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Review

Representing climate, disturbance, and vegetation interactions in landscape models

Robert E. Keane[a,*], Donald McKenzie[b], Donald A. Falk[c], Erica A.H. Smithwick[d], Carol Miller[e], Lara-Karena B. Kellogg[f]

[a] US Forest Service, Rocky Mountain Research Station, Missoula Fire Sciences Laboratory, 5775 Hwy 10 West, Missoula, MT 59808, United States
[b] US Forest Service Pacific Wildland Fire Sciences Laboratory, 400 N. 34th Street No. 201, Seattle, WA 98103, United States
[c] School of Natural Resources and the Environment, University of Arizona, 325 Biological Sciences East, Tucson, AZ 85721, United States
[d] Department of Geography, The Pennsylvania State University, 302 Walker Building, University Park, PA 16802, United States
[e] US Forest Service, Rocky Mountain Research Station, Aldo Leopold Wilderness Research Institute, 790 E. Beckwith Ave, Missoula, MT 59801, United States
[f] College of Forest Resources, University of Washington, Box 352100, Seattle, WA 98195-2100, United States

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ABSTRACT

The prospect of rapidly changing climates over the next century calls for methods to predict their effects on myriad, interactive ecosystem processes. Spatially explicit models that simulate ecosystem dynamics at fine (plant, stand) to coarse (regional, global) scales are indispensable tools for meeting this challenge under a variety of possible futures. A special class of these models, called landscape models (LMs), simulates dynamics at intermediate scales where many critical ecosystem processes interact. The complicated dependencies among climate, disturbance, and vegetation present a difficult challenge for LMs, however, because their simulation must reconcile processes and their interactions that occur at different spatial and temporal scales. In the absence of these interactions, key thresholds in ecosystem responses to changes in climate may go undetected or misrepresented. In this paper, we present a general strategy for constructing the next generation of LMs that ensures that interactions are modeled at appropriate scales of time and space, and that, when possible, processes representing these interactions are simulated mechanistically. We identify six key questions to frame this strategy and then provide guidance and possible solutions on the structure and content needed in future LMs to ensure that climate-vegetation-disturbance interactions are incorporated effectively.

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* Corresponding author. Tel.: +01 406 329 4846; fax: +01 406 329 4877.
E-mail address: rkeane@fs.fed.us (R.E. Keane).

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1. Introduction

Anticipating ongoing rapid climate change, ecologists are attempting to predict the effects of those changes on myriad ecosystem processes across various scales (Clark et al., 2001; Schumacher et al., 2006; Flannigan et al., 2009; Moritz et al., 2012). Traditional field methods of exploring ecosystem responses to climate change may provide insights at short temporal and small spatial scales, but they are often constrained by the time and expense of data collection, and their temporal and spatial scope often isn't sufficient to analyze the complex interactions among ecological processes, disturbance, and climate (Keane, 2012). Spatially explicit models that simulate the major biophysical processes that control ecosystem dynamics have the potential to explore these effects under possible future climates (Baker, 1989; Merriam et al., 1992; He, 2008; Perry and Millington, 2008). To be successful at future projections, such models must represent the dynamics of ecological interactions across multiple scales. Where possible, there should be feedbacks among model components, such as fire effects on tree establishment and development, and synergistic effects, such as combined effects of insects, disease, and fires on tree mortality. Otherwise, important ecosystem changes emerging from interactions could be missed or muted in simulated outcomes. More abstractly, but just as importantly, interactions between landscape pattern and process (Turner, 1989) change landscapes in ways that may not emerge from the simulation of one-way forcings that use empirical approaches (McKenzie et al., 2014).

There is no dearth of models that simulate ecological change at broad (regional, global) to fine (plant, ecosystem, stand) scales (King et al., 1989; Scheller and Mladenoff, 2007; Perry and Millington, 2008). Of these, landscape-scale (10^0–10^3 km^2) models are particularly important because their simulation is at spatial scales at which many ecosystem processes and linkages are manifest, as well as the scales at which most management decisions are made (Cushman et al., 2007; Littell et al., 2011; McKenzie et al., 2014). Hereafter we refer to these spatially explicit medium-scale models as landscape models (LMs). Finer-scale stand models have too limited spatial extent to adequately simulate important exogenous disturbances (Bugmann, 2001). Coarse-scale models, such as Dynamic Global Vegetation Models (DGVMs), often represent vegetation as plant functional types, which is inadequate for simulating successional shifts, community dynamics, and species-specific drivers of disturbance or responses to it (McKenzie et al., 2014).

LMs have expanded our understanding of complex ecological interactions over large areas and lengthy time spans (Perry and Enright, 2006; Scheller and Mladenoff, 2007; Perry and Millington, 2008). They are described and classified in a variety of ways related to their design and structure (see Keane et al., 2004; Perry and Enright, 2006; He et al., 2008; Scheller and Mladenoff, 2007; Baker, 1989; Shugart, 1998). Spatially explicit LMs are essential for understanding interactions between spatial pattern and ecological process (Turner et al., 1989a,b), which produce complex, emergent, and surprising behaviors, especially under new climates (Smithwick et al., 2003; Perry and Enright, 2006). LMs can simulate key pattern-process interactions across landscapes including propagule dispersal, disturbance propagation, and hydrologic flow (Gardner et al., 1999; Keane and Finney, 2003; Tague and Band, 2004; Schumacher et al., 2006; Seidl et al., 2011). Findings from LMs have addressed critical questions in ecosystem biogeochemistry, disturbance interactions, and wildlife dynamics (Cushman and McGarigal, 2007; Cushman et al., 2011; Loehman et al., 2011; Holsinger et al., 2014).

Few LMs simulate ecosystem processes with mechanistic detail at all scales; rather they balance trade-offs between model realism and manageable levels of complexity (McKenzie and Perera, 2015). For example, direct interactions of climate on vegetation may be represented more realistically by simulating daily carbon (photosynthesis, respiration), water (soil water availability, evapotranspiration), and nutrient (nitrogen, phosphorous) dynamics at the plant level, then scaling up to the landscape, than by simply simulating vegetation development annually with a state-and-transition model. The former approach, however, may introduce errors and biases, which are “smoothed” over in the latter, simpler model (Rastetter et al., 1991; McKenzie et al., 1996). A fully mechanistic design, where model algorithms use biological or physical relationships to represent simulated processes to the constraints of current scientific knowledge, may be difficult for both conceptual (inadequate science) and computational (inadequate computing resources) reasons. Mechanism is always relative to the next higher level in a hierarchy of processes; each mechanism itself has underlying mechanisms at lower levels (Grimm and Railsback, 2005). Emergent and novel landscape behaviors and phenomena are possible when multiple levels of mechanism are included in LM design as opposed to an empirical approach that imposes a deterministic landscape simulation (Railsback and Grimm, 2012). Representation of some highly complex biophysical processes may always require stochastic, empirical, or hybrid approaches (Falk et al., 2007; McKenzie et al., 2011). For examples, a fully mechanistic

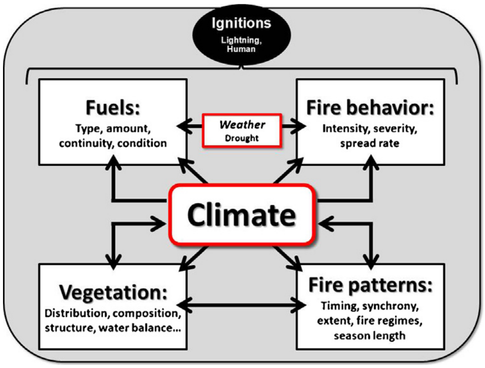

Fig. 1. An example of the complex interactions among climate, vegetation, and fire that governs landscape dynamics. Feedbacks (e.g., from vegetation or fire patterns back to climate) and synergies (e.g., combined effects of insect outbreaks and wildfires on forests not represented in this figure), are what separate true interactions from one-way forcings such as the effects of drought on wildfire.

representation of fire would require simulating heat fluxes at spatial scales of centimeters and a fully mechanistic simulation of photosynthesis would be done at the leaf or cellular scale, both of which are impractical for LMs.

