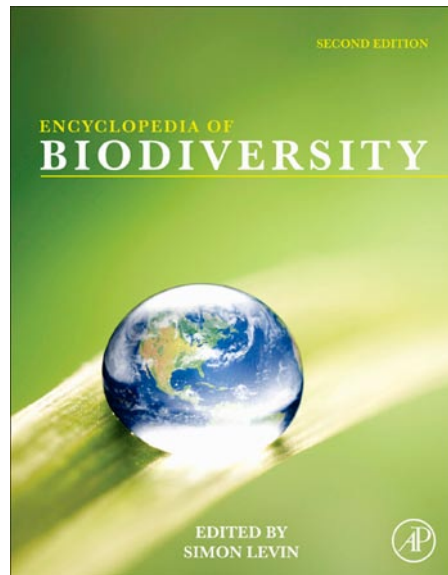


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## Landscape Modeling

Robert M Scheller, Portland State University, Portland, OR, USA

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### Glossary

**Disturbance** A relatively discrete event that results in mortality of plants or animals or an event that is uncharacteristically intense or long-lasting. Wildfire, tornados, and logging are disturbances that are generally stochastic in location and time. Floods or extended dry periods (droughts) are considered disturbances if they are unusually large or intense.

**Endogenous process** Process that emerges from biotic and abiotic interactions internal to the system of interest. Examples include vegetation growth and succession, dispersal of organisms within a landscape, and topographic influences on microclimate. Some human activities may be considered endogenous – for example, various crop rotation systems – if they are well established and responsive to local needs.

**Exogenous process** Process external to the system of interest. For landscapes, exogenous processes would include climate change or species migration into the landscape. Human activities may be considered exogenous if they are novel, permanent (e.g., housing development), or driven by external forces (e.g., the world market for timber).

**Geographic information system (GIS)** Computational system for storing, managing, manipulating, and displaying spatial data. Because landscape models are inherently spatial, strong links to GIS are either built into such models or are required to interface with the model input and output data. Many GIS, both free and commercial, are available for use with landscape models.

**Resolution** The resolution of information represented within a landscape model has three primary components:

spatial, temporal, and taxonomic. *Spatial resolution* refers to the smallest unit size or area represented (synonymous with *grain*). For vector data, resolution is the minimum mapping unit. For raster data, it is the cell size. *Temporal resolution* refers to the frequency at which various social or ecological processes operate. Common examples include hourly, daily, monthly, and annually. *Taxonomic resolution* is the degree of aggregation of species information. The smallest unit possible is species-specific information. *Taxonomic* aggregations typically used in landscape modeling include species, functional groups, potential vegetation types, and successional states.

**Scenario** A discrete suite of assumptions regarding future drivers of landscape change that are fed into a landscape model or models. The list of assumptions often includes future climate, future disturbance regimes, and future management or land-use policies. Multiple scenarios can be created to form a full factorial matrix that highlights experimentation and statistical rigor. Alternatively, fewer scenarios can be assembled into central “story lines” that highlight key management or policy options.

**Stochastic process** Process in which one or more simulated events or rates has values that are derived in part from a probability distribution function (e.g., Gaussian, Weibull, exponential). Therefore, such events or rates are not typically “random” (although random is a valid probability distribution function) but are unpredictable. Examples of simulated stochastic processes include the location of lightning strikes, daily maximum temperature, and wind speeds.

### Introduction

A sufficient understanding of the threats to biodiversity and the opportunities to preserve or enhance biodiversity requires an acknowledgment of the broader context within which the various components of biodiversity operate. Over the past several decades, managers have realized that consideration of only small watersheds or forest stands is not sufficient to maintain biodiversity (Hansson and Angelstam, 1991; White *et al.*, 1997; Foley *et al.*, 2005; Fischer and Lindenmayer, 2007; Lindenmayer *et al.*, 2008). Insufficient attention to the broader context within which an area of interest (e.g., a national park or wilderness area) resides can lead to population decline, local extirpation, or catastrophic disruption due to large, infrequent disturbance events (den Boer, 1981; Tilman *et al.*, 1994; Huxel and Hastings, 1999; Brashares, 2010; Spencer *et al.*, 2011). This broader context can be considered the *functional landscape*: an area large enough to capture all of those processes that maintain or reduce biodiversity and large

enough to provide sufficient habitat for populations of native species. A functional landscape is typically smaller than a biome but larger than a first-order watershed and several times larger than the maximum disturbance size (Baker, 1989a; Dunning *et al.*, 1992; Turner *et al.*, 1993, 1995; Forman, 1995).

Functional landscapes (*landscapes* henceforth) are an intuitive unit for studying and managing biodiversity. By encompassing most of the processes influencing biodiversity, landscapes afford the opportunity to practice inclusionary management that is more holistic and considerate of all relevant processes and elements (the individual components of a landscape – for example, forest patches, stream corridors, and grass or shrub fields). However, landscapes pose distinct challenges for ecologists and managers. Because of their size, they are inherently nonreplicable (Hurlbert, 1984). Also because of size, significant change at the landscape scale typically occurs over many decades: changes to composition, structure, or function emerge more slowly when averaged across large

numbers of each landscape element. Such long durations are generally not commensurate with the available funding for either research or management. For management, these concerns are particularly acute because trends occurring at a landscape scale are often difficult and expensive to reverse through restoration efforts. Borrowing a business aphorism, changing course at the landscape scale is akin to turning an oil tanker around: it happens slowly at best. And no one wants to be held accountable for running an ecosystem into the shoals of lost biodiversity or reduced ecosystem functioning.

