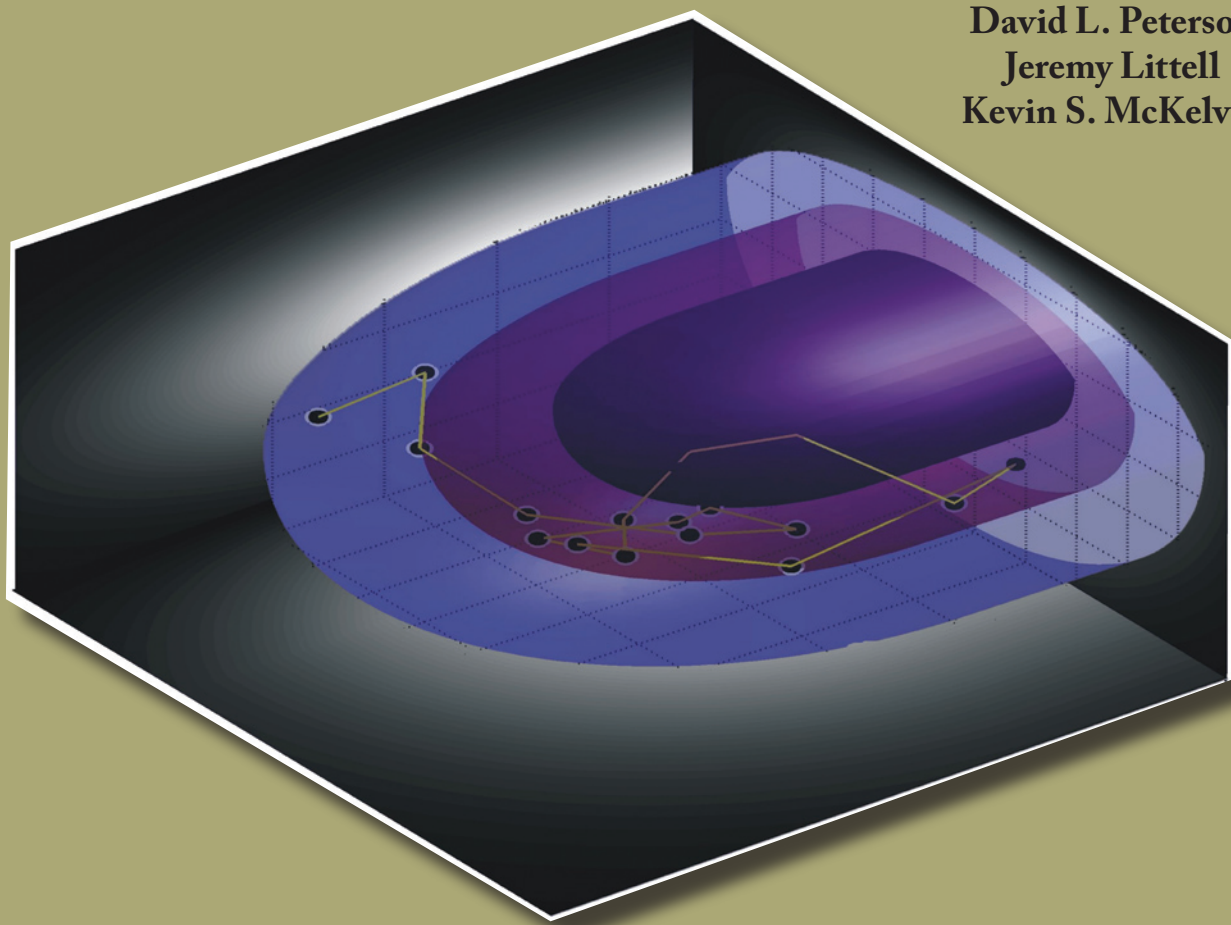


Research Agenda for Integrated Landscape Modeling

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Abstract

Reliable predictions of how changing climate and disturbance regimes will affect forest ecosystems are crucial for effective forest management. Current fire and climate research in forest ecosystem and community ecology offers data and methods that can inform such predictions. However, research in these fields occurs at different scales, with disparate goals, methods, and context. Often results are not readily comparable among studies and defy integration. We discuss the strengths and weaknesses of three modeling paradigms: empirical gradient models, mechanistic ecosystem models, and stochastic landscape disturbance models. We then propose a synthetic approach to multi-scale analysis of the effects of climatic change and disturbance on forest ecosystems. Empirical gradient models provide an anchor and spatial template for stand-level forest ecosystem models by quantifying key parameters for individual species and accounting for broad-scale geographic variation among them. Gradient imputation transfers predictions of fine-scale forest composition and structure across geographic space. Mechanistic ecosystem dynamic models predict the responses of biological variables to specific environmental drivers and facilitate understanding of temporal dynamics and disequilibrium. Stochastic landscape dynamics models predict frequency, extent, and severity of broad-scale disturbance. A robust linkage of these three modeling paradigms will facilitate prediction of the effects of altered fire and other disturbance regimes on forest ecosystems at multiple scales and in the context of climatic variability and change.

Keywords: climate change, climate regime, disturbance regime, modeling paradigms, empirical gradient model, mechanistic ecosystem model, stochastic landscape disturbance model

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Executive Summary

- The overall goal of the integrated modeling program described in this document is to obtain fine-scale predictions of ecosystem attributes across large geographical areas and project them over time under changing climate and disturbance regimes.
- Reliable prediction requires focus on mechanisms and responses and attention to spatial heterogeneity and temporal disequilibria.
- The fundamental unit of ecological analysis is the organism, and fundamental scales are those at which the organism strongly interacts with critical or limiting resources.
- A multi-scale approach is thus required, incorporating ecological conditions at the scale of treefall gaps, slope facets, catchments, and watersheds.
- Gradient analysis of environmental tolerances, ecosystem dynamics modeling, and landscape dynamics simulation modeling all contribute components required to predict the ecological responses of forests to changing climate and disturbance
- Many of the sources of uncertainty in gradient modeling can be mitigated by addressing biotic interactions, spatial dependence, and scaling relationships with multi-scale modeling and hierarchical variance partitioning within the driver-response paradigm.
- Predictive vegetation mapping predicts vegetation composition and structure across complex landscapes using gradient models describing relationships between existing vegetation and synoptically measured predictor variables to infer vegetation composition and structure at fine spatial scales across broad landscapes.
- Integration of multi-scale gradient modeling with process-based ecosystem dynamics modeling is needed to robustly predict future vegetation conditions at fine spatial scales.
- A major limitation of gradient and ecosystem models is the difficulty of incorporating large-scale disturbance processes.
- We suggest linking stochastic landscape dynamics models with ecosystem and gradient modeling to address large-scale disturbance, such as wildfire, within the context of individualistic species responses to biophysical drivers across space and through time.
- We outline four major steps to accomplish this integration.
- The first step is multi-scale gradient modeling of vegetation responses to limiting resources and conditions.
- The second step is gradient imputation to apply gradient models to produce predictive maps of current vegetation.
- The third step is to link ecosystem dynamics models to gradient modeling and imputation.
- The final step is to link landscape dynamics simulation to ecosystem dynamics and gradient models.
- There are a number of gaps in current understanding of ecological processes that must be overcome to complete this integration.
- This document identifies these gaps and proposes a research agenda to provide the required knowledge and lead to the integration of gradient, ecosystem, and landscape models to predict vegetation dynamics over broad landscapes under changing climatic and disturbance regimes.

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Introduction

Global climate is expected to change rapidly over the next century (Thompson and others 1998, Houghton and others 2001), affecting forest ecosystems both directly by altering biophysical conditions (Neilson 1995, Neilson and Drapek 1998, Bachelet and others 2001b) and indirectly through changing disturbance regimes (Baker 1995, McKenzie and others 1996, Keane and others 1999, Dale and others 2001, He and others 2002). Changes in biophysical conditions could lead to species replacement in communities and latitudinal and altitudinal migrations. Expected increases in the size, severity, and frequency of wildfires (Mearns and others 1984, Overpeck and others 1990, Solomon and Leemans 1997, IPCC 2001) will lead to changes in vegetation structure, species composition, and diversity (Christensen 1988, McKenzie and others 2004). The changes in distributions of plant species caused by changing climate, and associated changes in disturbance regimes, may have large impacts on many aspects of ecological diversity and function (Peters and Lovejoy 1992, Miller 2003).

Natural resource managers need reliable predictions of how changing climate and disturbance regimes will affect forest ecosystems at scales from stands to regions. To that end, a synthesis of modeling efforts and empirical approaches is needed to unify understanding of forest-climate-fire relationships across a range of spatial and temporal scales. Such a synthesis must simultaneously address several challenges. First, robust prediction of forest response requires researchers to focus on mechanistic relationships among organisms, processes, and drivers at appropriate scales in space and time. Second, spatial heterogeneity and temporal disequilibrium are fundamental attributes of forest systems (Davis 1986); thus, research must adopt flexible multi-scale approaches that address transient dynamics, time lags, and site history in the context of spatially complex landscapes. Third, spatially contagious disturbance processes

(e. g., fire and insect outbreaks) introduce discontinuities and spatial dependence into the temporal dynamics of ecosystems. Furthermore, the partially stochastic nature of individual disturbances often precludes mechanistic (deterministic) modeling, thereby introducing incongruities between model paradigms that are difficult to resolve.

To understand how climatic change influences vegetation, we need to predict the effects of these changes on disturbance regimes; likewise, to predict effects of climate change on disturbance regimes, we need to understand vegetation response (Clark 1993). Only by combining multi-scale studies of disturbance regimes with analysis of vegetation responses to biophysical gradients across time and space will it be possible to understand the interactions between climate change, forest vegetation, and disturbance regimes.

Here we focus on integrating stand- and landscape-level patterns of fire with site-level responses of vegetation to biophysical gradients. The major theme of this work is the primacy of associating mechanisms with responses at appropriate scales in spatially complex and temporally varying environments (Turner 1989, Levin 1992, Schneider 1994). **In this paper, we identify key issues whose resolution will facilitate analysis of forest-climate-fire relationships.** We then review three components of integrated modeling: gradient modeling of individual species responses, ecosystem dynamics simulation, and landscape disturbance simulation. We discuss the strengths and limits of each type of analysis and propose a synthetic approach to multi-scale analysis of forest ecosystem response to disturbance mediated climatic change. We focus on forest ecosystems and plant species in this paper; however, the issues and approaches discussed will be transferable to other ecological research efforts, such as wildlife species distributions and population performance.

Key Issues

There are several key issues that must be addressed to reliably predict future vegetation composition and structure under altered climatic and disturbance regimes. For example, past changes in climate often triggered disassembly of communities. Subsequently, communities reassembled unpredictably, producing mixtures of species that are rare or absent at present (Barnosky and others 1987, Bartlein and others 1997). Typically, displacement of entire vegetation zones or communities did not occur. Instead, species responded individually to climate change according to environmental tolerance, dispersal ability, and biotic interactions (Davis 1986, McLachlan and Brubaker 1995). Because species do not respond *en masse*, predicting changes in forest composition requires species-level resolution; all hierarchical levels above the species are transient.

Accordingly, we advocate addressing issues of vegetation response to climate and disturbance regime at the level of individual species and their interactions with key resources and limiting factors. Multivariate models characterizing the responses of individual species to gradients of ecological conditions are a primary tool in this effort. These multivariate models predict the response of individual plant species and the composition of plant communities. Importantly, they avoid questionable assumptions about the reality and stability of categorical vegetation types (Gleason 1926, Whittaker 1967).

Traditional gradient modeling predicts vegetation community composition and structure in an environment composed of multiple, but stable, gradients of biophysical conditions and resources. Static species-environment models, however, do not account for the influences of temporal dynamics and spatial complexity. Thus they often leave a considerable portion of the variance in vegetation structure and composition unexplained (Franklin 1995, Guisan and Zimmerman 2000, McKenzie and others 2003). Altered disturbance regimes compound the challenge. Disturbance regimes have been sensitive to past climate change (Clark 1990a). Due to feedbacks among species responses to biophysical conditions, spatial heterogeneity in the physical environment, vegetation succession, and fluctuating climatic and disturbance regimes, forest-climate-fire relationships lack stable point equilibria (Pickett and others 1994) and are highly sensitive to contingencies of history, landscape structure (Baker 2003), and the autecologies of individual species. Thus, predicting

individualistic species responses to changing climate and disturbance regimes requires quantification of their responses to non-equilibrium and spatially complex environmental conditions. Below we identify several of these key issues and discuss how they relate to the task of integrated landscape modeling of vegetation response to changing climatic and disturbance regimes.