Given the pressing need to understand complex ecosystem dynamics under future climates (Cushman et al., 2007) and a desire to inform the design and modification of regional and global models (Cary et al., 2009), we present tractable steps for the creation and evaluation of the next generation of LMs. To be effective at predicting climate change effects realistically, LMs must, at a minimum, simulate the core ecosystem dynamics of disturbance, vegetation, and biogeochemistry as they respond to environmental drivers (i.e., climate variability), and must also simulate their interactions across multiple scales (see Fig. 1 for example) (Bachelet et al., 2000; Purves and Pacala, 2008; de Bruijn et al., 2014).

Specifically, we ask and answer six questions that may guide future LM development under broader design protocols, such as ODD (see Grimm et al., 2006; Grimm et al., 2010) (Table 1). We address each in the context of a typical LM: a spatial domain of 10^0–10^3 km^2 (large enough to represent spatial processes important to climate change effects), spatial resolution of 30–100 m (matching the current generation of widely available remote-sensing products), multiple time steps (efficiently representing multiple ecological processes), and a temporal domain of 10^1 to 10^4 years (long enough to capture disturbance regimes and successional dynamics). A diagram (Fig. 2) is provided to illustrate the linkages across the six questions summarized in Table 1. We use the FireBGCv2 model (Keane et al., 2011) to illustrate some of the relevant properties of LMs in representing ecological interactions (Keane et al., 2004).

Not all LMs will require an exhaustive accounting of the considerations and recommendations provided here; indeed, some LMs may be designed for a specific simple research objective. Regardless of the scope of the modeling effort, consideration of the concepts in this paper should be useful particularly at the beginning stages of model development, as modeling objectives are defined and simulations are designed (Grimm et al., 2006). Our aim is to encourage the creation of new LMs that explore complex climate-change effects through explicit modeling of interactions. To ground this synthetic approach, we provide specific examples of design decisions that might be made, and provide possible avenues for incorporating our recommendations into new models. We summarize the design considerations and recommendations in Table 1. These considerations lead to a series of steps in LM development, which are illustrated in Fig. 2. While these suggestions are primarily to guide future model development, they can also be used by land managers and practitioners to evaluate existing models for future applications to ensure appropriate interactions are included.

2. Key questions

2.1. Question 1: How do we build a model to investigate climate, vegetation, disturbance, biogeochemistry, and their interactions?

The general design of an LM will dictate its utility for exploring current and future complex interactions, both known and unknown, and its flexibility to accommodate future research findings. The modeling approach, programming language, and software design will often govern the applicability of the model for diverse applications and across users. Five steps can be taken to facilitate designing effective, robust, and comprehensive LMs (Table 1).

2.1.1. Articulate simulation objectives clearly

A concise and comprehensive statement of modeling objectives is easily the most important, yet least appreciated, concept in the design and implementation of any LM (Keane, 2012). A clear objective allows the modeler to identify (1) variables to include in the model structure, (2) algorithms and their sequences during simulation, (3) input and output file structures, (4) critical ecosystem processes and feedbacks to simulate, (5) important interactions, and (6) most appropriate time steps. No single LM can be used for all circumstances because the objective would need to be so general and the scope so large that optimizing simulation design and structure would be impossible. With a clearly stated objective, however, the LM can be developed or adapted so that simulations can be completed successfully in the appropriate context and in a timely manner considering available computing resources. Grimm et al. (2006) and Grimm et al. (2010) use the term “purpose” in their ODD design protocol to emphasize the importance of a clearly stated rationale for model development.

We recommend using the SMART approach when formulating simulation objectives; objectives should be Specific, Measurable, Achievable, Relevant, and Time-Based (Doran, 1981). The purpose of the simulation effort should be explicitly stated in detail (specific) so the best model can be selected along with the most appropriate output variables and their desired spatial scale and temporal density (measurable) (Grimm et al., 2006). Modeling efforts can fail if existing state-of-knowledge precludes a mechanistic design, or the resources needed to build the model, such as data, trained personnel, and computing power, are lacking (achievable). The simulation of interactions across modeled processes is one important way to make climate change projections more realistic (relevant). And, while obvious, it is of utmost importance to link climate inputs to as many modeled ecological processes as possible to ensure all feedbacks are represented. Finally, the time allowed to develop and run the model should reflect the complexity of the processes included in model design (time-based).

2.1.2. Use a mechanistic approach where feasible

A mechanistic approach (as defined above) when possible, is a necessary first step to ensure that important landscape and ecosystem interactions are represented realistically in the simulation (Ford et al., 1994; Peng, 2000; Gustafson, 2013). For example, instead of using topography as a proxy variable to predict vegetation productivity, a mechanistic approach uses variables to represent the ecological and physical processes that affect productivity directly, such as seasonal temperature, soil properties and water availability, and evaporation (Fig. 3). Unfortunately, research has not yet identified all of these important biophysical relationships, and has done so in only some ecosystems. As such, compromises to a mechanistic approach must be made,

Table 1
Important considerations in building landscape models to simulate ecological interactions across multiple scales under climate change. Question and task numbers provide a crosswalk to Fig. 2.

Section number and question	Key tasks	Recommendations	How?
2.1 How do we build a model to explore interactions?	2.1.1. Define simulation objectives	Clearly articulate the modeling objective to design, select, and apply models; this will focus model design	Evaluate area of application, estimate available computing resources and modeling expertise; use SMART principles
	2.1.2. Use a mechanistic approach	Create models using fundamental biophysical principles if possible	Find available biophysical algorithms for local processes
	2.1.3. Define appropriate scales & organization	Identify and include those spatial, temporal, and organizational scales that support the simulation objective	Identify characteristic scales of selected process and implement to scales in LMs
	2.1.4. Identify software engineering concerns	Incorporate innovative software engineering methods into model development to create efficient simulation platforms that are flexible and facilitate future modifications	Emphasize understandability of code rather than efficiency; select robust compilers available on all hardware platforms; program using independent blocks of code
	2.1.5. Define data properties	Create data structures that support initialization, parameterization, and evaluation of models	Find all possible data sources for simulation area; create parameterization data sets; publish and post field data
2.2 What ecological processes should be included?	2.2.1. Biophysical template	Include spatial representations of topography, soils; also include hydrology if important to simulation objective	Merge DEM and soils layer to define static biophysical settings that are useful across all simulated processes; include hydrology in LM simulation
	2.2.2 Plant dynamics	Include succession (regeneration, growth, mortality) and productivity (NPP, GPP)	Match simulation detail to differential disturbance and climate impacts, often plant-level resolution; simulate those biophysical processes that control plant growth, regeneration, and mortality
	2.2.3. Disturbance	Include abiotic (fire, wind, severe weather, drought) and biotic (land use, insects, disease) disturbances	Select disturbances to match local conditions; simulate each phase of a disturbance: initiation, spread, termination, and effects
	2.2.4. Biogeochemistry	Include litter (decomposition, deposition), water (hydrology, evapotranspiration), and nutrient (nitrogen, phosphorous) dynamics	Mechanistically simulate the carbon, water, and nutrient flux
2.3. How should climate be represented?	2.3.1. Address multiple scales	Provide or simulate climate data at multiple scales of time and space	Develop algorithms to scale GCM down to the site, and to scale annual weather data to daily streams, and vice versa
	2.3.2. Develop parsimonious data stream	Include only those climate data important to ecological interactions	Use only those weather variables that are direct inputs to model algorithms
	2.3.3. Use alternative scenarios	Provide multiple climate scenarios for investigating interactions, thresholds, and phase shifts	Never simulate just one climate future (alternative scenarios) and never simulate just one run (replicate runs)
2.4. How best to represent interactions?	2.4.1. Identify important interactions	Design models so simulated processes share input/output variables	Review literature to discover those important processes that control disturbance and vegetation dynamics
	2.4.2. Develop methods to determine thresholds	Develop methods to identify important threshold shifts, tipping points, and phase transitions	Create statistical algorithms that test for significance in the time-series model output
	2.4.3. Simulate cross-scale interactions	Identify simulated processes that directly or indirectly cross spatial scales	Ensure LM algorithms have scaling functions to provide intermediate simulation results for use by important algorithms at finer or coarser scales
2.5. How can spatial patterns and processes be represented?	2.5.1. Identify spatial processes	Based on simulation objective and model design, identify those ecological processes that demand a spatial simulation, such as disturbance, seed dispersal, and hydrology	Use knowledge of simulated area to identify local spatial processes that must be included in LM design
	2.5.2. Reconcile time and space scales	Ensure time scales match spatial scales and the model's organizational scales	Solicit reviews of model design to find algorithms that may have scale discrepancies
	2.5.3. Integrate landscape structure	Integrate landscape ecology concepts and methods into model design to provide for spatial interactions	Build efficient modules that calculate various landscape metrics important for ecosystem dynamics
2.6. How can model be evaluated?	2.6.1. Identify data needs	Gather data for model initialization, parameterization, calibration, and validation	Find as many temporal and spatial datasets of field data as possible
	2.6.2. Develop methods for evaluation	Create new methods for the evaluation of the sensitivity, uncertainty, and importance of parameter and initial conditions	Conduct extensive sensitivity, validation, verification tests on LM and LM model components

and some processes may always have to be modeled empirically or stochastically due to high intrinsic uncertainty. For example, lightning-caused fire ignition is simulated stochastically in most LMs (Latham and Schlieter, 1989; Goldammer and Price, 1998) because of the lack of validated algorithms, high computational costs, and large error propagation from uncertainty in parameters. Thus, prior to building an LM, it is important to consider the plausible extent of a mechanistic design, given the simulation objective, available literature, and existing algorithms.