Because of these spatial and temporal challenges, both scientists and managers increasingly rely on landscape models to understand and predict change at these spatial and temporal scales. A landscape model is a mathematical and logical representation of a functional landscape that includes the subset of exogenous and endogenous processes expected to explain a majority of the coarse-scale spatial and temporal variability. These processes nearly always include disturbances and vegetative succession. A typical landscape model will include a representation of vegetative change (the author will discuss techniques in the following sections) and one or more stochastic disturbances: wildfire, development and urban expansion, forest management, windthrow, and so on. As with all models, an empirical foundation is necessary to derive the mathematical and logical abstractions of the real system.

Landscape models differ from other kinds of ecological model because they are spatially explicit, depicting the composition, arrangement, and geographic location of the various landscape elements. In practice, this means that the models are often closely linked to a geographic information system (GIS) for managing the spatial information. Results are often provided via maps of biodiversity or other conditions of interest, allowing an intuitive assessment of spatial variation. Maps are particularly valuable for communicating with stakeholders. Unfortunately, accompanying maps of uncertainty are seldom provided.

Landscape models also depict the spatial interactions among constituent elements. Spatial interactions are the lateral transfer of information, matter, or energy generated by ecological processes (Reiners and Driese, 2001). Movement of matter and energy includes the lateral transport of water and dissolved nutrients. The transfer of matter and energy may also be generated through disturbances. Wildfire is an archetypal spatial process because it releases and transfers energy and the size and duration of wildfire is highly dependent on the spatial configuration of fuels and topography (Hargrove *et al.*, 2000; Finney *et al.*, 2007; Schmidt *et al.*, 2008).

The lateral transfer of information is synonymous with species distributions and community composition and is transferred across the landscape through dispersal and migration. Similar to wildfire, dispersal is often highly dependent on landscape configuration and fragmentation (Miller *et al.*, 1997; King and With, 2002; Higgins *et al.*, 2003b; Iverson *et al.*, 2004; Scheller and Mladenoff, 2008). Without spatial interactions – or if spatial interactions are weak – landscape models can be reduced to a collection of individual units (e.g., stands), and these units could simply be multiplied by the area within the landscape that they represent. Further explication of when a spatially dynamic model (one that includes spatial interactions) is necessary is provided below (see Landscape Modeling Approaches).

By representing the dominant processes at a scale relevant to understanding and managing biodiversity and by representing the spatial configuration and interactions of a landscape, landscape models allow empirically derived knowledge to be extrapolated to larger spatial and temporal domains. Doing so, we can begin to engage in meaningful *ecological forecasting* (Clark *et al.*, 2001), providing managers and policy makers tools for enhanced decision making that incorporates knowledge about the future, however limited (Pielke, 2003).

Landscape models are frequently paired with scenarios that can be relatively simple narratives about future policies or conditions – for example, the *Millennium Ecosystem Assessment* (2005). Scenarios can also be framed within an experimental design with multiple factors along two or more gradients (e.g., three levels of fire rotation period  $\times$  three levels of harvesting in a full factorial design). Each individual scenario is then used to project how a landscape will change given the associated suite of assumptions about the frequency and intensity of the constituent processes (particularly of anthropogenic origin) (Carpenter, 2000). Typically, the results from each scenario are then compared with each other and with empirical data when available (see Conclusions). By comparing results among scenarios, the need for absolute accuracy is reduced as the *relative* merits of different policies or assumptions can still be assessed.

Although serving the utilitarian purpose of extrapolating knowledge to larger spatial and temporal domains, landscape models also enable a synthesis that is otherwise impossible. As knowledge about biodiversity expands and the threats to biodiversity multiply, the requisite number of processes that must be integrated and managed to preserve biodiversity grows exponentially. However, the human capacity to synthesize the effects of many processes, each operating at unique and often disparate scales, is limited. Landscape models allow many different processes to operate within and interact across a landscape. Patterns will emerge (*emergent behaviors*) that could not be anticipated using studies of isolated processes or intuition alone. For example, simulations of climate change in Siberia that included wildfire, logging, and insect mortality revealed that the expansion of harvesting in combination with increased insect activity will potentially have a far greater effect on forest composition than the direct effects of climate change alone (Gustafson *et al.*, 2010).

Because landscape models often incorporate multiple stochastic processes, they are also well suited for partitioning the total uncertainty of a landscape projection into its components: parameter, model, and inherent uncertainty (Haag and Kaupenjohann, 2001; Higgins *et al.*, 2003a; Millar *et al.*, 2007). Parameter and model uncertainty are artifacts of the modeling process and represent the current limits of knowledge about the system. Inherent uncertainty is the accumulated effect of all nondeterministic variation. For example, seed dispersal has significant inherent uncertainty as we can never know exactly how far an individual seed may travel. The exact time and location of lightning ignition of fires is similarly unknowable. Inherent uncertainty may seem to deflate ambitions for ever-increasing model accuracy. However, even if the accuracy of a given model projection is weak or unknown (as is the case for all projections of the deeper future), knowledge about the sources of uncertainty

(e.g., Allen *et al.*, 2000; Xu *et al.*, 2009) can be extremely valuable to managers. If a system has relatively low inherent uncertainty, then human agency will be relatively more effective. If the opposite is true, then caution is warranted before investing considerable resources into attempts at guiding or dictating landscape change.