Species Niche Relations Along Biophysical Gradients

Ecological theory suggests that species exhibit a unimodal response to limiting resources in n-dimensional ecological space (Whittaker 1967, Austin 1985, ter Braak 1986). The volume of ecological space in which the organism can survive and reproduce defines its “environmental niche” (Hutchinson 1957, ter Braak 1986, ter Braak and Prentice 1988, Ohmann and Spies 1998, Guisan and Zimmerman 2000). Quantification of niche space at the species level is a first step toward predicting the effects of climatic change and altered disturbance regimes on forest communities.

There are three levels of niche characterization important for linking forest vegetation response to climate and disturbance regime. The occurrence niche, which describes the combination of biophysical conditions that are occupied by each species, gives the broadest measure of species-environment relationships. Species occurrence may not perfectly reflect environmental suitability, however. Ecological conditions suitable for survival are typically broader than conditions necessary for reproduction and optimal growth. Thus, two additional niche characterizations are important. The second is the growth niche. A direct measure of current biological response of a species to the environment is the association of recent “performance” (for which growth rate is a useful proxy) with biophysical gradients. This growth niche describes rate of growth as a function of biophysical gradients, adjusted for factors such as stand age, tree age, and competitive position. Mature trees, for example, may persist for centuries and continue to accrue biomass in locations that are no longer optimal due to changing climate or biological interactions. These first two niches both describe behavior and distribution of mature organisms and can be combined into a “mature” niche. A third is the regeneration niche. Regeneration often is limited to a restricted subset of conditions (Figure 1). Modeling the biophysical conditions conducive to regeneration of

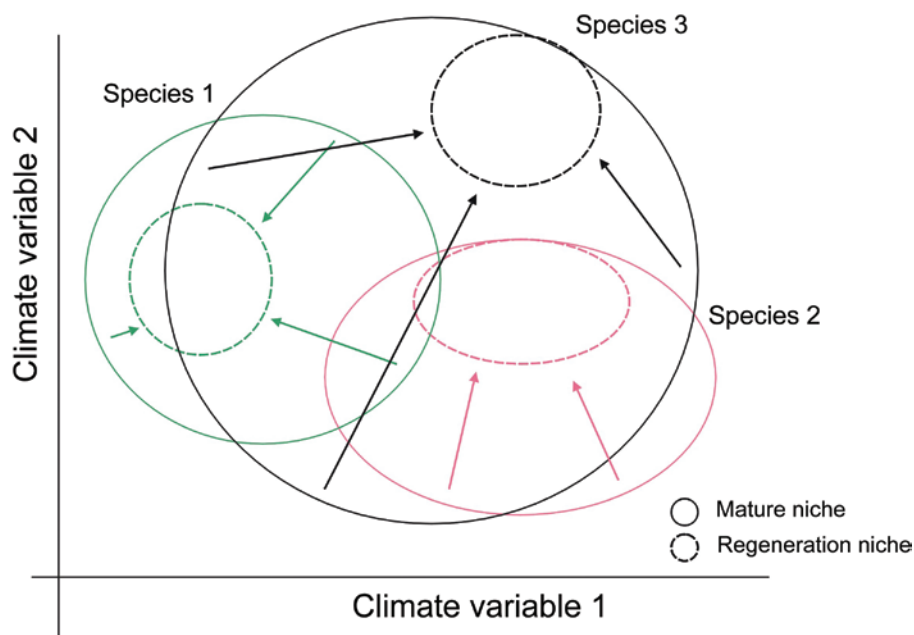


Figure 1. Hypothetical comparison of the “mature niche” (occurrence and growth) of three species with the “regeneration niche.” These three species overlap in the space of tolerable conditions once established, but not with respect to where they can initially establish.

each species is essential for projecting changes in species composition over time in response to changing climate and disturbance regimes.

These three environmental niches are described by an optimum and isoclines of tolerance in an n-dimensional environmental space. Often, the large number of factors that compose the niche can be reduced to a relative few that explain much of the variance in species responses. Multivariate gradient analysis (ter Braak and Prentice 1988) collapses environmental niche space into the few dimensions that maximize explanation of vegetation structure based on patterns of correlation between species and environmental conditions. This technique is heuristically powerful, but it can often obscure relationships between mechanism and response. Importantly, without clear linkages between cause and effect, reliable extrapolation to new conditions (e.g., warmer climate) is problematic. Therefore, it is preferable to identify *limiting factors*, which are key variables associated with species tolerance that explain substantial proportions of variance and make sense in terms of well-understood mechanisms. Gradient modeling based on limiting factors is likely to produce more interpretable predictions of species niche relationships and, most importantly, provide a robust means of predicting future responses in altered climatic and disturbance regimes.

Scale and Spatial Complexity

Biophysical gradients are clines in n-dimensional ecological space. In geographical space these gradients often form complex patterns across a range of scales. The fundamental challenge to integrating landscape

and community ecology is linking non-spatial niche relationships with the complex patterns of how environmental gradients overlay heterogeneous landscapes (Austin 1985, ter Braak and Prentice 1988, Littell and others, submitted). By establishing species optima and tolerances along environmental gradients, researchers can quantify the characteristics of each species’ environmental niche. The resulting statistical model can be used to predict the biophysical suitability of each location on a landscape for each species (Figures 2, 3). This mapping of niche suitability onto complex landscapes is the fundamental task required to predict individualistic species responses, and it is fundamentally important as a foundation for predicting effects of altered climate and disturbance regimes.

Spatial and temporal complexity

High levels of spatial and temporal variability are typically found in forest ecosystems systems. For example, site-level variation in air and ground temperatures, moisture, and nutrients are often high (Swanson and others 1988). This variability in environmental conditions strongly affects the distributions and abundances of plant species and the structure of plant communities across the landscape (Whittaker 1956, Swanson and others 1988, Bunn and others 2005a). Landform explains a large proportion of variability in successional pathways, even in areas having relatively little topographic relief (Host and others 1987) or biomass (Host and others 1988). The spatial structure of landscapes also has a major influence on the type, extent, severity, and frequency of disturbance events. Landforms and landscape structure affect the frequency and spatial pattern of natural

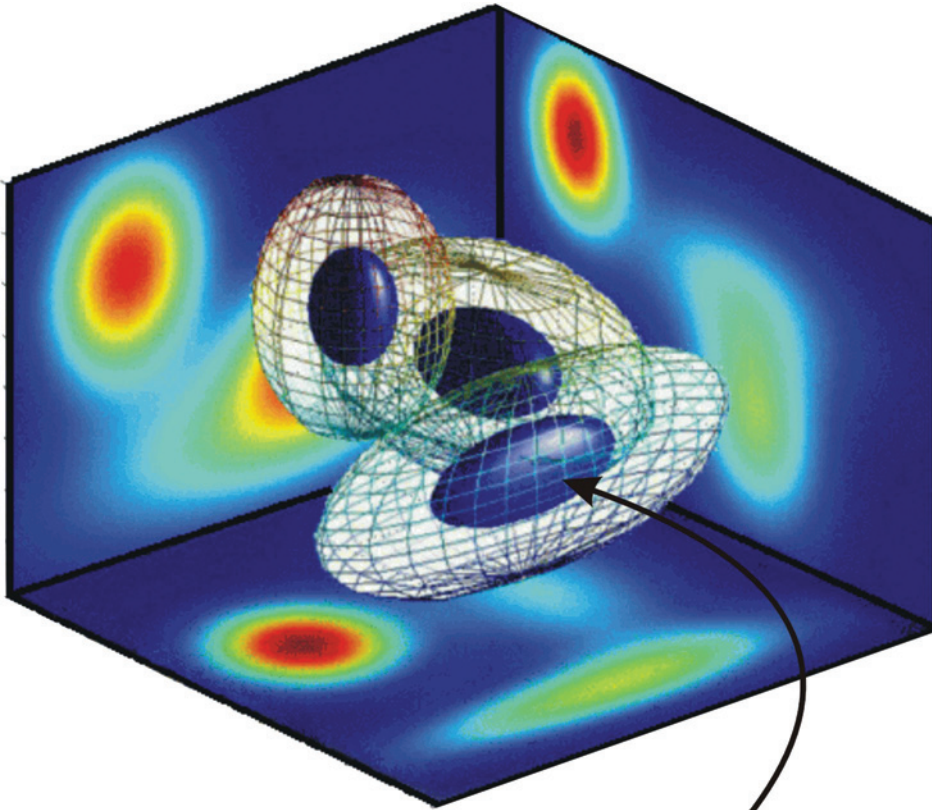
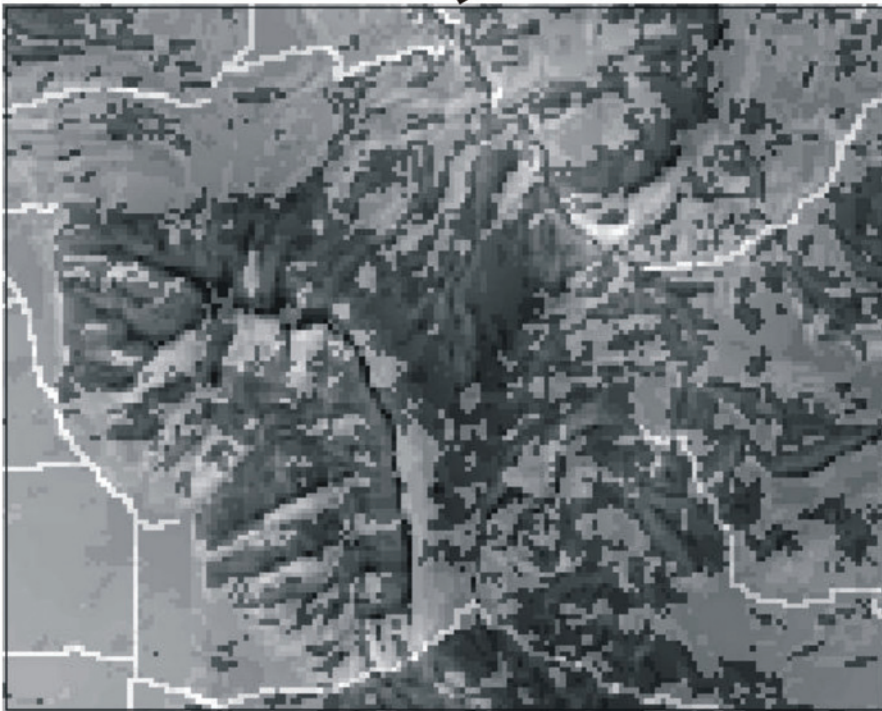
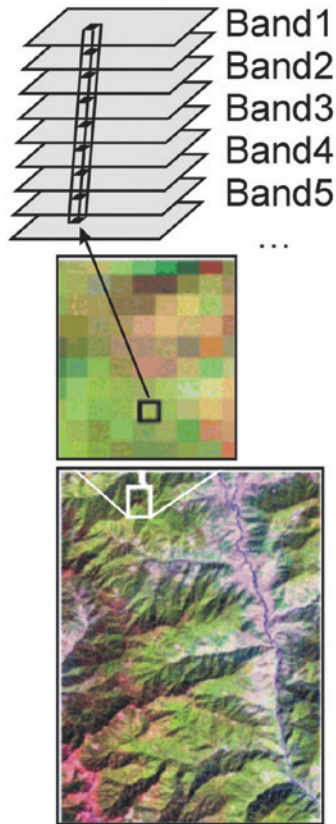


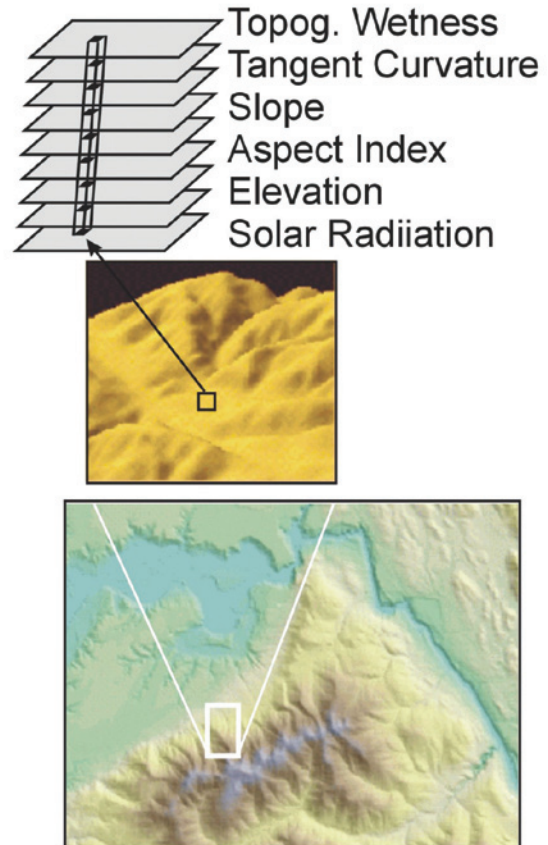
Figure 2. Organisms are influenced by multiple factors simultaneously. In this example, the tolerances of three species are mapped (top) in a 3D environmental space. The lower map shows the suitability of each cell in 2D geographic space for one of the species as a function of the three factors. Rigorously quantifying organism niches in ecological space is essential for predicting their distribution across landscapes. This linkage allows mapping of suitable conditions for each species.