Available information and the state of the science will dictate how mechanistic versus empirical an algorithm can be (Rastetter et al. 2003). Of course, there is often a mixture of empiricism and mechanism in many model algorithms. For example, theoretical models of plant growth that reflect biologically realistic (mechanistic) concepts of growth (Raymond and McKenzie, 2013, and citations therein) are nonlinear, with 2–4 parameters. As these parameters are fit to empirical data, such growth algorithms in LMs are hybrids of mechanistic and empirical modeling.

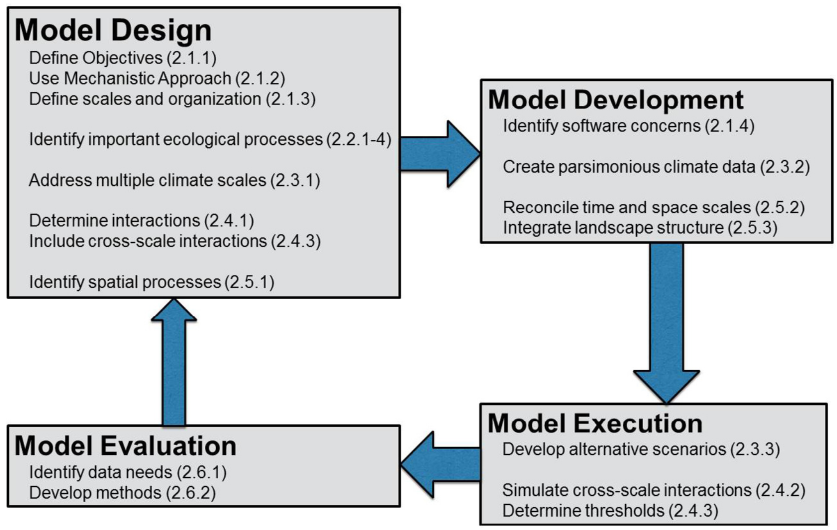

Fig. 2. Steps in the development of a landscape model (LM) that simulates climate, vegetation, and disturbance interactions. The numbers identify the task within the major questions detailed in Table 1.

A mechanistic approach is critical for modeling interactions because the driving processes in most mechanistic models, such as weather and climate, are overarching inputs for the biophysical algorithms in LMs and other models (de Bruijn et al., 2014). For example, temperature is a critical input to algorithms representing the processes that determine plant growth, namely photosynthesis and respiration. However, temperature is also important to many other ecological processes, such as decomposition, evaporation, and insect population dynamics that in turn determine fuel accumulation, moisture, and tree mortality (Fig. 3). Mechanistic designs that robustly represent linkages and feedbacks can simulate the environmental conditions of the future, which may involve novel combinations of biophysical drivers and responses that cannot be extrapolated from current statistical relationships.

2.1.3. Define appropriate spatial and temporal scales and levels of organization

Spatial and temporal simulation scales (e.g., grain, extent, time steps) must be selected to match those characteristic scales of native ecological processes. Vegetation development in boreal forests, for example, may be adequately represented in a mechanistic model by biomass growth of individual plants within 30 m pixels comprising a 50,000 ha watershed, and growth may be estimated using a simulation of photosynthesis and respiration at daily timesteps (Keane et al., 2011). Similarly, a 30 m pixel may adequately represent the scale of disturbance spread, soil, and hydrology processes over the watershed (Turner et al., 2004; Smithwick et al., 2009; Kashian et al., 2012). It is also important to identify appropriate sequences of simulation events across these scales so that

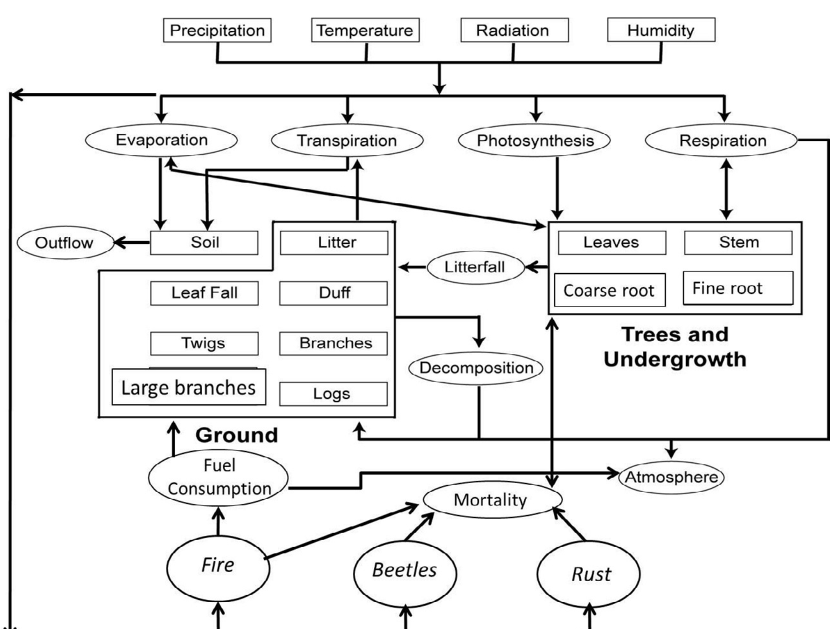

Fig. 3. Flow diagram of the mechanistic simulation of biomass in the FireBGCv2 model (Keane et al., 2011). Daily weather (precipitation, temperature, radiation, humidity) is used to drive evaporation and transpiration to simulate soil water dynamics and also photosynthesis and respiration to simulate biomass growth. This biomass is then allocated to leaves, stems, and roots to simulate plant growth and some existing biomass is shed from the leaves, stems, and roots to be deposited on the ground to simulate fuels dynamics.