Finally, landscape models also provide a critical heuristic function. The process of formulating, parameterizing, calibrating, and validating a landscape model requires the synthesis of multiple sources of data and models. A landscape model typically requires vast quantities of data that are processed in advance of conducting any simulations. For example, even the simplest landscape model requires remotely sensed data that are classified to a spatial and taxonomic resolution that are congruent with the questions at hand. More detailed or complex landscape models may require additional edaphic or topographic data or more detailed taxonomic data. In addition, formulating how the various processes will interact across space and time requires a deep understanding of the ecology of the system (and therefore modeling efforts often involve teams of scientists). Existing representations of processes may need to be altered or discarded if they were developed for a scale substantially different from the other model components. Validation requires more data still and is difficult to obtain for long-term or projected models. In total, the modeling process is dominated by data synthesis and analysis with a relatively small amount of time devoted to actual simulations.

## Landscape Modeling Approaches

When is a landscape model useful or necessary? Landscape models are useful when the representation of exogenous and endogenous processes, represented within a geographic framework, and with spatial interaction among landscape elements is required to project, understand, and manage landscapes for biodiversity. These are also the criteria the author used to select modeling approaches for review. There is an incredible diversity of landscape models – more than can be summarized here. These models span broad gradients of complexity, specificity, usability, and application. Many excellent reviews have been written summarizing the past and current state of landscape models (Baker, 1989b; Mladenoff and Baker, 1999; Keane *et al.*, 2004; Scheller and Mladenoff, 2007; Seidl *et al.*, 2011). More information about the mechanics of developing landscape models is also widely available (Maxwell and Costanza, 1997; Scheller *et al.*, 2010). Rather than an exhaustive and complete list, the author focussed on four of the most common approaches to formulating (or applying) landscape models: state-and-transition models, process models, hybrid models and multimodeling, and neutral models (an approach to applying models, rather than a type). The author will highlight their respective strengths and limitations and the appropriate domain of application for each.

Ideally, a model is no more complex than necessary to answer the given question. Given the enormous additional complexity introduced by the inclusion of spatial interactions (Shugart Jr., 1998; Strayer *et al.*, 2003), it is critical to decide when the representation of spatial processes – and therefore

the need for a landscape model at all – is justified. All ecosystems contain spatial interactions. The question is whether the policy, management, or ecological question can be answered with a simpler nonspatial model or whether the additional complexity is required. There are no absolute answers; however, general criteria can be outlined based on the strength of spatial interactions at the chosen model resolution and extent (Strayer *et al.*, 2003). If a spatial process is occurring at a resolution much finer than model resolution, then the process is often considered “noise” that can be safely averaged without loss of important information. For example, when modeling the effects of climate change on terrestrial systems at regional or continental systems (e.g., Bachelet *et al.*, 2003), the inclusion of the effects of competition among neighboring trees or fine-scale propagules dispersal would be unlikely to reduce uncertainty at the intended scale. Inclusion of the effects of tree species migration via dispersal may, however, be required if substantial range shifts are expected over the simulated duration. Similarly, if a spatial process naturally occurs across extents far greater than the focal extent, the process can be represented as a simple rate (potentially changing through time). For regional landscapes (or smaller), climate is often treated in this fashion even though we recognize that weather is a very spatially dynamic process.

All models are compromises. The data available to parameterize and validate models are limited, as are the resources (fiscal, temporal, and computational) available for developing and applying a model. Is it important that the model be able to run on a typical desktop computer? Is an intuitive user interface necessary for the intended user to be able to quickly implement the model? Each model developer must rank the priorities for resolving the question at hand.

Models must also compromise among processes for the allocation of complexity. For example, a landscape model with a fire component that represents hourly growth of a fire and flame lengths at a 1-m resolution necessarily devotes fewer resources to landscape processes that unfold over many decades (e.g., tree species migration). If the model developer devoted most resources to developing a model of individual trees, then the biogeochemical components may be simplified or lacking altogether. Each of the four types (Table 1) described in the following sections represent the compromises and such sacrifices. None of these model types is appropriate for all situations and questions.

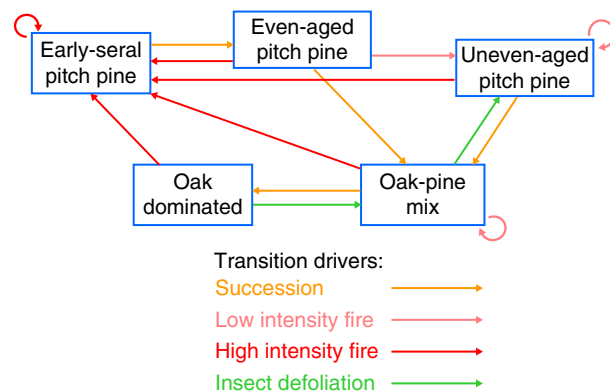
## State-and-Transition Models

State-and-transition models are typically used to address management questions for which distinct vegetative conditions or classes are readily identifiable and their relative abundance is an important consideration. For example, Pastor *et al.* (2005) modeled forest change in northern Minnesota as a function of harvesting using an age-dependent state-and-transition model. They concluded that a narrow range of harvest ages will reduce the amount of the landscape in a regeneration state, a result that is counter to emerging trends toward managing with a broader range of harvest ages.