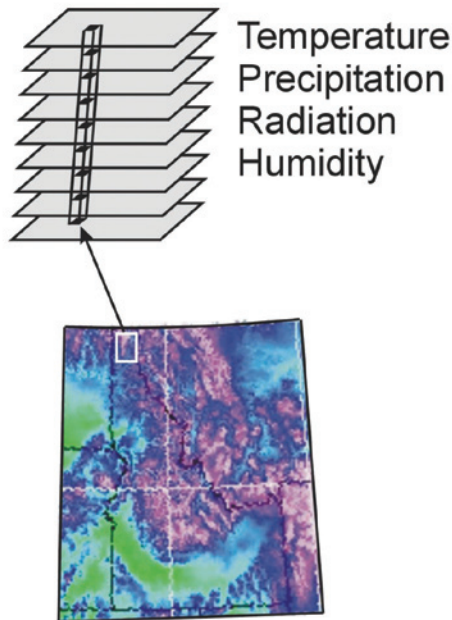
RS Image Bands



Topographical Indices



DAYMET Data



Disturbance / Geology

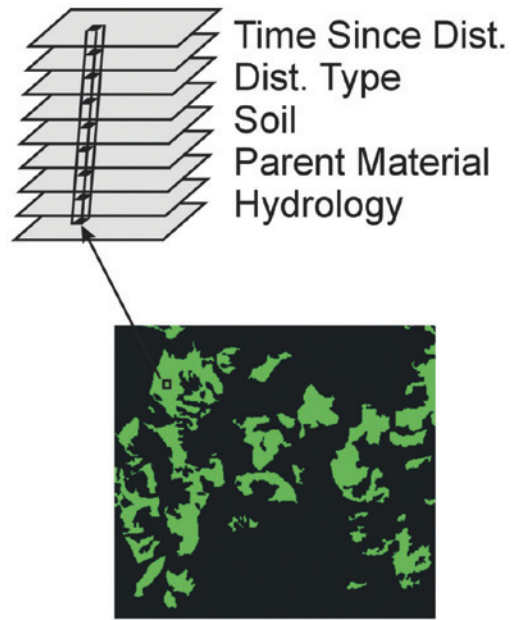


Figure 3. Predictor variables for gradient modeling are measured in the field or extracted from topographical, climatological, and remotely sensed data. For gradient models that are robust to climatic change, we eschew surrogate variables that are unchanging in ecological time in favor of those that reflect responses of the landscape to climatic variability. Examples of the latter are the 1-km DAYMET data (lower left) and modeled output such as soil moisture, evapotranspiration, and water balances (Thornton and others 1998, Wigmosta and others 1998, McKenzie and others 2003).

disturbances such as fire, wind, or bark beetle outbreaks. For example, in Labrador, fire and topography jointly influenced vegetation patterns (Foster and King 1986). Similarly, both topographic position and fire history contribute to susceptibility to wind damage (Foster and Boose 1992, Boose and others 1994, Kulakowski and Veblen 2002). Landscape context, i.e., patterns of local landforms, geomorphic processes, and existing biotic communities, influences both dispersal and biotic interactions (Host and others 1988, Swanson and others 1988, Bunn and others 2005b). Details of the spatial and temporal structure of forest ecosystems are important at a range of scales, but especially those that constitute the organisms' "operational environment" (Spomer 1973) where individual organisms directly interact with local topography and microclimate (Bunn and others 2003, 2005b), respond to successional dynamics, and experience disturbance (Whittaker 1967, Tilman 1982, Levin 1992, Schneider 1994).

Scale

There is no single correct scale of analysis for forest ecology. The fundamental unit of ecological analysis is the organism (Schneider 1994) and fundamental scales are those at which the organism strongly interacts with critical or limiting resources in its environment. Each species will respond to factors across a range of scales in space and time based on its life history strategy and ecological adaptations (Ball and Gimblett 1992, Ettl and Peterson 1995, Peterson and Peterson 2001). Ecological responses to biophysical gradients must be quantified at scales that match the biological interactions of individual organisms. Analyses at inappropriate scales risk missing or misconstruing relationships between mechanisms and responses (Wiens 1989, Cushman and McGarigal 2003). Biophysical conditions directly experienced by individual trees, for example, occur at the scale of treefall gaps, slope facets, or stands. Site-level conditions are necessary, but not sufficient, to explain current vegetation or predict future changes due to disturbances, species movements, and succession. While the scale of direct species-environment interactions is fundamental to understanding and prediction, one must also address the influences of landscape context, including landform, vegetation, and climate on ecosystem patterns and processes. Accounting for multiple interactions across ranges of spatial and temporal scales is the fundamental challenge to understanding relationships between forests, climate, and disturbance regimes (Levin 1992, Turner and others 2003). Thus, studies of relationships between forest communities, climate, and disturbance regimes should use multi-scale approaches that are directly tied to the dominant scales of organism interaction with the

environment. Where data allow, it is advantageous to quantitatively measure the relationships among driving factors across a range of scales simultaneously to identify these dominant scales and quantify interaction of factors across scale (e.g., Cushman and McGarigal 2003). Ideally, ecological analysis will therefore not be between hierarchical "levels," such as *populations*, *communities*, or *ecosystems*, but instead will focus on relationships among organisms and driving processes across continuous ranges of scale (Levin 1992, Littel and others, submitted).

Non-Equilibrium Dynamics and Disturbance

Disturbance is central to forest landscape dynamics (Cooper 1913, Leopold 1933, Watt 1947, Reiners and Lang 1979, Turner and others 2003). Many ecosystems are inherently non-equilibrial or depend on disturbances to maintain community structure and ecosystem function (White 1979, Mooney and Godron 1983, Sousa 1984, Glenn and Collins 1992, Collins and others 1998). Linking niche relationships of forest trees to current and future vegetation at the local and landscape levels is complicated by changing biophysical conditions through time, species invasion and succession, and the legacy of past disturbances (Peet and Loucks 1977, Pickett 1980). Older stand elements originated in a possibly quite different environment, creating a legacy of species composition and forest structure that may not be in equilibrium with current biophysical conditions or disturbance regimes (Baker 2003). In a changing climate, the plant communities established after disturbance may differ from those present at the time of disturbance. Mature trees usually tolerate short-term climatic fluctuations, and species best adapted to current climate may colonize only following disturbance (Dunwiddie 1986). Thus, adjustment of forest composition to climatic change may take centuries (Campbell and McAndrews 1993). Therefore, community composition and structure in older forests likely reflect a long sequence of climatic conditions and disturbances no longer present in the landscape (Baker 2003). If so, current biophysical conditions and disturbance regime will not fully explain existing forest structure (Clark 1990b).

Recovery following disturbance is sensitive to spatial patterns created by the disturbance and is influenced by biological legacies. The ecological characteristics of individual species play a key role in determining the biological effects of a disturbance and the nature of the following recovery (Connell and Slatyer 1977, Noble and Slatyer 1980, Peet and Christensen 1980, Pickett and others 1987, Halpern 1988). Species responses vary

depending on the kind and severity of a disturbance and its broader spatial and temporal context (Finegan 1984, Glenn and Collins 1992). Species life-history characteristics determine what the effects of disturbance size, heterogeneity, and distance from undisturbed sites may have on recolonization and subsequent succession (Denslow 1980, Hartshorn 1980, Miller 1982, Malanson 1984, Turner 1989, Peterson and Carson 1996). Ultimately, successional patterns of vegetation are constrained by the availability of seeds, which depends on species traits, plant health, long- and short-term weather, distance to seed source, and predation (Eis and Craigdallie 1983, Nepstad and others 1990, Johnson 1992, Aide and Cavelier 1994, da Silva and others 1996, He and Mladenoff 1999b).

Vegetation communities do not adjust immediately to altered disturbance regimes (Baker 1995). For example, the extent to which landscape heterogeneity controls fire spread determines the time required to fully burn through a landscape and reset both disturbance regime and succession (Givnish 1981, Foster 1983, Foster and King 1986, Baker 2003). Baker (1995) argued that the time required for fire regimes to adjust to climatic change may often exceed the time that climate is stable, creating a perpetual temporal disequilibrium between climate, fire regimes, fuel loads, and forest structure. If climate changes gradually in a directional way, then the fire regime will be perpetually adjusting to the new climate, constrained by the legacy of fuel loads and forest structures (Baker 1995, 2003).

Integrating Biophysical Niche Relationships With Disturbance Regimes

Biophysical niche relationships are inextricably linked to landscape disturbance. For example, although the ultimate cause of post-glacial vegetation change in the Pacific Northwest was climate, the proximate cause was altered fire regime (Cwynar 1987, Prichard 2003). A small change to a drier climate probably triggered a significant increase in fire frequency, allowing colonization by fire-adapted species (Cwynar 1987).

Existing vegetation and underlying biophysical gradients influence ecological processes across a

broad range of scales, from interactions of individual organisms with their operational environment to dynamics of landscape structure associated with climate, fire regime, and subsequent succession. The key to understanding and predicting these multi-scale dynamics across space and time lies in the responses of individual organisms to climate, other species, and disturbance across a range of spatial and temporal scales (Rowe 1981, Woodward 1987, 1988, Woodward and others 2004). We submit that the analysis of these dynamics has three parts. First, we require mechanistic understanding of the key drivers that limit occurrence, growth, and regeneration. Second, we need to explain current spatial patterns of distribution, growth, and regeneration across complex landscapes. Third, we need to understand how landscape spatial *processes*, i.e., disturbance and dispersal, condition these drivers, thereby modifying said *patterns*.

Recent research has provided substantial insight into this challenging task. In the following sections we review several major research approaches in the context of integrated vegetation modeling. Gradient analysis of niche relationships, ecosystems dynamics modeling, fire behavior and effects modeling, fire history research, landscape dynamics modeling, and global circulation modeling of climate have all contributed greatly. None of these approaches in itself is sufficient, however, to provide rigorous understanding or robust prediction of forest-climate-fire interactions. Below we suggest how progress might be made by integrating methods associated with several of these lines of research. Incorporating site history and environmental gradients into models of occurrence, growth, and regeneration provides a means to mechanistically understand and predict forest community dynamics at scales from stands to landscapes. The data-rich models arising from this integration can populate key parameters in process-based, ecosystem dynamics models. Finally, linking both types of models to spatially explicit simulations of alternative disturbance regimes provides a means to incorporate the influence of non-equilibrium conditions. This suite of models, properly integrated, can provide a coherent and practical approach for estimating the likely effects of climate change on forest ecosystems.

Review of Research Approaches

The Biophysical Niche and Gradient Modeling

All species occur in a characteristic, limited range of biophysical conditions. Within that range, a species will tend to be most abundant and have the highest growth and reproductive rates towards the center. A species not only requires a certain minimum amount of each resource but also cannot tolerate more than a certain maximum amount (Shelford 1931, Schwerdtfeger 1977). Therefore, each species performs best near an optimum (modal) value of a necessary environmental variable and cannot survive when the value diverges beyond its tolerance (Shelford 1931, Schwerdtfeger 1977). The relationships between a species performance and gradients of critical resources and conditions describe its fundamental niche (Hutchinson 1957). The composition of biotic communities changes along biophysical gradients because of how the niche relationships of the constituent species interact with the spatial structure of the environment and competing species (Hutchinson 1957, Whittaker 1967, Tilman 1982, Austin 1985). Species replacements occur as a function of variation in the environment (ter Braak and Prentice 1988) or with successional time (Pickett 1980, Peet and Loucks 1977).

When data are collected over a sufficient range of environmental conditions, species occurrence, abundance, and regeneration success will change nonlinearly along environmental gradients (Whittaker 1967, ter Braak 1986). It is therefore inappropriate to evaluate niche space using standard statistical methods that assume linear responses. The Gaussian response distribution has received most attention as a model for species responses to environmental gradients (ter Braak 1986). When species are measured along gradients of environmental variables that are critical and limiting, unimodal responses should be seen that are approximated by the Gaussian distribution (Guisan and Zimmerman 2000, Austin 2002).