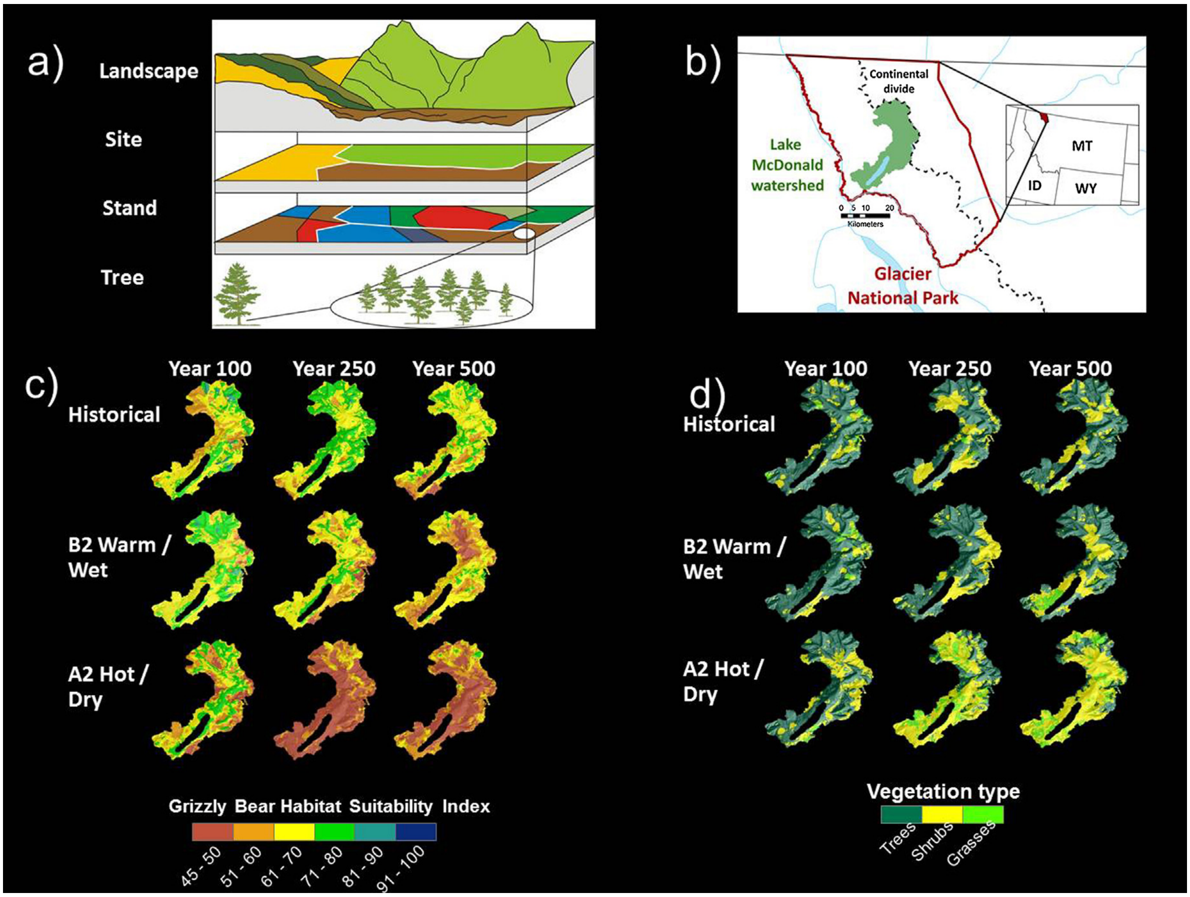

Fig. 4. Examples from FireBGCv2 (Keane et al., 2011), a mechanistic LM: (a) spatial and organizational scales included in the FireBGCv2 model (fire, dispersal, insects, diseases simulated at landscape scale; soil water, weather, and phenology simulated at site scale; fuel, undergrowth, and light dynamics simulated at stand scale; carbon allocation, cone production, and leaf area simulated at the tree level); (b) the MacDonald watershed in Glacier National Park, USA; (c) FireBGCv2 output showing habitat suitability for grizzly bears in MacDonald at three simulation years for three climates, and (d) vegetation changes in MacDonald at three simulation years for three climates.

the simulation will realistically replicate a chain of causation. Daily simulations of phenology, for example, may be needed to support the realistic simulation of foliar moisture to ensure that crown fires are not started when needles have unrealistically high moisture contents.

LM designs must represent many scales of space, time, and levels of biophysical organization to effectively simulate climate change impacts (Fig. 4). Inaccuracies and inconsistencies in predictions can result when ecological processes are simulated at inappropriate scales. Phenology algorithms, for example, may be simulated at weekly time-steps while photosynthesis may be simulated daily, and carbon allocation annually. To accommodate these different scales, the LM design could have routines that aggregate daily weather to monthly and annual time-steps, while preserving the fine-scale representation when necessary (Cleland et al., 2007). Much work remains to be done in cross-scale analysis of landscape dynamics (Milne et al., 2002; Falk et al., 2007).

2.1.4. Identify software engineering concerns

Creating an LM that can simulate complex interactions at different scales demands that a multitude of software engineering concerns be addressed (see Scheller et al., 2009). First, LM software design must match the hardware of the computers where the model will be used. Memory requirements, execution times, number of processors available, and input/output media are some of the many LM hardware and software design criteria that must be considered in the context of the simulation objective, as well as who will use the model and how. Design decisions should be revisited as new technologies, programming languages, and research results become available.

A sound programming approach should (1) support cross-platform design; (2) integrate thoroughly tested code from other sources; (3) be open source; (4) perform multi-threaded executions (run on many processors simultaneously); (5) employ a modular and transparent design with thoroughly commented code; (6) provide output from ensemble runs or different scenarios; and (7) provide clear and thorough documentation in manuals, technical guides, and other reference material. Because simulation projects are often limited by the available computing resources, many modelers write code to speed up computation. However, code optimized for speed may be difficult for others to understand thereby compromising the ability for others to update with the latest science. Computer programs representing LMs, therefore, must delicately balance software design and programming efficiency with transparency and the ease of program revision. This will greatly depend on whether the developers want the program to be (1) a dynamic platform for others to revise and use or (2) a static and stable platform to use without the ability for modification.

2.2. What processes should be included explicitly to explore interactions?

We recognize five categories of processes that are vital for investigating important climate–disturbance–biological interactions across multiple scales, listed in approximate order of significance for LM model function (Table 1, Question 2). Although listed as separate categories, there are, of course, linkages between these processes which are critical for LMs to simulate (see Fig. 3 for example).

2.2.1. Biophysical template and related processes

The biophysical environment, mostly represented by topography and soils, serves as a fundamental template for simulating biotic interactions and the response of vegetation to the variability of climate and disturbance. Few would argue that this template is essential in an LM, but care is needed to resolve the spatial and temporal scales at which it is represented, especially when representing interactions of climate with topography. Hydrological processes, in particular, are dynamic and sensitive to spatial variation and climate variability across a range of scales (Gleick, 1989; Blöschl and Sivapalan, 1995). LMs applied to landscapes with significant water transport may need to incorporate dominant water fluxes (e.g., snowmelt, evapotranspiration) and include representations of lateral and horizontal flow to inform algorithms for water use by vegetation.

Depending on simulation objectives, the biophysical template can be implemented at the scale of patches (vector layers with different polygon sizes matched to spatial pattern), *sensu* Tague and Band (2004), or pixels (raster layers), *sensu* Keane et al. (2011). Spatial characteristics of the soil environment (e.g., texture, hydraulic conductivity) that govern water availability can also be considered as attributes of topography and substrate, and this can enable simulations of plant water uptake or surface evaporative processes. Appropriate levels of aggregation in the model, both in the template of soils and topography as well as climatic and eco-hydrological drivers, are needed to represent biophysical controls on disturbance, plant dynamics, and fauna (see below). For example, in the case of fire spread which responds to both topography and fuel moisture, excessive coarse-graining can erroneously smooth discontinuities and make it difficult to realistically represent fire sizes and patterns.

2.2.2. Disturbance

Effects of future climate on landscapes may manifest most immediately in changes in disturbance processes and their effects on plant communities, rather than the direct effects of climate on vegetation dynamics (Allen et al., 2010; Littell et al., 2011). In many ecosystems, disturbances are more tightly connected with temporal meso-scale (annual to interannual) climatic fluctuations than is vegetation response (Bowman et al., 2009; Flannigan et al., 2009; Krawchuk et al., 2009), so much so that even coarse-scale modeling of vegetation response to climate now explicitly simulates disturbance (Thonicke et al., 2001; Arora and Boer, 2005; Prentice et al., 2011). Disturbance effects can occur at many spatial scales, directly or indirectly affecting soils, plants, and stands within landscapes (Pickett and White, 1985; Gardner et al., 1999). Moreover, many disturbances (fires, insect and disease outbreaks) can propagate both contagiously and discontinuously across space; both of these characteristics make their dynamic representation in LMs a challenge (Turner and Dale, 1992; Raffa et al., 2008).

An important decision in LM design is which critical disturbances to include in the simulation, because each unique set of simulated disturbances may yield different model results (Loehman et al., 2011; McKenzie and Perera, 2015). There are two key considerations: (1) the regional ecology, i.e., which disturbances affect the most area at the highest intensity, and (2) available information, i.e., whether the associated data and the state of the science are adequate to represent the disturbance realistically and robustly. Abiotic disturbances that can be important to represent in LMs are wildland fire (Bowman et al., 2009; Marlon et al., 2009; Falk et al., 2011), severe wind events (e.g., windthrow, blowdown, foehn winds: Westerling et al., 2004; Busing et al., 2009), drought (McDowell et al., 2008; Allen et al., 2010; Anderegg et al., 2012), and severe weather (e.g., freeze–thaw, early spring frost) (Dale et al., 2001), but landslides, avalanches, and erosion may be important locally. Biotic disturbances of interest include insect outbreaks (ideally including both endemic and epidemic population phases) (Reynolds and Holsten, 1994; Carroll et al., 2003; Jenkins et al., 2014), disease (Garrett et al., 2006), grazing (Finch, 2011; Riggs et al., 2015). Human-caused disturbances (e.g., logging, mining, and fire exclusion) represent a major source of landscape impacts in most ecosystems and should be included if important to the region and relevant to the simulation objective (Bowman et al., 2011).