State-and-transition models place each landscape element into one of a limited number of states (Cattalino *et al.*, 1979;

**Table 1** Four general landscape modeling approaches, example questions, and strengths and weaknesses

Model approach	Example question	Strengths	Weaknesses
State-and-transition	How will the relative abundance of discrete vegetation classes change through time?	Relatively straightforward logic; easier to parameterize; simplification facilitates collaboration; reduced computational requirements.	Less flexible responses to novel climates, introduced species, altered disturbance regimes; nonstationary landscape dynamics poorly represented.
Process	How will net biome production change if wildfire increases with climate change?	Highly flexible; ability to represent nonstationary landscape dynamics; can represent changing ecosystem process rates.	Steep parameterization requirements; requires specialized knowledge and therefore is less suitable for stakeholder engagement; high computational requirements.
Neutral	Are patch size or shape important determinants of population migration?	Assess strength of individual processes; location neutral and not context dependent; testing of multiple landscape configurations.	The results are more abstract; artificiality may render results less applicable to actual threats to biodiversity; lack of place-based output maps reduces stakeholder engagement.
Hybrid or multimodeling	Do landscape-scale fire dynamics influence carnivore population viability?	Integration of multiple domains (e.g., forests and animal metapopulations); integration across broader range of spatial and temporal scales; increased ability to assess sources of uncertainty.	High complexity can overwhelm modeler's ability to partition sources of variation; need to validate across multiple domains; communicating system behavior to nontechnical audiences is challenging.

**Figure 1** Conceptual diagram of a mid-Atlantic pine barrens state-and-transition model.

Klenner *et al.*, 2000; Acevedo *et al.*, 2001; Monticino *et al.*, 2002; Pastor *et al.*, 2005). These states typically represent the vegetative condition at a given time. For example, in the eastern US, a landscape element could be initially classified as even-aged pitch pine if satellite and field data indicate that the unit is dominated by *Pinus rigida* with an average age between 30 and 100 years (Figure 1). The transition to a different predetermined alternative state may occur if either a set amount of time has passed (succession) or a transition is triggered by a disturbance event. The even-aged pitch pine may transition to oak-pine mix 70 years after initiation unless a fire is simulated, changing it to early seral pitch pine or uneven-aged pitch pine, depending on fire severity (Figure 1).

Transitions among states may be dictated by disturbance as previously noted or may be determined via a transition probability matrix (Logofet and Lesnaya, 2000; Yemshanov and Perera, 2002). In this case, a state may transition to one of many possible alternate states based on a probability assigned to each transition. The combination of a fixed state and a transition determined in part by a stochastic process is considered a *semi-Markov* model.

The number of states and their taxonomic resolution (e.g., three classes of pitch pine vs. forest, prairie, and savannah), and the number of transitions is dependent on the objectives of the research or the management application. Shorter duration (<50 years) simulations often stratify a landscape into potential vegetation types with a suite of states for each type, whereas longer duration simulations may focus more on transitions among major land types (e.g., agriculture, forest, pasture, developed).

Because of the finite number of states (and therefore transitions), state-and-transition landscape models are conducive to rapid deployment and collaborative model construction. One of the most commonly used state-and-transition models, the Vegetation Dynamics Development Tool (VDDT), has an intuitive graphic interface that allows groups of scientists and managers to quickly visualize a model and focus their efforts on deliberately constructing the states and transitions that best represent the dynamics of their system (Hemstrom *et al.*, 2001; Shifley *et al.*, 2008). The relative simplicity also maximizes transparency and generates greater “buy-in” from local managers and stakeholders. This process of constructing state-and-transition models to engage a broader group of participants has been widely used by the Nature Conservancy in North America (Shlisky *et al.*, 2005).



However, the finite states also limit the inferential power of these landscape models. Most landscapes around the world today are in part dominated by one or more *nonstationary* processes, meaning that their frequency or magnitude is changing through time. Consequently, many states may cease to be significant components of their respective landscapes or the transitions among states may be substantially altered through time. Novel communities (states) may emerge due to climate change (Williams *et al.*, 2007) or invasive plant species. Invasive (or climatically released) insects may become the dominant process driving vegetative change (Ward and Masters, 2007; Kurz *et al.*, 2008).

### Process Models

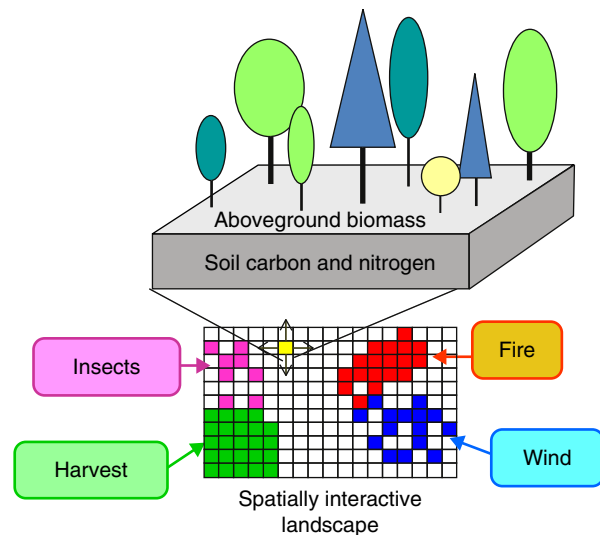
All landscape models represent one or more processes, and therefore this landscape model type is a misnomer. What distinguishes these models is that all processes, including succession, are explicitly represented and there are no fixed states or transitions. Rather, plant community composition is an emergent property itself. Depending on how succession is represented and on the taxonomic resolution, plant community composition may be a function of disturbance intensity and type, plant competition for light or nutrients, seed dispersal, and other species vital attributes (Mladenoff *et al.*, 1996; Roberts, 1996). Because composition is more nearly continuous, all other processes can be formulated to be more sensitive to the effects of plant community composition and diversity. In particular, ecosystem processes (e.g., aboveground net primary productivity, soil respiration) can more readily be incorporated as these generally require a tight coupling between vegetative composition, structure, climate and soils (Scheller *et al.*, 2011a).

Such landscape process models therefore have much greater flexibility to deal with nonstationary processes, notably climate change. Novel communities can emerge from the interplay between stochastic disturbance processes (themselves responding to climate), species vital attributes, and ecosystem processes that will dictate other physiological constraints (e.g., nitrogen availability, soil moisture, Scheller *et al.*, 2011a) (Figure 2). Such an approach is essential for projecting landscape capacity to sequester carbon and provide habitat further into the future (> 50 years).