Many studies have reported non-Gaussian responses of vegetation to environmental gradients (Mueller-Dombois and Ellenberg 1974, Austin and Cunningham 1981, Austin 1987). In many cases the measured environmental variables are not critical or limiting factors. In other cases, critical factors may be measured, but at incorrect scales that distort their relationship with species response. In such cases, species responses may appear to follow complex, multimodal patterns that cannot be modeled with the Gaussian distribution.

There are two general kinds of models used to evaluate species-environment relationships along environmental gradients (Table 1). In the first, the Pattern Matching Paradigm (PMP), the focus is on developing the most successful predictions of current patterns, rather than providing explanations for observed responses or means to predict future changes (e.g., Moisen and Frescino 2002). In the second, the Driver Response Paradigm (DRP), prior knowledge or preliminary modeling is used to identify critical and limiting environmental gradients and proper spatial and temporal scales for the modeling effort (e.g., McKenzie and others 2003). This second approach directly links species responses to driving mechanisms at appropriate scales, providing the strongest explanations of current conditions and predictions of expected future changes. There are advantages and disadvantages of both kinds of modeling, discussed below (Figure 4).

Pattern Matching Paradigm (PMP)

In PMP, the goal is to describe the strongest empirical correlations between measured vegetation conditions and a suite of independent variables describing aspects of the environment thought to be related to species occurrence or performance. A common objective is to produce maps of current vegetation composition and structure across broad geographical areas, rather than to explain

Table 1. Classification of biophysical modeling approaches. Machine-learning methods often have superior explanatory power or classification accuracy for pattern matching, whereas parametric models are more robust and appropriate for driver-response relationships.

	Predictor variables	
Statistical method	Pattern matching (Elevation, geographic coordinates, satellite spectra)	Driver-response (climate & climate-derived variables, biotic factors)

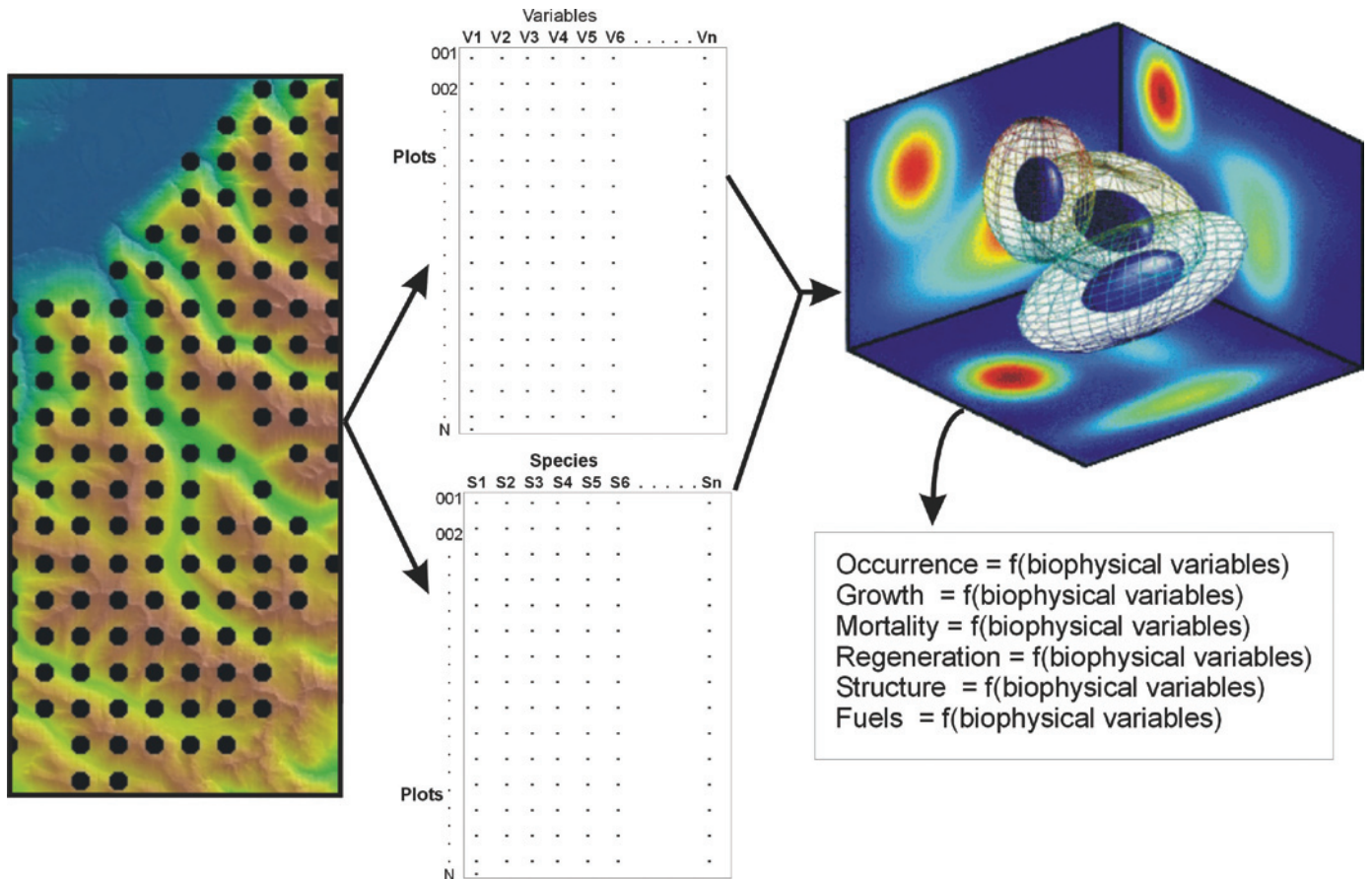


Figure 4. Whatever statistical modeling method is employed, there are three general steps in conducting biophysical gradient modeling. First, a large and representative sample of plots must be sampled for both vegetation response variables and biophysical driver variables. Second, these samples are compiled into matrices recording patterns of vegetation among plots and biophysical variables among plots. Third, these matrices, or selected vectors within them, are analyzed with canonical ordination or regression approaches to predict the realized niche structure and functional response of the vegetation variables to biophysical variables at multiple spatial scales. These models produce functions describing the quantitative relationships between response variables and biophysical variables, and provide parameters for modeling ecosystem dynamics and landscape disturbance. They also provide the relationship space for imputation.

observed patterns on the basis of relationships between environmental drivers and species responses.

A variety of methods have been used in this kind of modeling, including gradient modeling and machine-learning or expert-system methods (Frescino and others 2001, Moisen and Frescino 2002, Ohmann and Gregory 2002, Olden and Jackson 2002). Generalized additive models (GAMs—Hastie and Tibshirani 1986), that include non-parametric terms to extend the generalized linear model, have often proven quite effective in predicting current vegetation (Moisen and Edwards 1999, Frescino and others 2001, Moisen and Frescino 2002). Classification and regression trees (CART) use binary recursive partitioning to divide the data into branches that maximize the relationship between predictor and response variables (Morgan and Sonquist 1963, Breiman and others 1984). CART was one of the least successful of the five modeling techniques compared by Moisen

and Frescino (2002) for predicting forest composition and structure. This may be because CART imposes a categorical model structure on continuous gradient responses. Predicted responses for new observations in CART are limited by its hierarchical structure to those already estimated by the original model (Clark and Pregibon 1992). Multivariate adaptive regression splines (MARS; Friedman 1991) generalize the piecewise categorical functions of CART into continuous functions by fitting multivariate splines and matching the values at the boundaries of the regions. MARS and GAM were the most successful methods tested by Moisen and Frescino (2002).

A recent implementation of a genetic algorithm—the Genetic Algorithm for Rule-set Prediction (GARP—Stockwell and Peters 1999)—has proven successful in modeling the ecological niches of both plant and animal species across a wide range of ecosystems (Peterson

and others 1999, Anderson and others 2003, Oberhauser and Peterson, 2003). GARP generates a set of rules for predicting presence or absence, each of which applies to a portion of the data. Some of these rules (“logit” rules) are rule-based analogues to logistic regression, whereas others determine presence or absence of a species based on ranges of predictors or on whether one or more predictors takes on a unique value or values. In contrast to classical models, not all rules apply to every data point. For a full description of the GARP algorithm, see Stockwell and Noble (1992) or Stockwell and Peters (1999).

Such flexible non-parametric or machine-learning statistical methods can optimize the fit of one pattern to another, providing a means of producing predictions across broad spatial extents, but they have limited ability to distinguish drivers and responses and are vulnerable to overfitting (Venables and Ripley 2002). Such fine-scale model fitting may offer high performance for predicting within a single data set but is less successful in 1) identifying the form of underlying mechanistic relationships, 2) extrapolating or interpolating beyond the samples, or 3) making predictions for the future under altered conditions. Thus, while pattern-fitting approaches equal or exceed parametric models in prediction accuracy, they are more difficult to interpret with respect to limiting factors, are less parsimonious in variable selection, and often are computationally expensive (Stockwell and Peters 1999, McKenzie unpubl. data¹). Further, they often perform better in simulation studies than with real data, giving a false sense of accuracy and robustness to extrapolation (Moisen and Frescino 2002). The strengths of PMP are for prediction within a given time and space; the lack of mechanistic underpinnings is far less critical for interpolation than for extrapolation, and the flexibility of the algorithms allows precise fit to specific data sets. However, evaluating the effects of future climates on a forested landscape or applying models developed in one area to produce predictions in another are clearly extrapolative in nature, and PMP is likely to produce erratic results when used in this context.

The Driver-Response Paradigm (DRP)

DRP seeks to identify limiting factors and the functional relationships between these limiting factors and vegetation responses using gradient modeling (Figure 5). By focusing on limiting factors it is possible to interpret

species-environment relationships with more confidence than is possible using PMP. Importantly, gradient modeling is better grounded in ecological theory than more complex approaches using machine-learning techniques (ter Braak and Prentice 1988). Parametric gradient models also provide better discrimination among the niches of closely related species (Doebell and Dieckmann 2003) and are more amenable to multi-scale and hierarchical analysis (Cushman and McGarigal 2003) than non-parametric or machine learning approaches. Finally, in the integrated modeling environment we propose below, clearly defined species responses to biophysical gradients are essential because they are used to specify parameters in ecosystem models. We therefore propose a combined approach that nests mechanistic biophysical modeling of limiting factors within a more general gradient modeling framework (Figure 3). Multi-scale, hierarchical gradient modeling facilitates both mechanistic understanding and robust extrapolation for landscape mapping.

DRP gradient modeling and limiting resources

There are three major challenges to obtaining suitable predictor variables for parametric DRP gradient modeling. First, one must identify the key factors that govern the responses of each species across space, time, and biophysical conditions. Second, one must be able to obtain accurate measurements of these factors, or appropriate surrogates, for a large number of sample locations distributed across a representative combination of biophysical conditions in broad landscapes. Third, these measurements must be made at the scales at which the species is most strongly responding to the limiting factor; measurements at other scales may not produce clear or consistent predictions (Wiens 1989).

Examples of key limiting resources are energy and water. Energy and water limitations interact to affect water balance at the level of sites and individual organisms (Stephenson 1990, 1998). Indeed, water balance is a key variable in both ecosystem simulation models (Neilson 1995) and empirical gradient models, though indirectly in the latter via energy and water variables. Hawkins and others (2003) suggest that energy and water balances and their interactions globally affect species distributions and patterns of species richness. Milne and others (2002) used terrain modeling to quantify a threshold between energy-limited and water-limited ecosystems in the Interior Columbia River Basin. Much of the biophysical gradient modeling heretofore accomplished, including that of Milne and others (2002), was either in clearly water-limited systems—e.g., arid mountains or shrublands—or in extreme environments in which biotic interactions are less important than abiotic

¹ Unpublished manuscript on file at Pacific Wildland Fire Sciences Lab, Seattle, WA.