An adequate simulation of disturbance must address the four phases of disturbance dynamics explicitly – initiation, spread, termination, and effects – to ensure all interactions and governing factors are properly addressed. *Initiation* of most disturbances, such as wildfire, is usually represented using stochastic algorithms because it involves the complex multi-scaled interaction of vegetation condition (e.g., fuel loading) with the current (e.g., wind, humidity, temperature) and antecedent weather (e.g., drought, dead fuel moisture), topographic position, and the disturbance source (e.g. lightning) (Cary et al., 2006a,b; Gardner et al., 1997). In the case of insect outbreaks, initiation often progresses from the endemic phase as landscape composition interacts with past and present climate variability, to the epidemic stage where insect populations are active at coarse spatial scales and the degrees of effect make detection over landscape scales difficult (Raffa et al., 2008; Meigs et al., 2011; Jenkins et al., 2014). Similarly, the initiation of apparent drought effects on vegetation may lag quantitative climatic variables by several years, especially in species that have evolved tolerance to episodic drought (Allen et al., 2010).

Spread of disturbances involves multiple spatial processes that are typically simulated using cell automata or vector-based approaches. Some disturbance agents (wildfires, insect outbreaks) spread contagiously across the landscape along environmental gradients, whereas other disturbances (drought, windthrow, severe weather events, human disturbances) may not be contagious and are externally forced (Bentz et al., 2010; McKenzie and Kennedy, 2012). The progression of wildfires, for example, can be modeled based on wind speed and direction, fuel type, mass and moisture, and topography, all of which can be represented specifically in a fire-spread algorithm. Similarly, the spread of insect outbreaks over landscapes is governed by species-specific (insect and host) factors of population density, seasonal temperature, host density and size distributions, and multiple other factors (Raffa et al., 2008; Jenkins et al., 2014).

All spread functions need an algorithm that *terminates* the process, which is often the most difficult to construct under a mechanistic design because it is difficult to determine which complex interaction governs the cessation of a disturbance event (Keane et al., 2004). For example, wildfire spread may be constrained by factors that inhibit combustion, such as reduced temperatures, increased relative humidity and precipitation leading to higher fuel moistures, changes in fuel mass or type, and combinations of these factors. Insect outbreaks may terminate due to both endogenous (population dynamics) and exogenous (host availability, seasonal weather, predation) factors (Raffa et al., 2008).

Ultimately, routines that simulate the *effects* of disturbances on all other modeled processes and state variables are the only ways to link disturbance impacts to direct and indirect ecosystem response (Keane et al., 2004). Approaches for simulating effects include the extremely simplistic (fire occurrence results in tree death), stochastic (statistically derived probability of fire-mortality functions), and mechanistic (heat from fire is pulsed to tree cambium through bark using physical equations to simulate mortality) (see Keane et al., 2004).

2.2.3. Plant population dynamics

Every phase of a plant's life history – seed production, dispersal, establishment, growth, mortality, and reproduction – is influenced both directly and indirectly by climate (Huston and Smith, 1987) and therefore warrants inclusion in LMs. Regeneration (establishment) is arguably the demographic phase most sensitive to changes in climate, but growth and mortality of established individuals can also be affected strongly by persistent or strong departures from the climate to which they are adapted (Allen et al., 2010; Williams et al., 2010). Plant community dynamics integrate key interactions among species populations, including competition, facilitation, and other outcomes that govern post-disturbance community trajectories (Temperton et al., 2004).

Ideally, LMs should resolve scale differences in plant life-history processes so that fine scale variables, such as biomass, can interact with coarser scale plant development and succession in the simulation (Pastor and Post, 1986). To do this, LMs may represent plant dynamics at different scales (e.g., stands, species, cohorts, populations, or individuals) simultaneously (Mladenoff and Baker, 1999) and plants can be represented by different state variables (e.g., tree diameter, stem carbon, cohorts) (Grimm et al., 2010). For example, plant mortality from disturbance may be both species- and size-specific, requiring some accounting for the variability of each (McDowell et al., 2008). Characteristics of individual plants can then be scaled up to simulate canopy dynamics (e.g., light attenuation, interception, and transpiration), organic matter deposition, and reproductive potential (seed production, seed dispersal by animal, wind, and water). Species- and population-level information must include the most critical life-history attributes (life span, shade tolerance, drought tolerance, disturbance adaptations, plant defenses), and demographic population parameters (germination, seed production, fecundity). LMs that build plant dynamics from underlying processes will be more successful in allowing for unexpected outcomes under future disturbance and climate regimes compared to models that are based on pre-determined states or transitions.

2.2.4. Biogeochemistry

Biogeochemical processes – primarily the transformation, flow, and storage of water, nutrients, and carbon, across ecosystem components – provide important linkages across most climate, vegetation, and disturbance processes thereby allowing direct simulation of many interactions (King et al., 1989; Rastetter et al., 1991; Smithwick, 2011). Biogeochemical processes can also be tied closely to management objectives and thus can inform climate-change mitigation and adaptation. For example, landscape-level carbon stocks and water yield can be linked to timber-harvest or fuels management scenarios (Holsinger et al., 2014) (Fig. 5). Biogeochemistry regulates vegetative growth, thereby controlling carbon exchange between the terrestrial biosphere and the atmosphere (Bonan, 2008), and can dictate susceptibility of vegetation to disturbance. The detail of biogeochemical representation in LMs may differ by ecosystem, geographic area, climate, and disturbance regimes, but a core set of biophysical processes (evapotranspiration, decomposition, nutrient cycling, photosynthesis, respiration) is fundamental (Fig. 3). One critical area of concern in most LMs is characterizing belowground dynamics (e.g., levels of soil, microbial communities, and roots). Belowground processes regulate plant water and nutrient uptake but these are often modeled indirectly through leaf demand and stoichiometry (Smithwick et al., 2013, 2014). Interactions between other biota (e.g., ungulates, insects) and water, carbon, and nutrient processes are likely important in many landscapes though not often included in LMs (Schneider and Root, 2002).

2.3. How should climate be represented in LMs?

Climate has two distinct roles in an LM. First, it drives energy- and water-sensitive processes, such as hydrology, plant growth and mortality, disturbance, and watershed processes. Second, it provides a dominant bioregional context within which key ecosystem processes operate. For example, ecosystem processes are different in maritime versus continental climate zones; ecoregions are influenced differently by ENSO, PDO and other quasi-periodic modes of the climate system depending on location and terrain; extreme events (droughts, floods, storms) influence terrestrial processes differently in every region. An LM ideally would represent climate with spatial resolutions fine enough to capture interactions across climate-dependent biotic and abiotic processes. In most areas of interest, statistical downscaling models can extrapolate some historical climate parameters to landscape scales by calibrating with Remote Automated Weather Stations (RAWS) and other instrumental data. Historical climate can also be modeled using combinations of instrumental data and paleoecological reconstructions (e.g. from tree rings: Hughes et al., 2011). Future projections of climate (e.g. CMIP5, Mearns et al., 2013) are becoming increasingly more accurate and fine-scale, and can be used to drive future landscape dynamics where appropriate.

To capture the role of climate in ecological interactions, it is important to represent climate and its variability at scales that best match the spatially explicit simulation of disturbance, hydrology, and vegetation dynamics. This will likely involve three key compromises: (1) accept the inherent errors and uncertainties of climate dynamics downscaled from global climate models, which may be quite large in some areas (Salathe et al., 2008; Abatzoglou and Brown, 2012); (2) accept that the LM will not include land-surface feedbacks to the climate system, in contrast with coarser-scale global vegetation models (Quillet et al., 2010; McKenzie et al., 2014); and (3) recognize that climate models generally represent only a small number of physical variables that may influence landscape processes; relative humidity and local variation in precipitation, for example, are difficult to simulate accurately at sub-kilometer scales. Given these general constraints, we identify four guidelines for representing climate in an LM (Table 1), the specifics of which will depend on the objectives of particular modeling studies.