The added flexibility does, however, come at a substantial cost. The data required to parameterize such models is orders of magnitude greater than for state-and-transition models. And the process of constructing and parameterizing these landscape models is at best a specialized skill and at worst hopelessly opaque to anyone outside of the discipline. Policy makers, managers, and stakeholders can feel removed from the modeling process and are generally unable to assess the quality of the research. The important drivers that may emerge – N availability, litter lignin content – are not readily measurable by land managers and often only loosely related back to the task of managing for biodiversity.

### Hybrid and Multimodeling

An emerging trend is the combination of one or more modeling approaches to understand and project changing



**Figure 2** Conceptual diagram of a process landscape model, emphasizing ecosystem processes and spatially dependent disturbances.

biodiversity. In particular, hybrid models and multimodeling offer the opportunity to include processes or interactions across a broader range of spatial, temporal, or taxonomic resolutions than might be possible with a single modeling approach.

To better understand vegetation change, hybrid models have been deployed to represent finer-scale processes using a different modeling paradigm than is used to represent broader landscape process interactions. For example, competition among individual trees and subsequent growth may be simulated using an individual tree model (Robinson and Ek, 2003; Seidl *et al.*, in press) or a gap model (Pastor and Post, 1988; Seidl *et al.*, 2005). These fine-scale models can be stitched together spatially to form a continuous landscape (e.g., Urban *et al.*, 1991; Bragg *et al.*, 2004). Alternatively, individual tree data can be averaged using ecological field theory and scaled up to allow for the efficient calculation of processes that operate at larger spatial or temporal scales (e.g., Seidl *et al.* in press). The advantage of hybrid forest models is the inclusion of individual trees, their growth, and competition with neighbors. The challenge is the additional parameterization and data required. To date, these data are seldom captured by the remote sensing tools available, and hybrid models have been limited to relative small landscapes (< 10,000 ha).

*Multimodeling* (or *model coupling*) has also been extended to assessing animal populations. The challenges of overlaying stochastic animal populations on top of the existing stochastic disturbance dynamics are considerable. However, advances in software and computer power have accelerated the ability to consider both changing habitats and changing populations simultaneously (Larson *et al.*, 2004; Akcakaya *et al.*, 2005; Shifley *et al.*, 2008). For example, to project changes in the population of fisher (*Martes pennanti*) in the southern Sierra Nevada, California, USA, a landscape change model was coupled with a metapopulation model (Spencer *et al.*, 2011; Syphard *et al.*, 2011). As a result, two of the largest sources of uncertainty were incorporated: wildfire and fisher dispersal.

By doing so, a more accurate estimate of inherent uncertainty was achieved (Scheller *et al.*, 2011b).

### Neutral Models

Neutral models are not a model type in and of themselves but rather a unique application of landscape models (Gardner *et al.*, 1987; With and King, 1997). Neutral modeling is the process of applying a landscape model to a strictly hypothetical landscape. In this case, the complexity inherent in parameterizing an actual landscape is jettisoned in favor of a focus on the processes themselves. A neutral modeling approach allows for much more precise testing of model sensitivity to landscape configuration and community composition than is possible on a real landscape. The goal of neutral landscape modeling is a more fundamental understanding of the processes that control landscape change across *all* landscapes rather than the narrower domain of a real landscape. Real landscapes simply never contain the full range of possible landscape configurations and species that may inform longer-range management efforts. As an example, Huxel and Hastings (1999) used neutral models to examine how the placement of restoration efforts (adjacent to existing habitat vs. random placement) could significantly influence habitat restoration success. Attempting to find a suitable suite of similar landscapes (with replication) for such experimentation would have been impossible.

Although further removed from the immediacies of landscape management, neutral models can potentially inform managers about potential solutions or enhancements that are not immediately apparent from an examination of current conditions (Huxel and Hastings, 1999; With *et al.*, 1999; King and With, 2002). The risk is further detachment from management relevancy: maps of actual landscapes and geographically grounded projections of landscape change remain extremely powerful tools for communicating the science of landscape change.

### Conclusions

The limitations to landscape models are similar to that of all models, with one important caveat. All models are limited (or strengthened) by the empirical foundation on which they are built: by the data underlying their formulation, the data available to parameterize a model in a novel setting, the computational limits to complex simulations, and the software limitations to managing complex algorithms and architectures. With limited experience, I assume these limitations also apply to models of beating hearts and hurricane trajectories.

However, landscape models, like climate change models, are additionally limited by the ability to validate results. When projecting more than a few years into the future, validation of model results – the cross-check against reality that has made weather forecasting so successful – requires the continual collection of spatially explicit data through time (Rastetter, 1996; Rykiel, 1996; Haag and Kaupenjohann, 2001; Gardner and Urban, 2003). If projecting more than 10 or 20 years,

validation would require patience and funding not typically afforded the average scientist or manager. In addition, it is important to remember that because of stochastic events, the actual observed landscape is but one of many possible outcomes that could have occurred. Rarely will a single model simulation match reality. Thus, even assuming that spatial data are collected, validation should be against confidence intervals generated by running the model many times (e.g., model replication).

Complete validation may be the gold standard of modeling (as double-blind experiments are to medicine), but it is only one route to building confidence in the knowledge gained from models. Other avenues for building confidence in landscape model results include the validation of individual processes, model documentation, model transparency (e.g., closed vs. open source), and repeated application across diverse systems. Deploying a rigorous software engineering process during the development stage can maximize model verification (*sensu*; Aber, 1997) and has become more important as model complexity has increased (Scheller *et al.*, 2010).