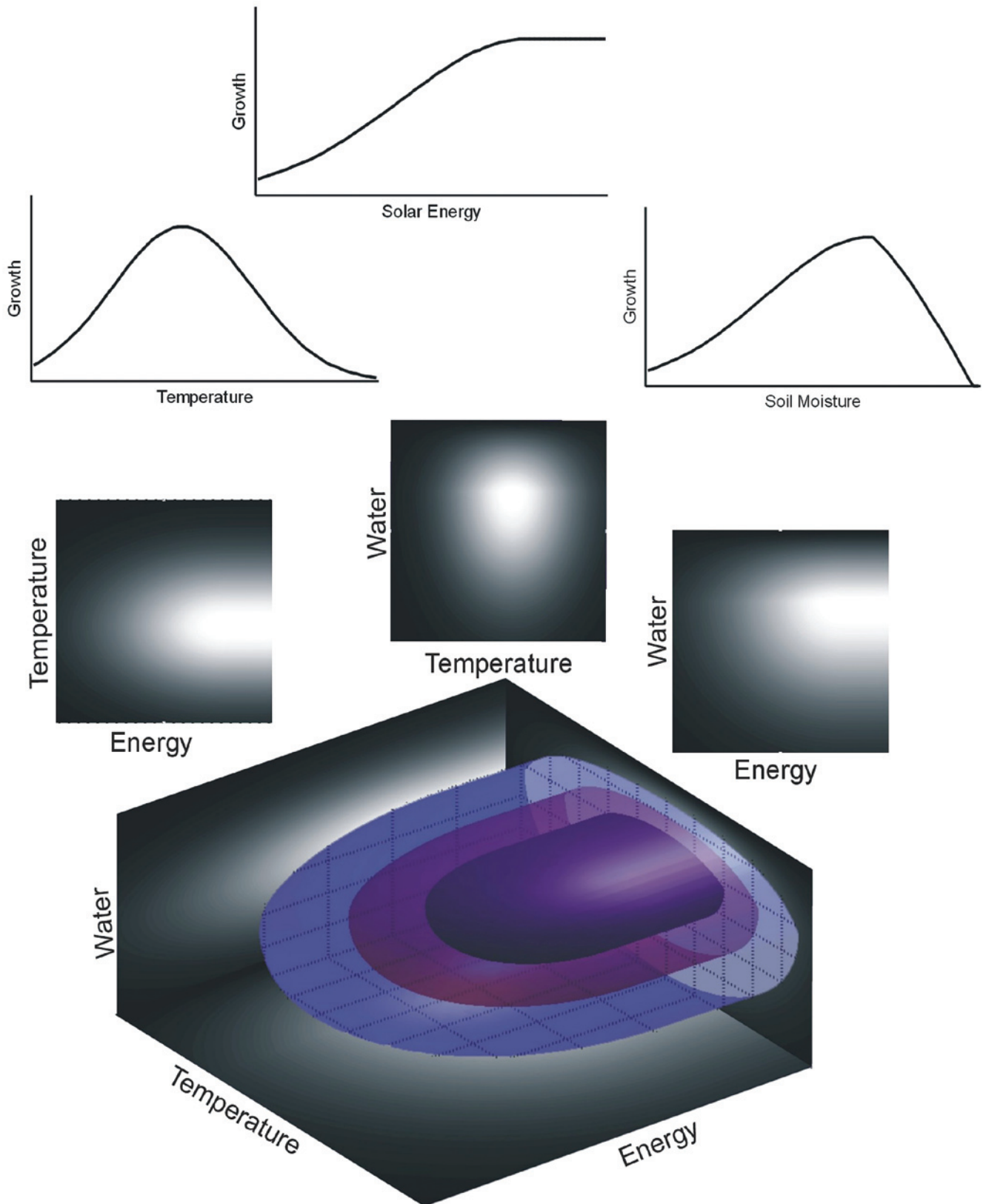


Figure 5. The strongest inferences about causality and the most robust predictions to new locations or future conditions are obtained from modeling the occurrence or performance of each species along gradients of limiting biophysical variables. In this example, the limiting biophysical variables are water, temperature, and energy and the response variable is annual growth. Each species will have unique response curves along each of these critical resource gradients. Response curves for a hypothetical species are shown at the top. The bivariate response surfaces for each pair of these resources are shown in the middle, and the trivariate response volume is shown at the bottom. In the response volume, the outer blue shell represents a 25% of maximum growth isocline, the purple shell a 50% of maximum, and the inner lavender shell 75% of maximum growth rate. By modeling species responses directly on limiting biophysical variables, one can link mechanistic relationships between driving variables and biotic responses directly.

limiting factors (Austin and others 1994, Franklin 1998, Bolliger and others 2000a, McKenzie and others 2003). Correlations between individual species responses and moisture may, in many other systems, be more difficult to identify due to the confounding effects of biotic interactions (i.e., competition—McKenzie and others 2003), or may be correlated with other controlling factors. For example, Peterson and Peterson (2001) found that spring snowpack clearly limited growth of mountain hemlock (*Tsuga mertensiana*) in the upper elevations of its range in the Pacific Northwest, but at drier lower elevations growth was limited by moisture deficits. At high elevations, abundant moisture in the form of snow was correlated with reduced light and temperature leading to differential responses to moisture with changing elevation. Biotic interactions and correlations with other limiting factors can cause the effects of any limiting factors to be increased or decreased under climatic change, and within a specific species may differ across its range. In general, however, unimodal response functions identify limiting factors at both ends of a species' range, if sampled gradients are broad enough to span all or most of that range.

Once the key limiting factors are identified it is essential to obtain accurate measurements or predictions of these factors for each sample plot. This usually will require measurements or estimates of each driving variable at hundreds to thousands of individual locations across complex landscapes for which existing vegetation and disturbance history are also quantified. The challenge is obtaining direct measurements of climatic and edaphic variables for such large and dispersed grids of sample plots. A combination of approaches, including networks of sensor stations placed on the sample grid and spatial modeling relationships between terrain and climatic conditions, will provide the most reliable inferences. In the research agenda section at the end of this document we identify several alternative approaches for obtaining these key independent variables for large and dispersed sample grids across complex landscapes. Once these driving variables have been obtained for all sample plots, the next main consideration is what approach to use for gradient modeling. In this regard there are two major alternatives, univariate and multivariate gradient modeling.

Univariate and Multivariate Approaches to Gradient Modeling

Parametric gradient models of species-environment relationships can be fit in both univariate and multivariate frameworks. Individual species responses to environmental gradients can be quantified using generalized linear models by specifying polynomial or other

nonlinear terms in the linear predictor (Forsythe and Loucks 1972, McCullagh and Nelder 1989, Guisan and others 2002). Lenihan (1993) fit two- and three-dimensional response surfaces to boreal tree species distributions using logistic regression and biophysical variables (snowfall, degree days, minimum temperature, soil moisture deficit, and evapotranspiration). Austin and others (1994) successfully modeled Australian vegetation by modeling unimodal response with a right-skewed beta function. Bolliger and others (2000b), modeling subalpine species in Switzerland, and McKenzie and others (2003), modeling conifer species in the Pacific Northwest, USA, identified *proxy sets* of predictor variables (Booth and others 1994), grouping variables associated with expected limiting factors of energy (mean temperature, growing degree days, soil temperature, etc.) and moisture (precipitation, snowfall, soil moisture, etc.). Only one variable from each set was allowed as a predictor, reducing collinearity and clarifying potential limits to growth or distribution. McKenzie and others (2003) also fit unimodal response curves successfully for the majority of species tested.

When the number of species is large, it may be impractical to conduct separate analyses for each. It is also challenging to combine separate analyses to quantify species interactions and niche separation, particularly when there are more than 2-3 environmental variables. Additionally, regression is often limited in studying vegetation responses to biophysical gradients because vegetation data contain many zeros, violating the assumption of normal error distribution implicit in many regression techniques. In addition, environmental variables are often highly correlated, violating assumptions of independent predictor variables implicit in most regression approaches. These challenges can be most readily addressed in a multivariate context.

In a multivariate context, canonical ordination (ter Braak 1986, ter Braak and Prentice 1988, Palmer 1993) uses a heuristic mathematical approximation to a Gaussian response curve, applied simultaneously to each species. Canonical ordination is unaffected by zero values in the species data and is quite robust to inter-correlation among predictors (Palmer 1993). Thus, if species react to the same linear combinations of environmental variables according to a common response model, canonical ordination is an attractive alternative to individual regression models (ter Braak and Prentice 1988).

The decision whether to use constrained ordination or a series of separate regressions depends on if there is an advantage to analyzing all species simultaneously (ter Braak and Prentice 1988). Constrained ordination

assumes that species react to the same biophysical gradients, while, in regression, a separate composite gradient is constructed for each species. Regression, therefore, allows more detailed and accurate prediction and calibration. Single-species models often yield better predictions than a multi-species model for the same species (Guisan and others 1999). However, single-species regressions lose information about the co-occurrence of multiple species within samples (Gottfried and others 1998), whereas constrained ordination makes use of this information in the weighted averaging algorithm (Ohmann and Gregory 2002). Also, multi-species constrained ordination ensures that predicted plant communities are realistic assemblages of species and structures. If all species distributions were modeled independently and then assembled into communities, it is likely that unrealistic collections of species would be predicted (Moeur and Stage 1995).

Uncertainties in Gradient Modeling

Despite their theoretical and practical advantages, past applications of gradient modeling have usually left a substantial proportion of the variance in species abundance or occurrence unexplained (e.g., Ohmann and Gregory 2002, McKenzie and others 2003). We identify three types of error associated with gradient models. The first two are partially avoidable within the paradigm, whereas the third is intrinsic to the paradigm and necessitates integration with other paradigms:

1. Technical issues requiring better quality control and minimization of error.
 - a) *Model assumptions are inappropriate for the covariance structure within the data.* Lack of fit appears in strongly patterned residuals or unequal variances, particularly at the ends of ranges (Littell and others, submitted).
 - b) *Response or predictors or both not accurately measured.* This is likely, for example, when data-poor extrapolations are made to unsampled sites, when predictor variables are assumed to be homogeneous across complex terrain, or when questionable allometry is used to calculate response variables.
2. Limitations partially resolvable within the paradigm. Addressing the first two of these requires coupled models within the paradigm. Addressing the second two requires some additional creative thinking about driver-response vs. pattern matching methods. We take up these topics up later in this section.
 - a) *Biotic interactions are not considered.* For example, in energy-limited systems with high biomass and

productivity, such as mesic low-elevation forests, the majority of trees are buffered from the “true” biophysical environment but limited by competition for scarce resources (energy, e.g., light) by more dominant individuals.

- b) *Spatial dependence is not considered.* This is not a problem in the mechanism-response relation per se, but a question of adding another statistical coupling to take advantage of knowing true degrees of freedom and weighting observations accordingly.
- c) *The use of surrogate variables* leads to imperfect coupling of driver and response (Figure 6). Much past gradient modeling has been based on correlating patterns of species in the environment to spectral, topographic, or other spatial variables. These predictor variables are not themselves actors on the organisms. Organisms respond to limiting resources that may vary in correlation with these surrogates, but not to these surrogates themselves. In complex environments, it is common that the surrogate relationship between organism responses and these proxy variables is non-stationary across space, time, and biophysical context. This increases model imprecision and can lead to spatial bias. It also prevents mechanistic understanding of relationships between species and the limiting resources that actually drive their responses. Reliable understanding and prediction requires that the variables that govern species response must be directly measured and associated with organism performance.
- d) *A scale mismatch* between the action of the driving variable, the response of the organism and the scales at which the variable and the organism are measured obscures or distorts the nature of the species-environment relationship (Figure 7). The response of organisms to driving variables will be expressed over a limited range of scales. Incorrect scale of measurement of the driving variable or the organism responses may lead to incorrect conclusions about the importance and nature of the relationship between that factor and that organism (Wiens 1989). Scaling issues pertain to both response and predictor variables. Often, the response variable is predicted at a different scale than it was measured, requiring data aggregation that is a source of substantial error (Rastetter and others 1992). Increasing spatial scale in prediction can be achieved through spatial imputation of results at the native grain (see Imputation section below), which maintains the scaling relationships

