documentation of the South Florida Water Management Model Version 5.5. Page 305. South Florida Water Management District, West Palm Beach, FL.
- Siteur, K., Mao, J., Nierop, K.G.J., Rietkerk, M., Dekker, S.C., Eppinga, M.B., 2016. Soil water repellency: a potential driver of vegetation dynamics in coastal dunes. *Ecosystems* (in press).
- Sivakumar, B., 2009. Nonlinear dynamics and chaos in hydrologic systems: latest developments and a look forward. *Stoch. Env. Res. Risk A* 23, 1027–1036.
- Smirnov, N., 1948. Table for estimating the goodness of fit of empirical distributions. *Ann. Math. Stat.* 279–281.
- Stark, C.P., Passalacqua, P., 2014. A dynamical system model of eco-geomorphic response to landslide disturbance. *Water Resour. Res.* 50, 8216–8226.

- Suding, K.N., Gross, K.L., 2006. The dynamic nature of ecological systems: multiple states and restoration trajectories. *Foundations of Restoration Ecology*, pp. 190–209.
- Sugihara, G., May, R., Ye, H., Hsieh, C., Deyle, E., Fogarty, M., Munch, S., 2012. Detecting causality in complex ecosystems. *Science* 338, 496–500.
- Takens, F., 1981. *Dynamical Systems and Turbulence (Detecting Strange Attractors in Fluid Turbulence)*.
- Thiery, J.M., D'Herbes, J.-M., Valentin, C., 1995. A model simulating the genesis of banded vegetation patterns in Niger. *J. Ecol.* 83, 497–507.
- Thomas, R., Nicholas, A.P., 2002. Simulation of braided river flow using a new cellular routing scheme. *Geomorphology* 43, 179–195.
- Tilman, D., 1982. *Resource Competition and Community Structure*. (Mpb-17). Princeton University Press.
- Topping, C.J., Hansen, T.S., Jensen, T.S., Jepsen, J.U., Nikolajsen, F., Odderskær, P., 2003. ALMaSS, an agent-based model for animals in temperate European landscapes. *Ecol. Model.* 167, 65–82.
- Tucker, G.E., Hancock, G.R., 2010. Modelling landscape evolution. *Earth Surf. Process. Landf.* 35, 28–50.
- Tuljapurkar, S., Caswell, H., 2012. *Structured-population Models in Marine, Terrestrial, and Freshwater Systems*. Springer Science & Business Media.
- Turing, A.M., 1952. The chemical basis of morphogenesis. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* 237, 37–72.
- USEPA (U.S. Environmental Protection Agency), 2010. Chesapeake Bay Phase 5.3 Community Watershed Model. EPA 903S10002 - CBP/TRS-303-10. U.S. Environmental Protection Agency, Chesapeake Bay Program Office, Annapolis, MD.
- van de Koppel, J., Crain, C.M., 2006. Scale-dependent inhibition drives regular tussock spacing in a freshwater marsh. *Am. Nat.* 168, E136–E147.
- Volterra, V., 1928. Variations and fluctuations of the number of individuals in animal species living together. *J. Cons. Int. Explor. Mer* 3, 3–51.
- Voroney, R.P., Van Veen, J.A., Paul, E.A., 2011. Organic C dynamics in grassland soils. 2. Model validation and simulation of the long-term effects of cultivation and rainfall erosion. *Can. J. Soil Sci.*
- Watts, D.L., Cohen, M.J., Heffernan, J.B., Osborne, T.Z., 2010. Hydrologic modification and the loss of self-organized patterning in the ridge–slough mosaic of the Everglades. *Ecosystems* 13, 813–827.
- Weerman, E.J., Van de Koppel, J., Eppinga, M.B., Montserrat, F., Liu, Q.-X., Herman, P.M., 2010. Spatial self-organization on intertidal mudflats through biophysical stress divergence. *Am. Nat.* 176, E15–E32.
- Werner, B.T., 1995. Eolian dunes: computer simulations and attractor interpretation. *Geology* 23, 1107–1110.
- Werner, B.T., 2003. Modeling landforms as self-organized, hierarchical dynamical systems. *Prediction in Geomorphology*, pp. 133–150.
- Willgoose, G., 2005. Mathematical modeling of whole landscape evolution. *Annu. Rev. Earth Planet. Sci.* 33, 443–459.
- Willgoose, G., Bras, R.L., Rodriguez-Iturbe, I., 1991. A coupled channel network growth and hillslope evolution model: 2. Nondimensionalization and applications. *Water Resour. Res.* 27, 1685–1696.
- Wilson, J.A., Acheson, J.M., Metcalfe, M., Kleban, P., 1994. Chaos, complexity and community management of fisheries. *Mar. Policy* 18, 291–305.
- Ye, H., Beamish, R.J., Glaser, S.M., Grant, S.C.H., Hsieh, C., Richards, L.J., Schnute, J.T., Sugihara, G., 2015. Equation-free mechanistic ecosystem forecasting using empirical dynamic modeling. *Proc. Natl. Acad. Sci.* 112, E1569–E1576.
- Yoo, K., Amundson, R., Heimsath, A.M., Dietrich, W.E., 2005. Process-based model linking pocket gopher (*Thomomys bottae*) activity to sediment transport and soil thickness. *Geology* 33, 917–920.
- Zhang, D., Narteau, C., Rozier, O., 2010. Morphodynamics of barchan and transverse dunes using a cellular automaton model. *J. Geophys. Res. Earth Surf.* (2003–2012), 115.
- Zhang, D., Narteau, C., Rozier, O., Courrech du Pont, S., 2012. Morphology and dynamics of star dunes from numerical modelling. *Nat. Geosci.* 5, 463–467.