2.3.1. Address multiple spatial and temporal scales of climate variation

LMs should incorporate climate explicitly across multiple scales of space and time to ensure that simulated ecosystem dynamics are responding to climate variability at the appropriate scale(s) of space and time (Root and Schneider, 2002). For example, phenology may need a daily time step at 30-m spatial resolution or finer (White et al., 1997), whereas decomposition may be modeled adequately with monthly time steps at 1-km resolution (Means et al., 1985). Similarly, daily or hourly values may be required for simulating some processes (e.g. photosynthesis, fire spread), whereas seasonalized (3-month) aggregates may be sufficient for others (e.g. insect outbreaks, stand dynamics). Even if all scales are not simulated explicitly, some robust surrogates will be needed for the processes at scales that are not represented. This could come from an established coarse-graining procedure. For example, in a long-term (multi-century) simulation model, explicit fire spread can be replaced by drawing from fire-size distributions that are sensitive to aggregate (annual) climate indexes (Keane et al., 2011).

2.3.2. Develop parsimonious data streams

Mismatches between the resolution of weather data and the finest resolution of key model processes can complicate and compromise LM simulations. Choice of weather variables (temperature,

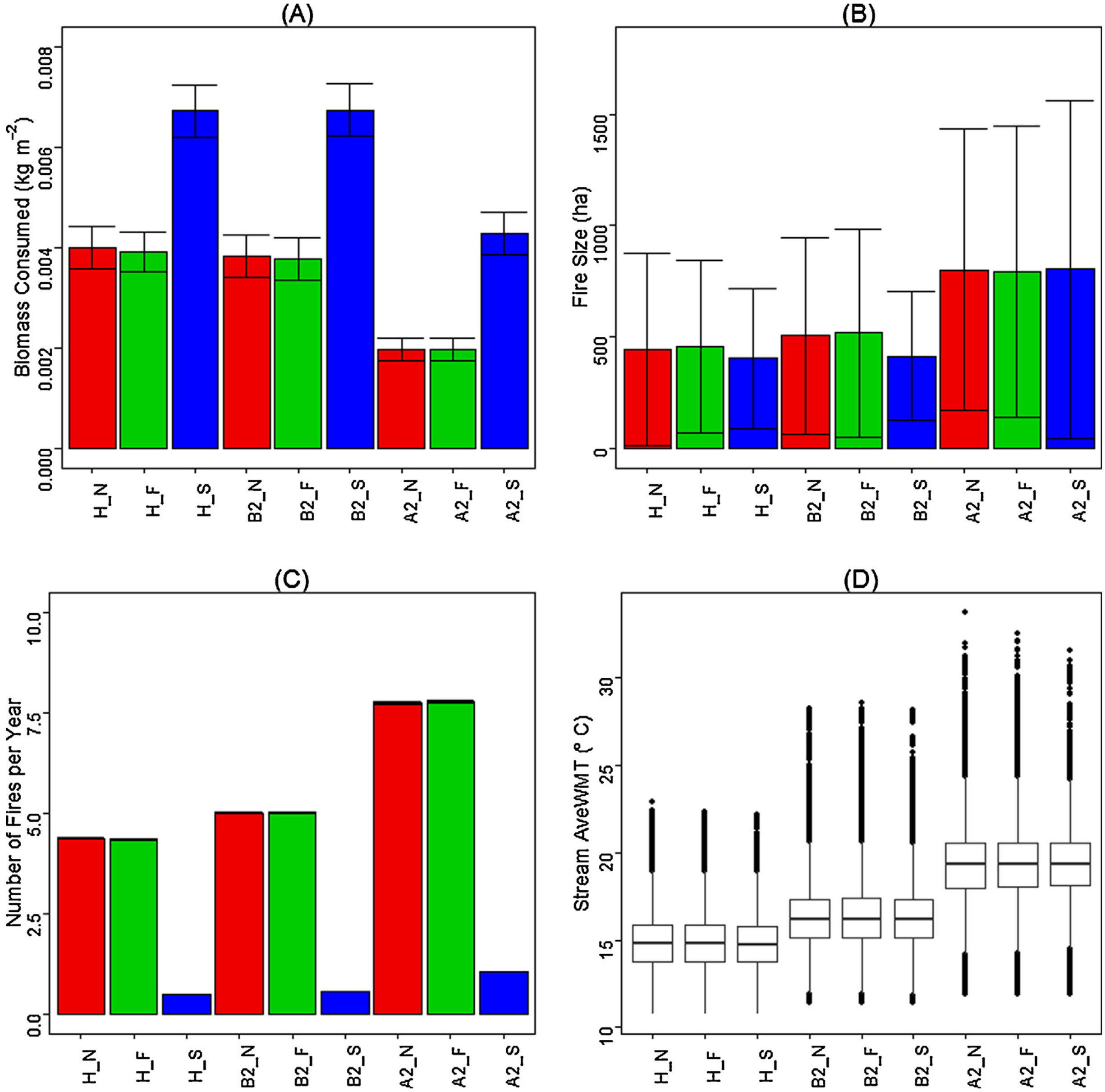

Fig. 5. Mean and standard errors for (a) biomass consumed by fire as a proxy for fire severity, (b) fire size, (c) number of fires per year, and (d) boxplots for average weekly maximum temperature stream (AveWMT) for each of nine climate/fire management scenarios symbolized on the *x*-axis by combining climate abbreviations (H is historical climate, B2-warm, moist and A2-hot,dry) with fire management abbreviations (N is no fire management, F is fuel treatment, S is suppression). This illustrates that the interactions of biomass consumed with area burned and fire frequency to influence tree mortality that may influence stream temperature (FireBGCv2 model output from Holsinger et al., 2013).

precipitation, wind, radiation, humidity) and their representation at the appropriate scales is a key decision in LMs design. Does weather need to be input for multiple vertical levels (e.g., ground, canopy height, boundary layer)? Can the variables be input as discrete classes or continuous variables? Should hourly values be used, or can daily or monthly means, minima, and maxima suffice? Too much weather data may slow LM simulations, so it is important that only the weather variables most important to the ecological interactions of interest be represented explicitly in model inputs with others generated within the LM.

2.3.3. Use alternative future climate scenarios

An investigation of potential climate change effects on disturbance and vegetation should never rely on a single projection of future climate. The portfolio of climate projections used in LMs should represent the range of outcomes in General Circulation Models (GCMs). Ensemble projections, such as the Coupled Model Intercomparison Project, Phase 5 (CMIP5—Taylor et al., 2012) and the Representative Concentration Pathways (RCPs—Moss et al., 2010; Vuuren et al., 2011), can be used to bracket the range of climate variation thereby not neglecting climate forcings that might move ecosystems across thresholds of change (sometimes rapid or irreversible) as simulated in the LM (McKenzie et al., 2014). These products are used extensively in successive reports of the International Panel on Climate Change (IPCC) (2013), which establishes important connections between the climate and landscape dynamics research communities.

2.4. How can an LM represent ecological interactions?

Although many LMs represent critical ecological processes, especially vegetation, climate, and disturbance, interactions among these ecosystem components should be emergent behaviors resulting from changes in the basic processes outlined above. We propose here that interactions be modeled at the scales and levels of detail at which their dynamics actually unfold. Apparent interactions can emerge with the outcomes of climate forcings on vegetation or disturbance, and also interactions can be artifacts of parallel chains of causation. For example, simulated changes in live forest biomass after fire and concurrent insect outbreaks will surely be correlated, but this is a statistical interaction rather than an ecological one, and is not robust to changes in the vegetation dynamics. Here is where a mechanistic approach is more desirable: the interactions to model explicitly are fire-caused vulnerability to beetles, for example, or conversely, increased flammability from insect-killed foliage and branchwood. We identify three design considerations to help ensure that LMs are able to explore these interactions and their causal factors.