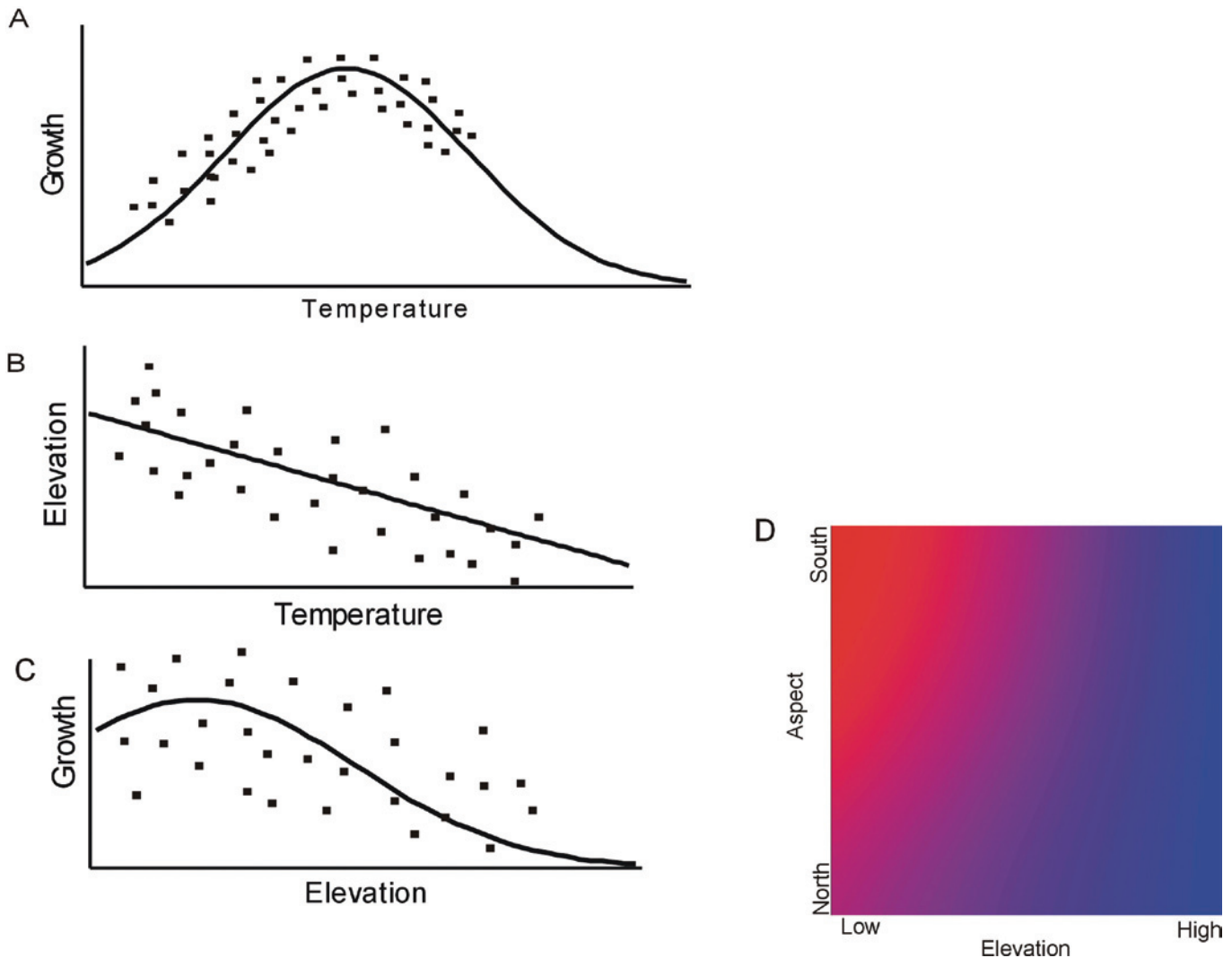
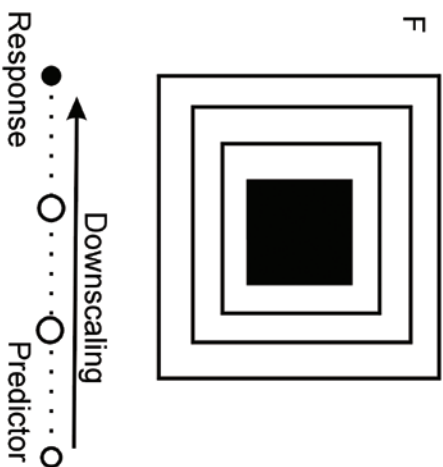
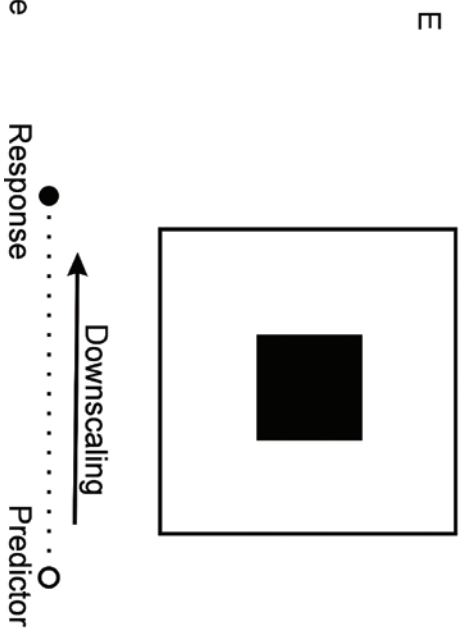
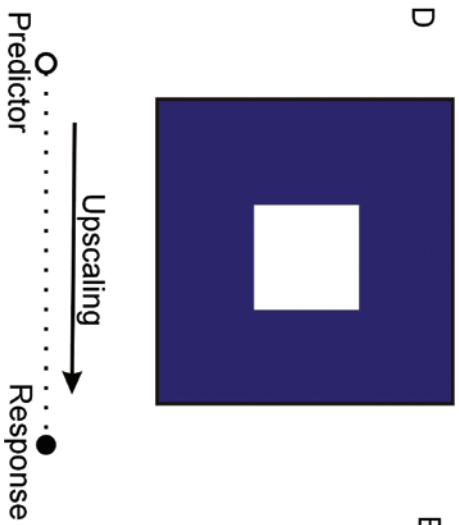
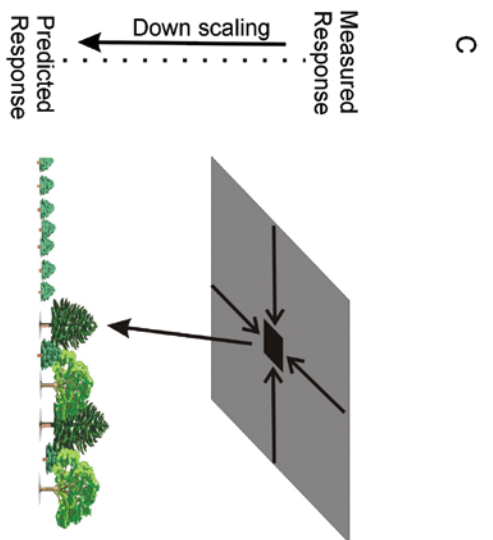
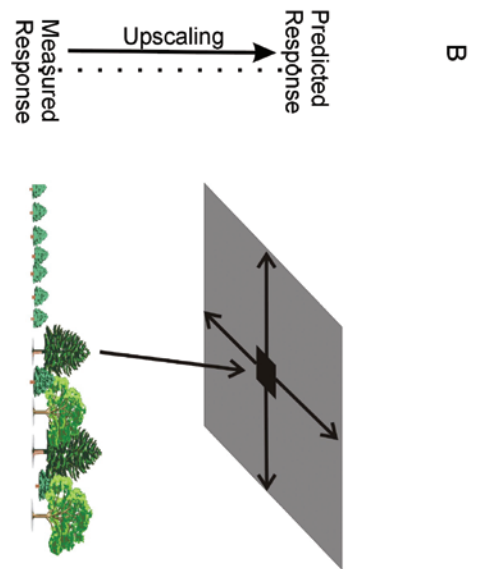
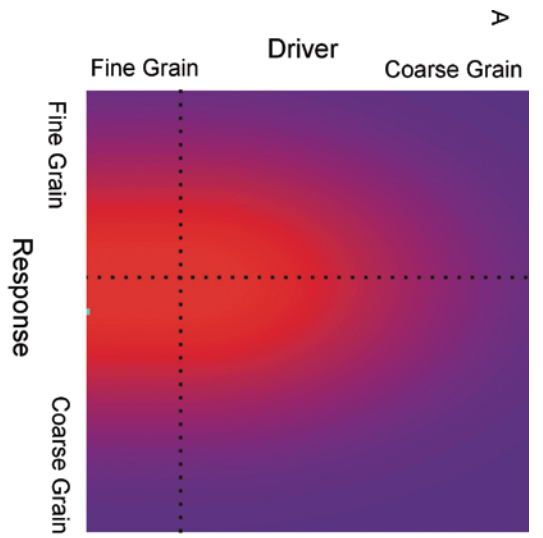


Figure 6. A. Relationships between biological responses and limiting biophysical variables usually have high predictive power and low residual deviance. B. In contrast, relationships between limiting biophysical variables and spatial surrogates, such as elevation for temperature, usually have somewhat weaker relationships and higher residual deviance. C. Relationships between the surrogate and the biological response compounds the imprecision in both A and B, resulting in weaker relationships with high residual deviance. There are many factors that influence temperature regimes across complex landscapes in addition to elevation. D. For example, elevation and aspect interact to influence local temperature regime. The interaction of several factors results in low predictive power for any particular surrogate variable.

Figure 7. The strength and nature of relationship observed between a response variable and a predictor variable will change as functions of the scale of each (A). Scaling response variables is problematic and requires either upscaling (e.g., plot-level vegetation response to predicted landscape-level aggregate properties) (B), or downscaling (e.g., 1-km scale measured response data to plot-level predicted response) (C). These extrapolations require information at multiple scales. Forest plots are rarely nested across a broad range of scales, for example. The errors associated with scaling response variables are avoided by making predictions at the same grain at which response variables were measured. Spatial scope can then be achieved by imputing model predictions across large spatial extents at the native grain of the response variable (see Imputation section). Scaling predictor variables, in contrast, is an essential task in modeling species-environment relationships. The grain at which environmental data are most strongly related to the response of the dependent variable may be finer (D) or coarser (E) than the grain of the response variable. Haphazard selection of scales of variables leads to equivocal conclusions. Ideally, the grain of the response variable should be fixed at an appropriate level and modeled across spatial and temporal extents (F). The predictor variables ideally would be measured at the finest possible grain over the largest possible extent. Partial bivariate scaling (Figure 7F and Figure 9) could then be used to identify the neighborhood extent around sampling units at which the predictor variable has the strongest relationship with the response variable.



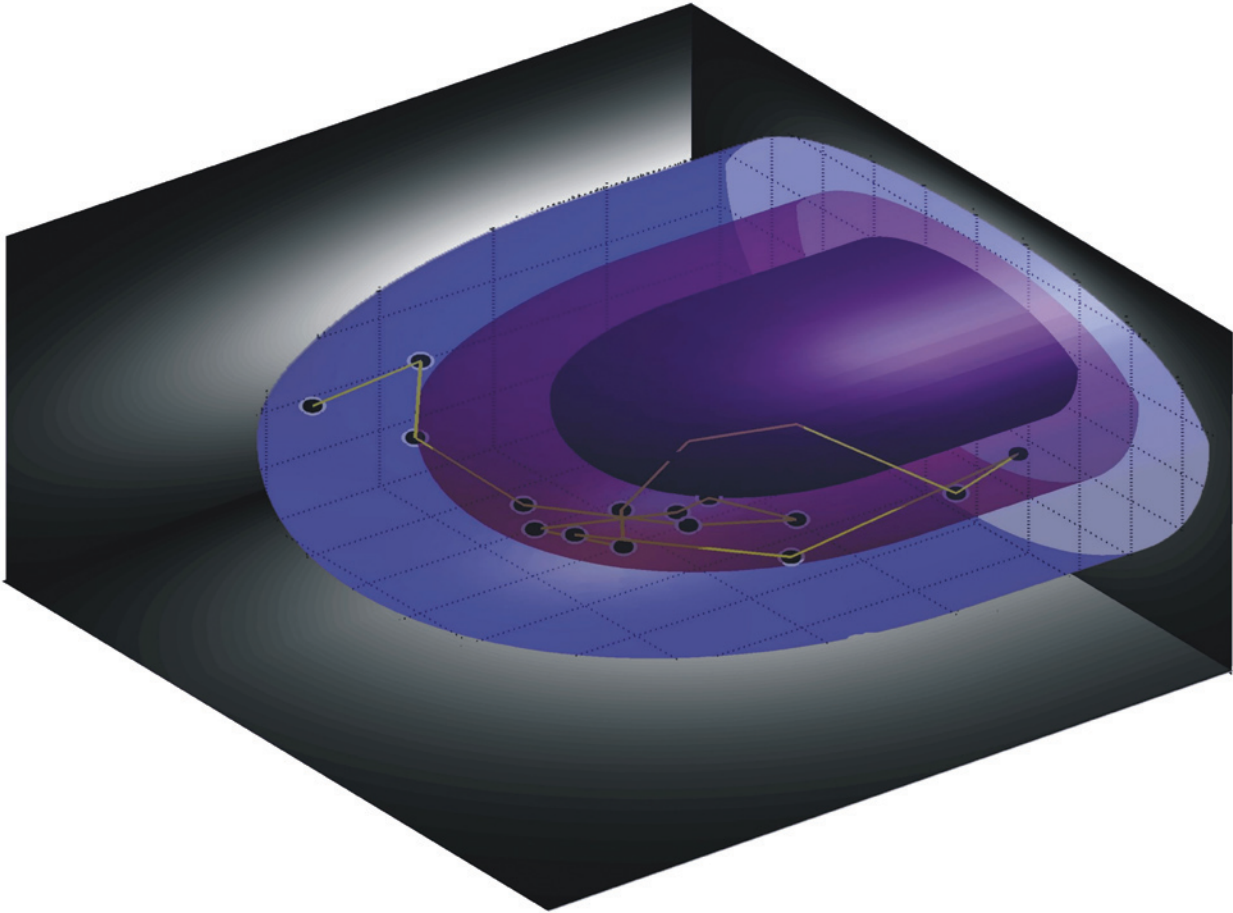


Figure 8. Biophysical conditions at each location in a landscape fluctuate over time on seasonal, annual, and decadal time scales. Thus the biophysical character of a location cannot be adequately represented by measurements taken at a single time. The current vegetation at the site reflects the results of a variety of nonequilibrium processes over various temporal scales, so it is essential to address temporal variability. In this figure the axes represent the limiting resources of water, temperature, and solar energy. The surfaces reflect the concentric 25th, 50th, and 75th percentile of maximum annual growth for a hypothetical species along those three limiting resources. The black dots represent sequential measurements of biophysical conditions at a single plot. The trajectory illustrates variable biophysical conditions over time. The pathway of the trajectory through the growth isoclines indicates temporal changes in the suitability of this single plot location for growth of the species.

between patterns and processes while extending predictions across broad spatial extents. Scaling predictor variables is an equally important issue. The relationship between a predictor and a response variable will change as a function of the extent over which the predictor variable is measured. It is important to identify the scale(s) at which this relationship is strongest. Bivariate scaling (Figure 9) is a formal approach to determine the scales at which environmental variables are most strongly influencing the response of vegetation at the scale at which the vegetation is sampled.