It is incumbent on those who build and apply landscape models to follow a few general principles. First, quantify model sensitivity. There is little value obtaining precise leaf nitrogen estimates if wildfire explains 90% of the variation in species composition. Conversely, if leaf nitrogen is the controlling variable, more effort can be placed on obtaining empirical estimates.

Second, the inability to validate the complete landscape does not preclude the validation of individual processes. Often available knowledge about individual processes (tree growth rates, wildfire spread, logging patterns) is large and should be rigorously utilized.

Third, replication is essential. The existence of inherent uncertainty in reality and the incorporation of stochastic processes into models ensures that no single model simulation will be broadly representative of the future.

Fourth, communicate uncertainty. Although maps of projected landscape change are powerful tools for communication, it is essential that the underlying uncertainty be expressed through time series with replicate standard errors, probability surface maps, or similar approaches.

Similarly, it is incumbent on the managers and policy makers to be aware of these principles and to recognize those model applications that do or do not adhere to them. Unfortunately, many managers and policy makers instinctively distrust model results and do not engage in the process. This is perhaps in part due to inadequate education and outreach on the part of those who conduct modeling research (Pielke, 2003). It is also true that model results have often been presented as *predictions*, which imply a high level of accuracy, and the degree of uncertainty has been underrepresented. Modelers need to articulate what managers can learn from models while acknowledging that we live in a “black swan” world (Taleb, 2007).

As the collective challenge to preserve biodiversity increases, tools that enable learning about the future are increasingly valuable. Landscape models – in conjunction with well-formulated scenarios – offer a route to understanding and managing biodiversity across large areas and long

durations. The relentless increase in spatial data (particularly from remote sensing), computing power, and the sophistication of landscape models has enabled scientists and managers to look further into the future and with greater accuracy than ever before. Continued success and improvement is possible, dependent on the ability of scientists to provide a transparent, collaborative, and rigorous system that maximizes learning while acknowledging uncertainty.

## Appendix

### University Courses

1. Landscape Ecology
2. Forest Ecology
3. Simulation Modeling

**See also:** Biodiversity in Logged and Managed Forests. Climate, Effects of. Computer Systems and Models, Use of. Disturbance Regimes and the Historical Range of Variation in Terrestrial Ecosystems. Dynamic Global Vegetation Models. Forest Ecology. Land-Use Issues. Modeling Biodiversity Dynamics in Countryside and Native Habitats. Modeling Terrestrial Ecosystem Services. Succession, Phenomenon of. Timber Industry