2.4.1. Identify important interactions among biotic, abiotic, and climatic variables

Unexpected landscape changes, often resulting from non-linear interactions among climate, vegetation, and disturbance factors, are of great societal and scientific interest (Peters et al., 2004; Hastings and Wysham, 2010; McKenzie and Kennedy, 2012). Modelers clearly must identify an economical list of important state variables to model, and then simulate the fluxes to and from these state variables to capture the characteristic variability that emerges from complex interactions. For example, grazing may decrease biomass (fuel) that will reduce fire intensity, which reduces tree mortality from fire, thereby increasing transpiration and reducing water availability (Bachelet et al., 2000; Asner et al., 2004; Koerner and Collins, 2013) (Fig. 5). Though intuitive, exploring those complex interactions across heterogeneous landscapes is more difficult where mediating factors (e.g., soil type, climate) may differ across space and qualitatively change the signs and magnitudes of interactions.

Of particular concern are processes that govern the principal feedbacks between vegetation, disturbance and climate (Green and Sadedin, 2005). Including variables that are common to different processes provides critical structure for simulating these principal feedbacks (Green and Sadedin, 2005). Clearly, vegetation biomass is necessary to model both grazing and fire processes in the example above, but vegetation biomass itself is dependent on multiple finer-scale processes driving biological production. Similarly, stand density and crown loading would be critical for representing mountain pine beetle and fire so these should be included or available in any simulation to address their interactions (Turner and Bratton, 1987; Jenkins et al., 2008). Variables that integrate multiple underlying processes, such as biomass for vegetation, can be directly used in other processes, such as fuel loading for fire or forage for grazing, thereby enabling direct simulation of interactions.

2.4.2. Simulate cross-scale interactions

In addition to structuring models to include direct and indirect critical interactions at one scale, LMs should also be designed to explore explicitly the cross-scale interactions of climate, vegetation, and disturbance (Peters et al., 2004; Falk et al., 2007) (Fig. 4). For example, climate and its variability are often modeled at coarser scales as a top-down forcing factor that induces synchronous responses at regional scales and interacts with fine-scale bottom-up controls (e.g. frost pockets, inversions, topographical shading effects on fuel moisture and mass). As such, climate variability influences both productivity and disturbance, thereby affecting landscape heterogeneity (Agee, 1998). In another example, Temperli et al. (2013) found predicted changes in climate affected the sign and strength of cross-scale disturbance interactions among beetles and wind to create unforeseen landscape behaviors. And in savanna ecosystems, interacting effects of CO_2 fertilization, seed dispersal, and grazing should all be considered for their net effects on complex vegetation dynamics such as woody plant encroachment into grasslands, or post-fire successional pathways (Asner et al., 2004).

2.4.3. Develop methods to determine thresholds and phase transitions

Unexpected landscape changes, often resulting from non-linear interactions among climate, vegetation, and disturbance factors are of great societal and scientific interest (Peters et al., 2004; Hastings and Wysham, 2010; McKenzie and Kennedy, 2012). Simulations provide an opportunity for modelers to test hypotheses about conditions that may lead to such ecosystem 'surprises' (Doak et al., 2008). We expect that the complex nonlinear responses produced by interactions in LMs will result in unanticipated landscape shifts and ecosystem phase transitions. Modelers need methods and algorithms, both implemented within an LM and used in post-simulation analyses, to not only detect these phase transitions, but also to identify the causal mechanisms behind tipping points (Lenton et al., 2008). In southwestern US ponderosa pine forests, for example, fire exclusion has created dense canopies that may burn severely, converting forests to semi-permanent shrublands by eliminating pine seed source and creating unfavorable microsites for tree establishment (Savage and Mast, 2005; Williams et al., 2010). Such a type conversion can create a new system state that is itself resilient to change. Since ecosystem interactions may initiate phase transitions (Allen, 2007; Falk, 2013), there has been considerable effort to detect their causes, but most answers to date apply only to specific unusual cases (Hastings and Wysham, 2010). A simulation approach may enable experiments with disturbance and climate generators for LMs to identify the climatic and weather dynamics that bring landscapes to thresholds or tipping points, but there are few analysis techniques to uniquely identify when a threshold has been simulated. This is a difficult task, because in any complex simulation model there are many attributes across multiple scales that may confound straightforward experiments (Keane et al., 2011; McKenzie et al., 2014; McKenzie and Perera, 2015).

2.5. How can spatial patterns and processes be represented in landscape simulations?

There are many fine-scale (tree and stand) processes that depend on landscape pattern characteristics and our understanding of these spatial structural interactions continues to grow (Jordan et al., 2008; Churchill et al., 2013). The initiation, spread, termination, and effects of contagious disturbances, for example, are often more dependent on spatial patterns of patches than stand-level characteristics. The growth and ultimate size of wildfires depends on the spatial continuity of fuels. We suggest three important considerations for LMs related to spatial patterns and processes (Table 1).

2.5.1. Identify important spatial processes

Spatial processes that are contagious and respond to landscape patterns such as corridors, connectivity, and edges, (Cushman and McGarigal, 2007; Gonzalez et al., 2008; Brudvig et al., 2012) are important to distinguish in the design of a LM. One challenge is to decide if a disturbance actually needs a spatially explicit module. For example, do mountain pine beetle outbreaks that last for a few years require a spread component for century-long simulations? LMs can recognize different sources of spatial heterogeneity (e.g. derived from disturbance, ecological processes, or the abiotic template), but detailed representation of spatial processes may be limited to those that have been extensively studied, such as wildland fire spread, or those that exert a great influence on future landscape dynamics, such as seed dispersal.

2.5.2. Reconcile spatial and temporal scales

The inherent spatial scales represented in an LM must be reconciled to the ecosystem processes being simulated, and the time scales built into the model must be appropriate for their simulation. Tree regeneration, for example, might require spatially explicit seed dispersal simulations that occur once a year at the landscape level, as well as a daily time step for phenology and growth of individual plants to properly reflect climate interactions on reproductive potential, seed maturity, and subsequent regeneration. Similarly, simulations of fire behavior at a fine 10 m^2 resolution may produce more realistic fire perimeters, size distributions, and severity estimates than simulations done at a 1 km^2 resolution because the processes that govern fire spread operate at fine temporal scales (minutes to hours) (Keane and Finney, 2003). It is also important to represent boundary conditions and edge effects of multiple interacting disturbances at the appropriate scale, especially when the ecological process is non-stationary (Keane, 2012).

2.5.3. Integrate landscape structure and arrangement

The quantification of landscape patch patterns (landscape metrics) (Fortin, 1999) and surface properties (Goetz et al., 2009; McGarigal et al., 2009) remains a key priority in landscape ecology. Some research studies have incorporated landscape metrics in their design, particularly when stratifying samples (Cardille et al., 2005; Cardille and Lambois, 2009). LMs can then use such results to simulate the effect of landscape structure and arrangement on landscape dynamics (Stewart et al., 2013). For example, raster spread models of forest insects might accelerate spread rates if the computed contagion metric for some landscape characteristic, such as old growth tree hosts, was above some threshold identified in a field experiment or estimated by experts. Ideally, an LM will have a pre-designed interface with programs available for analysis of landscape pattern such as FRAGSTATS (McGarigal et al., 2002) and METALAND (Cardille et al., 2005) and use these concepts, tools, and metrics to simulate cross-scale spatial interactions.

2.6. How do we test and evaluate LMs?

Construction and use of an LM demands specially designed testing and validation phases, because without these steps, models can easily generate outputs that have no guarantee of accuracy, reliability, or realism. With increasing simulation detail and resolution, especially resulting from mechanistic approaches, the intrinsic uncertainties associated with each modeled process may be compounded. These uncertainties can be difficult to reconcile via standard approaches such as comparing model output to raw observations (McKenzie et al., 1996; Rastetter, 1996). Even though this step seems obvious, some LMs remain untested and unevaluated, often because of the lack of validation data, a temporal or spatial scale mismatch between model output and validation data, or the difficulty in testing un-replicated landscape dynamics (Shifley et al., 2008) (see Section 2.1.5). Un-replicated landscape simulations that use stochastic functions represent only one realization of complex process and their interactions; one run may appear quite different from another, or from "reality", even when the dynamics generating them are essentially the same (Deser et al., 2012). We present two important tasks when evaluating LMs (Table 1).