3. Limitations requiring integrating gradient modeling with other paradigms

e) Lag effects and non-equilibrium dynamics compromise the interpretation and power of equilibrium models. Lag effects incorporate the entire history of the site prior to the point at which vegetation and biophysical limiting factors were measured. These effects persist across a vast range of temporal scales. Species occurrence on a site will be related not only to current moisture and temperature gradients, but also to the separation of the North American continent from Europe

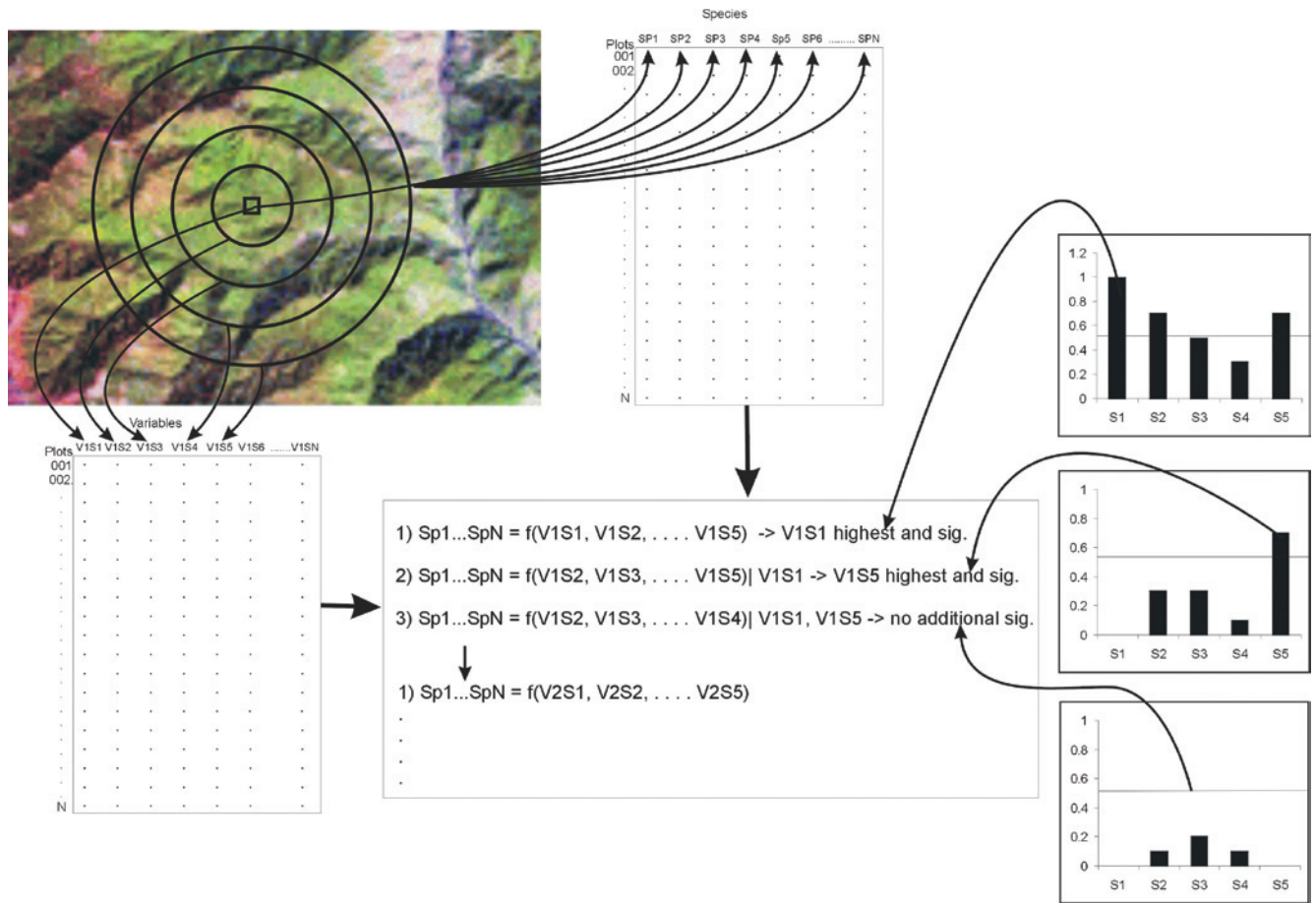


Figure 9. Partial bivariate scaling to identify the appropriate scales for each explanatory variable. This example illustrates the process for a single hypothetical explanatory variable measured over five spatial scales. In the image in the upper left, the square represents the footprint of the sample plot, and the concentric rings each of four radii around the plot. The variable is extracted from each of these five spatial scales. Across plots, we derive a matrix of plots by variable-by-scale combinations (lower left), and a matrix of plots by species (upper right). Bivariate scaling associates the patterns in the species among plots with the values of the variable-by-scale among plots. The first step is to model the species response as a function of all scales of the variable 1). In this example, scale 1, 2, and 5 have statistically significant explanatory power, and scale 1 has the largest marginal explanatory power. Scale 1 is selected. In step 2, the model is rebuilt using scales 2-5 as explanatory variables and scale 1 as a covariable. In this step, scale 5 is found to be the only significant scale and is selected. In step 3 no additional significant scales are selected. Scales 1 and 5 are selected for inclusion in the model building and the process is repeated for the next explanatory variable.

(millions of years), presence of ice-age refugia (thousands of years), fire history (hundreds of years), and more immediate influences such as the seasonal, annual, and decadal climatic variability. Any particular plot will follow a trajectory through biophysical conditions, and thus species tolerance, space (Figure 8), and composition and growth will be strongly influenced by past events.

f) *Limiting factors are not stationary.* Even if one could solve the problem of lag effects within an equilibrium model, the parameters of gradient models would be expected to change over time. For example, if limiting factors change, so will the key

predictor variables (Peterson and Peterson 2001). For dynamic modeling, then, gradient models are best utilized for establishing initial conditions and for building transfer functions to take landscape outputs in future time-steps back to fine-scale ecosystem attributes (see below).

Biotic Interactions, Hierarchical Variance Partitioning, Multi-Scale Modeling, and Spatial Dependence

Many of the sources of error and imprecision detailed above can be mitigated within the gradient modeling

approach by addressing biotic interactions, spatial dependence, and scaling relationships with multi-scale modeling (Thompson and McGarigal 2002), and hierarchical variance partitioning (Cushman and McGarigal 2003, Cushman and Wallin 2002, Cushman and McGarigal 2004). The relationships between a species and an important environmental variable will appear only when measurements are made at appropriate spatial scales (Wiens 1989). Thus it is essential to optimally match the scale of environmental pattern in each predictor variable to vegetation response. In the past, most efforts have been restricted to single scales of analysis, often arbitrarily imposed by the scale of available data (e.g., TM or AVHRR imagery). Much effort has recently been committed to determining which methods are most effective at identifying the correct scale for associating environmental variation to species responses; *partial bivariate scaling* (Thompson and McGarigal 2002, Grand and others 2004) is among the most effective.

Partial bivariate scaling

In partial bivariate scaling, the patterns of the response variables (vegetation composition and structure) are associated with multiple environmental variables, each measured across a range of spatial scales. A priori, we have no basis to assume which spatial extent surrounding the sampled plot is the scale at which the environmental variable is most strongly related to vegetation response. Accordingly, it is best to measure each environmental variable across a broad range of radii surrounding the plot. Partial CCA or partial regression is then used to determine the scale(s) at which each predictor variable is most related to vegetation response (Figure 9). Separate models are constructed for each predictor variable, with each model including variables at each spatial scale. Canonical ordination or regression then identifies the spatial scale with the largest marginal relationship between the response and any predictor variable. If there is no scale at which a variable is significant then that variable is dropped. If the most influential scale is a significant predictor, the process is repeated, treating the previously identified scale as a covariate. If additional scales are found to be significant predictors then they too are selected and partialled out, and the process is continued until no more scales contribute significantly to prediction. In practice, one or at most two significant scales are usually associated with each variable, and many variables have no significant explanatory power and are dropped (Grand and others 2004).

Hierarchical gradient modeling

Once the appropriate scales have been identified for each variable, gradient models are then built using step-wise approaches incorporating significant variables at the identified scales. In this model building, it is often useful to use hierarchical variance partitioning (Cushman and McGarigal 2003, Cushman and Wallin 2002, Cushman and McGarigal 2004). Hierarchical variance partitioning is a statistical method that breaks down the explanatory power among multiple sets of explanatory variables into their individual components (Figure 10). The method translates a hierarchical or multi-scale conceptual model into a statistical decomposition of variance. The decomposed model allows one to assess the relative importance, confounding, and interaction among variables. This facilitates ecological understanding of the relationships between mechanisms and responses across scale and organizational levels. Hierarchical model partitioning is particularly useful for the specific challenges facing research on relationships among forest vegetation, fire, and climate. It allows quantitative assessment of the relative predictive abilities and interactions of 1) local “fine-filter” measurements of environmental conditions in the field and “coarse-filter” environmental conditions extracted from synoptic GIS, 2) mechanistic limiting factors and the potpourri of other available surrogate variables, 3) abiotic environmental conditions and biotic interactions, 4) spatial dependence, and 5) time lag effects.

Biotic-interactions and time lag effects—Hierarchical, multi-scale gradient models can also incorporate biotic interactions, succession, disturbance history, and temporal disequilibria between current vegetation and the environment (Figure 10). Both temporal and environmental variables are included as separate predictor sets and partitioned to quantify the relative effects and interaction of time since disturbance, disturbance type, and environmental gradients. For example, the effect of competition upon a target species can be seen as a local modification of environmental conditions by other species (Tilman 1990). Biotic interactions can be modeled directly, where vectors of proportional composition are a multivariate response (Aitchison 1986, Billheimer and others 2001, Cumming 2001). Although this technique is of theoretical interest, it may prove difficult to apply to any but the simplest compositional patterns (but see Cumming 2001). For example, McKenzie (unpublished) was able to explain negligible variance with this approach using the same data (McKenzie and others 2003) that produced robust gradient models for individual species.