## References

- Aber JD (1997) Why don't we believe the models. *Bulletin of the Ecological Society of America* 232–233.
- Acevedo MF, Aulan M, Urban DL, and Pamarti S (2001) Estimating parameters of forest patch transition models from gap models. *Environmental Modelling & Software* 16: 649–658.
- Akcakaya HR, Franklin J, Syphard AD, and Stephenson JR (2005) Viability of Bell's Sage Sparrow (*Amphispiza belli* ssp. *Belli*): Altered fire regimes. *Ecological Applications* 15: 521–531.
- Allen MR, Stott PA, Mitchell JFB, Schnur R, and Delworth TL (2000) Quantifying the uncertainty in forecasts of anthropogenic climate change. *Nature* 407: 617–620.
- Bachelet D, Neilson RP, Hickler T, et al. (2003) Simulating past and future dynamics of natural ecosystems in the United States. *Global Biogeochemical Cycles* 17: 1–21.
- Baker WL (1989a) Landscape ecology and nature reserve design in the Boundary Waters Canoe Area, Minnesota. *Ecology* 70: 23–35.
- Baker WL (1989b) A review of models of landscape change. *Landscape Ecology* 2: 111–333.
- Bragg DC, Roberts DW, and Crow TR (2004) A hierarchical approach for simulating northern forest dynamics. *Ecological Modelling* 173: 31–94.
- Brashares JS (2010) Filtering wildlife. *Science* 329: 402–403.
- Carpenter SR (2000) Ecological futures: Building an ecology of the long now. *Ecology* 83: 2069–2083.
- Cattellino PJ, Noble IR, Slatyer RO, and Kessell SR (1979) Predicting the multiple pathways of plant succession. *Environmental Management* 3: 41–50.
- Clark JS, Carpenter SR, Barber M, et al. (2001) Ecological forecasts: an emerging imperative. *Science* 293: 657–660.
- den Boer PJ (1981) On the survival of populations in a heterogeneous and variable environment. *Oecologia* 50: 39–53.
- Dunning JB, Danielson BJ, and Pulliam HR (1992) Ecological processes that affect populations in complex landscapes. *Oikos* 65: 169–175.
- Finney MA, Selia RC, McHugh CW, Ager AA, Bahro B, and Agee JK (2007) Simulation of long-term landscape-level fuel treatment effects on large wildfires. *International Journal of Wildland Fire* 16: 712–727.
- Fischer J and Lindenmayer DB (2007) Landscape modification and habitat fragmentation: A synthesis. *Global Ecology and Biogeography* 16: 265–280.
- Foley JA, Defries R, Asner GP, et al. (2005) Global consequences of land use. *Science* 309: 570–574.
- Forman RTT (1995) Some general principles of landscape and regional ecology. *Landscape Ecology* 10: 133–142.
- Gardner RH, Milne BT, Turner MG, and O'Neill RV (1987) Neutral models for the analysis of broad-scale landscape pattern. *Landscape Ecology* 1: 19–28.
- Gardner RH and Urban DL (2003) Model validation and testing: Past lessons, present concerns, future prospects. In: Canham CD, Cole JJ, and Lauenroth WK (eds.) *Models in Ecosystem Science*, pp. 184–203. Princeton, New Jersey, USA: Princeton University Press.
- Gustafson EJ, Shvidenko AZ, Sturtevant BR, and Scheller RM (2010) Predicting global change effects on forest biomass and composition in south-central Siberia. *Ecological Applications* 20: 700–715.
- Haag D and Kaupenjohann M (2001) Parameters, prediction, post-normal science and the precautionary principle – a roadmap for modelling for decision-making. *Ecological Modelling* 144: 45–60.
- Hansson L and Angelstam P (1991) Landscape ecology as a theoretical basis for nature conservation. *Landscape Ecology* 5: 191–201.
- Hargrove WW, Gardner RH, Turner MG, Romme WH, and Despain DG (2000) Simulating fire patterns in heterogeneous landscapes. *Ecological Modelling* 135: 243–263.
- Hemstrom MA, Korol JJ, and Hann WJ (2001) Trends in terrestrial plant communities and landscape health indicate the effects of alternative management strategies in the interior Columbia river basin. *Forest Ecology and Management* 5504: 1–21.
- Higgins SI, Clark JS, Nathan R, et al. (2003a) Forecasting plant migration rates: Managing uncertainty for risk assessment. *Journal of Ecology* 91: 341–347.
- Higgins SI, Lavorel S, and Revilla E (2003b) Estimating plant migration rates under habitat loss and fragmentation. *Oikos* 101: 354–366.
- Hurlbert SH (1984) Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54: 187–211.
- Huxel GR and Hastings A (1999) Habitat loss, fragmentation, and restoration. *Restoration Ecology* 7: 309–315.
- Iverson LR, Schwartz MW, and Prasad AM (2004) How fast and far might tree species migrate in the eastern United States due to climate change? *Global Ecology and Biogeography* 13: 209–219.
- Keane RE, Cary GJ, Davies ID, et al. (2004) A classification of landscape fire succession models: Spatial simulations of fire and vegetation dynamics. *Ecological Modelling* 179: 3–27.
- King AW and With KA (2002) Dispersal success on spatially structured landscapes: When do spatial pattern and dispersal behavior really matter? *Ecological Modelling* 147: 23–39.
- Klenner W, Kurz W, and Beukema S (2000) Habitat patterns in forested landscapes: Management practices and the uncertainty associated with natural disturbances. *Computers and Electronics in Agriculture* 27: 243–262.
- Kurz WA, Dymond CC, Stinson G, et al. (2008) Mountain pine beetle and forest carbon feedback to climate change. *Nature* 452: 987–990.
- Larson MA, Thompson III FR, Millspaugh JJ, Dijak WD, and Shifley SR (2004) Linking population viability, habitat suitability, and landscape simulation models for conservation planning. *Ecological Modelling* 180: 103–118.
- Lindenmayer D, Hobbs RJ, Montague-Drake R, et al. (2008) A checklist for ecological management of landscapes for conservation. *Ecology Letters* 11: 78–91.
- Logofet DO and Lesnaya EV (2000) The mathematics of Markov models: What Markov chains can really predict in forest successions. *Ecological Modelling* 126: 285–298.
- Maxwell T and Costanza R (1997) A language for modular spatio-temporal simulation. *Ecological Modelling* 103: 105–113.
- Millar CI, Stephens NL, and Stephens SL (2007) Climate change and forests of the future: Managing in the face of uncertainty. *Ecological Applications* 17: 2145–2151.
- Millennium Ecosystem Assessment (2005) *Ecosystems and Human Well Being: Scenarios*, 596 pp. Washington, DC: Island Press.
- Miller GS, Small RJ, and Meslow EC (1997) Habitat selection by Spotted Owls during natal dispersal in western Oregon. *Journal of Wildlife Management* 61: 140–150.
- Mladenoff DJ and Baker WL (1999) Development of forest and landscape modeling approaches. In: Mladenoff DJ and Baker WL (eds.) *Spatial Modeling of Forest Landscape Change*, pp. 1–13. Cambridge, UK: Cambridge University Press.
- Mladenoff DJ, Host GE, Boeder J, and Crow TR (1996) LANDIS: A spatial model of forest landscape disturbance, succession, and management. In: Goodchild MF,