2.6.1. Identify data needs

A basic but essential step in testing spatial models is to obtain comprehensive data sets that can be used for initialization (i.e., inputs), parameterization, calibration, or validation (Jenkins and Birdsey, 1998). These data sets should have been previously assigned a measure of reliability or variability and be stored in a standardized format (Fuentes et al., 2006). Spatially explicit time-series data of sufficient quality, ecological detail, and depth to validate landscape models are vital for model calibration (Pielke et al., 1997). This quality will improve as more comprehensive geo-referenced field data are collected using scientifically credible methodologies and stored in standardized formats (Huntzinger et al., 2011, 2012; Hurtt et al., 1998, 2010). Large-scale terrestrial ecology data sets including field- and remotely sensed products are increasingly available (e.g., ORNL-DAAC); temporal depth varies from years to decades.

Every effort should be made to incorporate the most recent ecological data as they become available to initialize, parameterize, calibrate, optimize, and assess the LM (LeBauer et al., 2013). New sophisticated methods, such as data assimilation and uncertainty analysis, are emerging as possible validation and evaluation tests. Data assimilation includes prior data to constrain parameter and model uncertainty (Wolf et al., 2011). This is especially important given that ecological understanding about disturbance interactions is constantly improving and the data and logic to drive such models are constantly evolving (Raffa et al., 2008; Turner, 2010). The recent expansion of remote-sensing products provides a valuable resource for land-cover change, land-surface phenology, and patches of disturbance, across large areas at fine spatial resolution (Kennedy et al., 2010; Zhu and Woodcock, 2014). We expect that remotely sensed data will soon become essential inputs for LMs, as they continue to serve as validation data for simulation output.

2.6.2. Develop methods for evaluation

The field of spatial simulation modeling critically needs comprehensive frameworks, standards, and methods to test and evaluate models. Common evaluation approaches, such as sensitivity analysis and accuracy assessments, are important but difficult to complete in a spatial context (Kleijnen et al., 1992; White et al., 2000; Couto, 2003). Simulation times for comprehensive sensitivity analyses are excessive, often requiring from a hundred to a million replicates (Nathan et al., 2001), especially in rigorous Monte-Carlo frameworks (Soetaert and Petzoldt, 2010). Accuracy assessments are difficult because long-term independent spatially explicit data are non-existent for many parts of the US (Rausche et al., 2000) as well as worldwide. Grimm et al. (2014) provide excellent examples of how to document model validation and evaluation.

As spatial domains of LMs get larger, and the dynamics of interactions are modeled explicitly as we have proposed, model evaluation needs to adopt appropriate metrics at appropriate levels of aggregation. We shall no longer be able to compare LM output to observations on a cell-by-cell, or even patch by patch, basis. Replicating these specifics raises the "middle-number problem" (McKenzie et al., 2011); in LMs, the cumulative error of many inexact computations is overwhelming and therefore will produce unrecognizable outcomes. As models become more complex and simulations reach further into the future over larger landscapes, available testing information is even more limited, so expectations must evolve. We believe the solution lies in a realistic coupling of the questions posed by an LM with its evaluation. For example, suppose we are testing an LM by running it at equilibrium on a known landscape with the idea of evaluating its use for future projections. We would not expect to replicate exactly the species composition and total live biomass of every pixel, but we would certainly like to recover the proportional composition of the landscape, and the mean per-cell and variance of biomass.

Nor would we expect every realization of the LM to get these things exactly. A broader view is needed, necessitated by model complexity. Paradigms from the climate and air-quality modeling communities may be helpful here. For example, ensemble

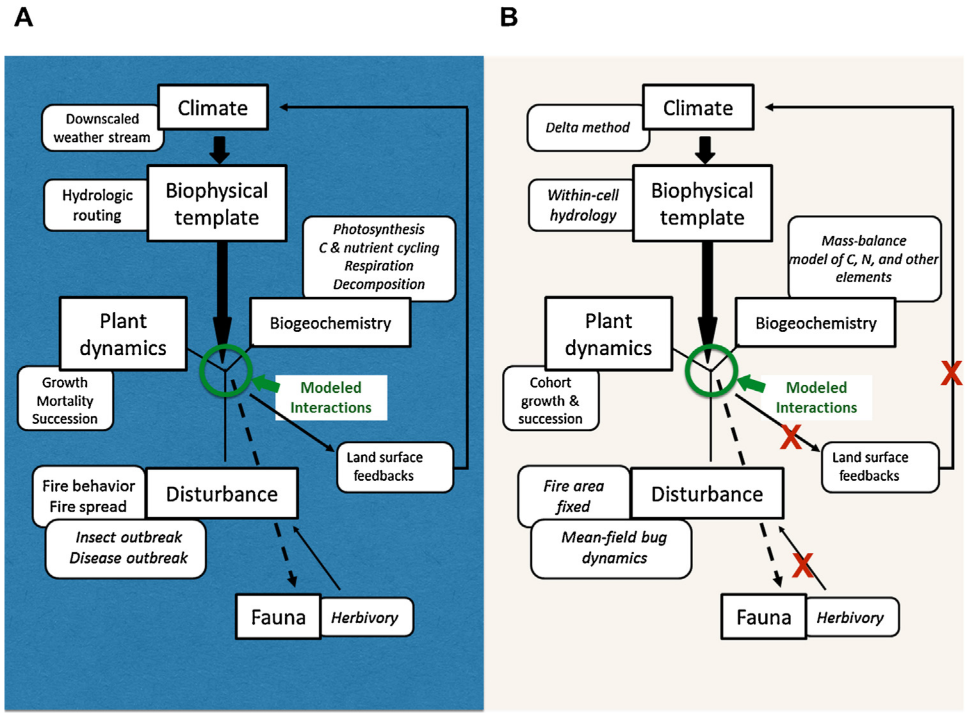

Fig. 6. Two variants on the detail and complexity of an LM whose components are the processes identified for explicit inclusion in the text. Criteria for choices include (1) articulating simulation objectives clearly, (2) choosing model structures to be as mechanistic as possible, (3) defining spatio-temporal scales and levels of organization, (4) identifying software engineering concerns, (5) defining data properties (A) In the fully mechanistic ideal, all processes would be implemented with the finest attention to detail. The key to dynamics is the modeling of interactions, represented in the center but incorporating too many forcings and feedbacks to be illustrated here. (B) In most LMs for most objectives, a less than full representation of all possible processes will be the parsimonious choice. Here many processes are represented with less detail than in A, but modeling interactions is still critical to understand landscape outcomes.

averaging (Dennis et al., 2010), linked to the Bayesian paradigm, looks at multiple outputs and weights their importance based on both observations and prior knowledge. Model evaluation becomes an iterative interactive process, whereby algorithms and parameters are subjected to scrutiny at varying levels of aggregation. Another paradigm worth exploring is multi-criteria optimization (Kennedy and Ford, 2011). LMs, or their ensembles, are evaluated for their skill in reproducing means, variances, pattern metrics, or other outcomes simultaneously.

More practically, we recommend that a concerted effort be made to create a landscape modeling web site that contains standardized test landscapes so that modelers can compare results generated from their models to other model results. Model comparisons are an important means of model validation and we recommend that this practice be employed with future LMs (Cary et al., 2006a,b; Cary et al., 2009).

3. Conclusion

Ultimately, the design of any LM is a process informed by (1) the quality of the underlying science and (2) the technical and creative ability of the modeler to implement this understanding quantitatively (Fig. 6). The quality of the underlying science is determined by experimentation and observation that informs a mechanistic understanding of key processes and is published in peer-reviewed journals. Modelers depend on the advancement of this scientific understanding to improve existing models, and thus are dependent on advances in complementary disciplines. On the other hand, modelers are also limited in the extent to which evolving ecological understanding can be feasibly incorporated into existing model structures. Especially on the 'edge' of scientific advances, there is often a lack of quantitative descriptions of qualitatively described processes (Clark and Gelfand, 2006). There are also limitations of data parsimony and availability, and engineering restrictions, which may hinder the incorporation of new knowledge into existing model structures (Fig. 6). More theoretical issues, such as temporal and spatial scale reconciliation (Urban, 2005), pose additional challenges to the modeling community. The balance of data needs versus model advancement reflects a general imperative for cross-fertilization between field ecologists, who provide data and equations to modelers, and modelers, who must then integrate that knowledge to provide descriptions of phenomena at different spatial and temporal scales. A challenge is the enhanced communication between modelers, ecologists, and climatologists. After all, a significant part of spatial model development is learning from the building process and this new knowledge is important to future efforts. Although the recommendations presented in this paper are by no means exclusive or comprehensive, we hope that they provide a direction for future LM development and assessment.

Acknowledgments

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