- Steyaert AH, Parks BO, *et al.* (eds.) *GIS and Environmental Modeling: Progress and Research Issues*, pp. 175–179. Colorado, USA: GIS World Books, Fort Collins.
- Monticino MG, Cogdill T, Acevedo MF (2002) Cell interaction in semi-Markov forest landscape models. *Integrated Assessment and Decision Support*, Lugano, Switzerland, pp. 227–232.
- Pastor J and Post WM (1988) Response of northern forests to CO<sub>2</sub>-induced climate change. *Nature* 334: 55–58.
- Pastor J, Sharp A, and Wolter P (2005) An application of Markov models to the dynamics of Minnesota's forests. *Canadian Journal of Forest Research – Revue Canadienne De Recherche Forestiere* 35: 3011–3019.
- Pielke RAJ (2003) The role of models in prediction for decision. In: Canham CD, Cole JJ, and Lauenroth WK (eds.) *Models in Ecosystem Science*, pp. 111–138. Princeton, New Jersey, USA: Princeton University Press.
- Rastetter EB (1996) Validating models of ecosystem response to climate change. *BioScience* 46: 190–198.
- Reiners WA and Driese KL (2001) The propagation of ecological influences through heterogeneous environmental space. *Bioscience* 51: 939–950.
- Roberts DW (1996) Modelling forest dynamics with vital attributes and fuzzy systems theory. *Ecological Modelling* 90: 161–173.
- Robinson AP and Ek AR (2003) Description and validation of a hybrid model of forest growth and stand dynamics for the Great Lakes region. *Ecological Modelling* 170: 73–104.
- Rykiel EJJ (1996) Testing ecological models: The meaning of validation. *Ecological Modelling* 90: 229–244.
- Scheller RM, Hua D, Bolstad PV, Birdsey RA, and Mladenoff DJ (2011) The effects of forest harvest intensity in combination with wind disturbance on carbon dynamics in Lake States mesic forests. *Ecological Modelling* 222: 144–153.
- Scheller RM and Mladenoff DJ (2007) Forest landscape simulation models: Tools and strategies for projecting and understanding spatially extensive forest ecosystems. *Landscape Ecology* 22: 491–505.
- Scheller RM and Mladenoff DJ (2008) Simulated effects of climate change, tree species migrations, and forest fragmentation on aboveground carbon storage on a forested landscape. *Climate Research* 36: 191–202.
- Scheller RM, Spencer WD, Rustigian-Romsos H, Syphard AD, Ward BC, Strittholt JR (2011) Effects of fire and fuels management on Fishers (*Martes pennanti*) in the southern Sierra Nevada, California. *Landscape Ecology* 26: 1491–1504.
- Scheller RM, Sturtevant BR, Gustafson EJ, Mladenoff DJ, and Ward BC (2010) Increasing the reliability of ecological models using modern software engineering techniques. *Frontiers in Ecology and the Environment* 8: 253–260.
- Schmidt DA, Taylor AH, and Skinner CN (2008) The influence of fuels treatment and landscape arrangement on simulated fire behavior, Southern Cascade range, California. *Forest Ecology and Management* 255: 3170–3184.
- Seidl R, Fernandes PM, Fonseca TF, *et al.* (2011) Modelling natural disturbances in forest ecosystems: A review. *Ecological Modelling* 222: 903–924.
- Seidl R, Lexer MJ, Jager D, and Honninger K (2005) Evaluating the accuracy and generality of a hybrid patch model. *Tree Physiology* 25: 939–951.
- Seidl R, Rammner W, Scheller RM, Spies T, Lexer MJ (in press) Simulating ecological complexity: A scalable, individual-based process model of forest ecosystem dynamics. *Ecological Modelling*.
- Shifley SR, Thompson III FR, Dijk WD, and Fan Z (2008) Forecasting landscape-scale, cumulative effects of forest management on vegetation and wildlife habitat: A case study of issues, limitations, and opportunities. *Forest Ecology and Management* 254: 474–483.
- Shlisky AJ, Guyette RP, Ryan KC (2005) Modeling reference conditions to restore altered fire regimes in oak-hickory-pine forests: Validating coarse models with local fire history data. In: *Proceedings of the EastFIRE Conference*, Fairfax, VA.
- Shugart Jr. HH (1998) *Terrestrial Ecosystems in Changing Environments*. Cambridge, UK: Cambridge University Press.
- Spencer WD, Rustigian-Romsos H, Strittholt J, Scheller RM, Zielinski W, and Truex R (2011) Using occupancy and population models to assess habitat conservation opportunities for an isolated carnivore population. *Biological Conservation* 144: 788–803.
- Strayer DL, Ewing HA, and Bigelow S (2003) What kind of spatial and temporal details are required in models of heterogeneous systems? *Oikos* 102: 654–662.
- Syphard AD, Scheller RM, Ward BC, Spencer WD, and Strittholt JR (2011) Simulating landscape-scale effects of fuels treatments in the Sierra Nevada, California. *International Journal of Fire Management* 20: 364–383.
- Taleb NN (ed.) (2007) *The Black Swan: The Impact of the Highly Improbable*. New York: Random House.
- Tilman D, May RM, Lehman CL, and Nowak MA (1994) Habitat destruction and the extinction debt. *Nature* 371: 65–66.
- Turner MG, Gardner RH, and O'Neill RV (1995) Ecological dynamics at broad scales. Ecosystems and landscapes. *BioScience* S-29: 443–449.
- Turner MG, Romme WH, Gardner RH, O'Neill RV, and Kratz TK (1993) A revised concept of landscape equilibrium – disturbance and stability on scaled landscapes. *Landscape Ecology* 8: 213–227.
- Urban DL, Bonan GB, Smith TM, and Shugart HH (1991) Spatial applications of gap models. *Forest Ecology and Management* 42: 95–110.
- Ward NL and Masters GJ (2007) Linking climate change and species invasion: An illustration using insect herbivores. *Global Change Biology* 13: 1605–1615.
- White D, Minotti PG, Barczak MJ, *et al.* (1997) Assessing risks to biodiversity from future landscape change. *Conservation Biology* 11: 349–360.
- Williams JW, Jackson ST, and Kutzbach JE (2007) Projected distributions of novel and disappearing climates by 2100 AD. *Proceedings of the National Academy of Sciences* 104: 5738–5742.
- With KA, Cadaret SJ, and Davis C (1999) Movement responses to patch structure in experimental fractal landscapes. *Ecology* 80: 1340–1353.
- With KA and King AW (1997) The use and misuse of neutral landscape models in ecology. *Oikos* 79: 219–229.
- Xu C, Gertner GZ, and Scheller RM (2009) Uncertainties in the response of a forest landscape to global climatic change. *Global Change Biology* 15: 116–131.
- Yemshanov D and Perera AH (2002) A spatially explicit stochastic model to simulate boreal forest cover transitions: General structure and properties. *Ecological Modelling* 150: 189–209.