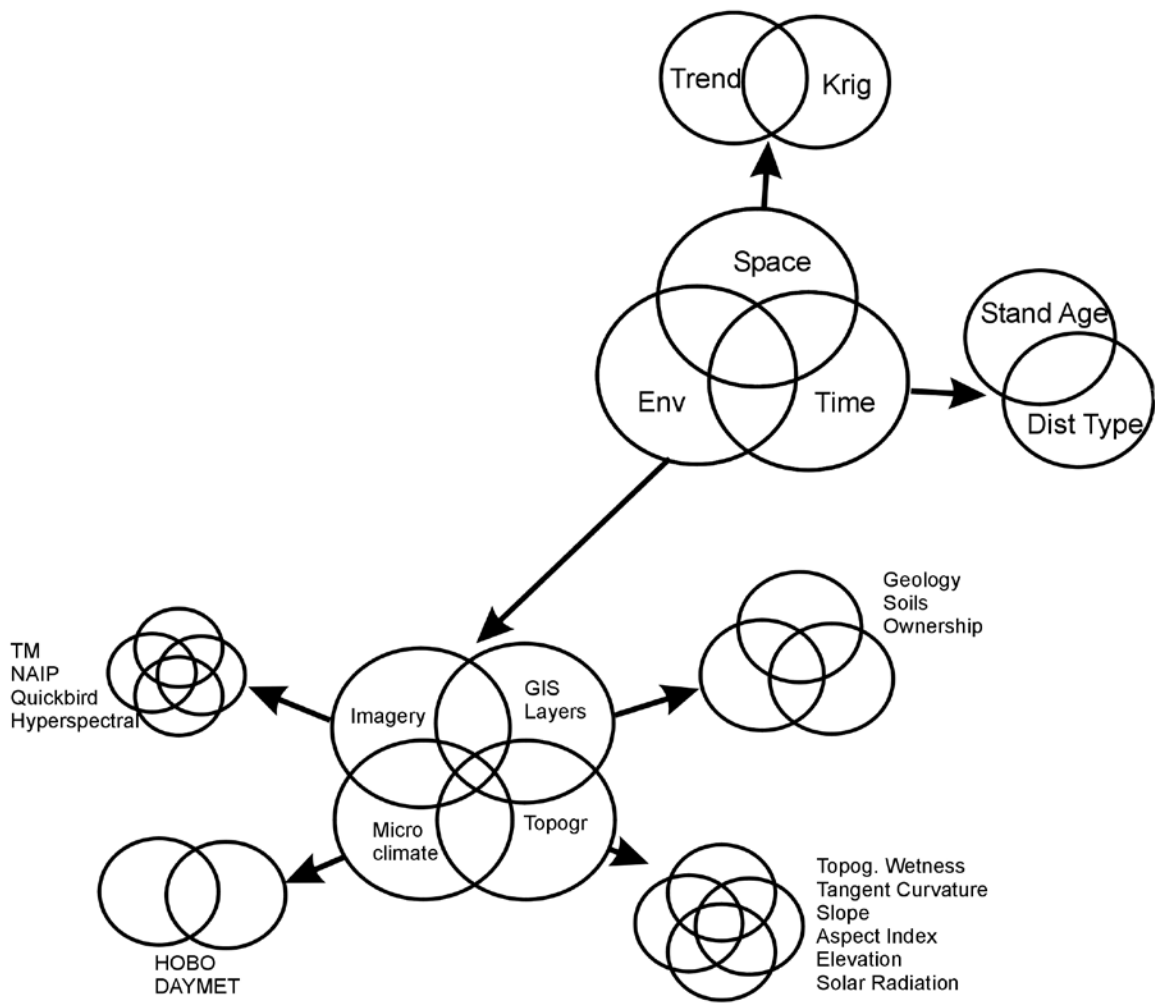


Figure 10. Hierarchical model building and decomposition. In regression and canonical ordination, subsets of variables are partitioned to quantify their independent and interactive influences. In this example, we hierarchically build a model to explain vegetation composition and structure based on spatial, temporal, and environmental factors. Each of these data sets in turn contains nested subsets. By decomposing the relationships among these components we can quantify the relative importance, interaction, and confounding among multiple explanatory variables derived at different spatial scales and different organizational levels. This provides a means to both build the most powerful predictive models, but also to gain the most complete insight into the importance and shape of the relationship between each driving factor and vegetation response.

An analogous indirect method is to estimate proportional composition of individual species via a GLM of the binomial family, as is used to predict probability of presence/absence. Like the methods of Aitchison (1986) and others, this approach requires a non-zero value for every species in every observation or plot so it is difficult to apply in real ecosystems. A more practical approach may be a canonical ordination method such as canonical correspondence analysis, where individual species' optima and tolerances in multidimensional gradient space are constrained both by predictor variables (linearly) and by changes in species composition itself (via unimodal functions), thereby implicitly incorporating biotic interactions among species. Hierarchical variance

partitioning of canonical ordination models provides a means of addressing species interactions by including appropriate biotic variables among the environmental predictor sets. It is then possible to separate the effects of abiotic environmental control from the effects of species interactions (Figure 10).

Success in this effort will depend on samples from combinations of all pertinent biophysical contexts with and without past disturbance types of interest. The database of sample plots must contain the full combination of species occurrences along environmental gradients. Quantifying competition and species interactions requires measurement of performance of each species in each biophysical context both in the presence

and the absence of the putative competitors. For example, vegetation responses are highly sensitive to the details of site level resources and disturbance history (Bunn and others 2003). Seed dispersal depends on release height, topography, wind speed and direction, tree density, and seed morphology (Johnson and others 1981, Van der Pijl 1982, Green and Johnson 1996). Cycling of organic matter and nutrients depends on litterfall, atmospheric deposition, and decomposition (Waring and Schlesinger 1985), which are highly influenced by local stand conditions, history, and biophysical context. In a hierarchical gradient model, these local influences can be separated from coarse-scale influences, rather than just combined with them in interaction terms, and the variance attributable to each can be precisely quantified (Cushman and McGarigal 2004). Such an approach partially overcomes errors associated with spatial scale mismatches and temporal lag effects.

Spatial Dependence and Autocorrelation—Biotic response along environmental gradients has two components of spatial dependence: spatial biotic processes within the community and the spatial structure of environmental factors (Legendre 1993). Spatial dependence among observations reduces degrees of freedom in a model and can drastically change significance levels. Because many ecological processes exhibit spatial autocorrelation to some degree, ignoring spatial dependence where non-negligible can distort ecological inference. The core statistical techniques in gradient modeling (multiple regression, GLMs, canonical ordination in its regression phase) carry assumptions of independence. Violation of these assumptions does not bias estimation *per se*, but it does render significance tests unreliable. Explicit consideration of spatial dependence can improve model estimation and in some cases predictive power. For example, Miller and Franklin (2002) improved predictive models for shrub species in the American Southwest by combining GLMs (including a preponderance of unimodal functions) with indicator Kriging (Isaaks and Srivastava 1989).

Hierarchical gradient modeling with direct ordination can account for spatial dependence in several ways. First, one can include spatial variables, such as the terms of a trend surface analysis, as predictor variables. By partitioning the models one can determine the amount of variance attributable to independent environmental control, spatially structured environmental control, and biotic spatial autocorrelation (Borcard and Legendre 1994). Alternatively, Wagner (2004) integrated geostatistical spatial modeling with direct canonical ordination to address spatial autocorrelation in community patterns. This allows the ordination results to be portioned by

distance and integrated with geostatistics. The diagnostic tools provided by direct multi-scale ordination (*sensu* Wagner 2004) allow ecologists to distinguish between spatial dependence and spatial autocorrelation and to check assumptions of independent residuals, stationarity, and scale-invariant correlation.

Not all biophysical gradient models will benefit from incorporating spatial dependence, however. Spatial autocorrelation will be evident in sample data only if its range (more precisely, the range of its empirical variogram) is much greater than the average geographic distance between observations. In complex terrain, observations have to be very close in space for this to be true. For example, McKenzie and others (2003) tested for spatial dependence indirectly by computing empirical variograms of the residuals from their gradient models, finding no mean change in covariance from adjacent plots to those separated by kilometers. However, in imputation (see below), predictions are made for all pixels across all lag distances. Accounting for spatial dependence will be of great importance in producing the most accurate imputed maps of expected vegetation conditions across complex landscapes.

Existing FIA sample protocols use a sub-plot design that could be utilized to provide a measure of spatial autocorrelation by comparing vegetation, climate, disturbance, and biophysical environments between sub-plots. FIA plot structures allow autocorrelation to be computed at 2 lag-distances (36.6 and 63.4 m). Additional plots could be added to provide additional scales at which autocorrelation could be measured. Spatial autocorrelation itself can then be modeled as an autoregressive gradient function of disturbance and biophysical environment.

Implementing Multi-scale Gradient Modeling with Canonical Ordination—Multi-scale and hierarchical gradient modeling has been developed using partial canonical correspondence analysis (ter Braak 1986, Cushman and McGarigal 2003, 2004). Partial CCA is a particularly useful tool for analysis of temporal, multi-scale, or hierarchical relationships (e.g., Cushman and McGarigal 2003). Partial CCA can be used to separate the effects of environmental control from the autogenic changes in the community related to successional time. It is also an ideal tool with which to identify the scales at which each biophysical variable is most strongly related to the species responses (Figure 4) and to partition the effects of variables from multiple data sources and organizational levels (Cushman and McGarigal 2003, Figure 5). Thus partial CCA provides a rigorous framework to quantitatively link vegetation responses to the influences of environmental factors across a range of spatial scales, temporal dynamics, and succession

and to partition the effects of factors measured across multiple levels of organization. Bivariate scaling and hierarchical gradient modeling should be possible using alternative approaches such as GAM and nonlinear regression. However, more development is required before the potential of these other methods is known. At this time, multi-scale, hierarchical gradient modeling is the only well-developed tool allowing proper linkage of the patterns and processes across spatial scales and over time essential to the task of predicting relationships between climate, fire regimes, and forest ecosystems.

Predictive Vegetation Mapping: Univariate Prediction and Multivariate Gradient Imputation

Spatially explicit predictions of species composition and the structure of forest vegetation are needed at broad spatial scales (Moisen and Frescino 2002, Ohmann and Gregory 2002). A detailed spatial prediction of current vegetation composition and structure is the foundation on which predictions of the effects of future climate and disturbance regimes are based and evaluated. This information is obtained through predictive vegetation mapping (Franklin 1995). Predictive vegetation mapping uses relationships between observed patterns of species occurrence, obtained from a large, representative sample of field plots, and synoptically measured predictor variables.

Most efforts at predictive vegetation mapping have been based on classification of satellite imagery. Categorical, patch-based classifications are limited to general characteristics of upper canopy (Cohen and others 2001, Wolter and others 1995, Woodcock and others 1994) and cannot reflect the continuously varying structure of the plant community. If a minimum patch size is imposed, small scale features may vanish. Perhaps even more importantly, classification results is a necessary compromise between information loss and categorical error rates. As the numbers of classification types increase, error rates also increase (Hunsaker and others 2001, McGarigal and Cushman 2005). Thus classified maps are limited to relatively few, broadly defined patch types.

An alternative approach is to predict detailed vegetation conditions at each cell across the landscape based on a gradient model (Van Deusen 1997). There are two main approaches for predictive vegetation mapping. If univariate models are used the model itself can produce predictions for each unsampled location based on the value of predictor variables at each location. For example, Frescino and others (2001) used generalized

additive models to predict forest presence, lodgepole pine (*Pinus contorta*) presence, basal area, shrub cover, and snag density in the Uintah Mountains of Utah. The input data was provided by the Interior West Resource Inventory, Monitoring and Evaluation Program database, and consisted of forest vegetation measurements taken from 0.4 ha plots. The explanatory variables included downscaled PRISM precipitation data, elevation, aspect and slope, geology, geographic location, classified TM imagery, unclassified TM imagery, and AVHRR imagery. All variables were rescaled within GIS to a cell size of 0.4 ha. Their results indicate that TM data, elevation, and geology are significantly related to the response variables, but predictive accuracy was low. Prediction accuracy for forest vs. non-forest was 88% and was 80% for lodgepole pine. Only 62% of predictions for basal area, shrub cover, and snag density fell within 15% of measured values.

Moisen and Frescino (2002) compared five modeling approaches for predicting forest presence: spruce-fir forest, biomass, tree age, quadratic mean diameter, and crown cover. Vegetation training data were from FIA plots at a spatial resolution of 0.4 ha. The explanatory variables included elevation, slope, aspect, geographic location, AVHRR data, and TM-classified land cover data. All predictions were made to 1-km output pixels. The modeling approaches included simple linear models, GAM, CART, MARS, and artificial neural networks (ANN). Models built on simulated complex nonlinear responses indicated that MARS and ANN performed best. In contrast, models built using measured data appeared to favor GAM and MARS. Predictive success was relatively low overall, however. Kappa values for predicting forest vs. nonforest ranged between 0.3 and 0.8. Correlations between observed and predicted values for continuous variables were relatively low, with none over 0.6. Few models produced maps with more than 50% of predicted values within 25% of actual.

When a multivariate approach is adopted, in which the responses of multiple species are simultaneously predicted based on combinations of predictor variables, it is not possible to use the model to directly predict expected values of each species. When a multivariate gradient model is used, gradient imputation (Figure 11—Ohmann and Spies 1998, Ohmann and Gregory 2002, Wimberly and Ohmann 2004) provides an efficient means of estimating expected values for dependent variables at unsampled locations based on the complex of environmental gradients at those locations. Gradient imputation has several technical advantages over alternative methods. First, gradient models utilize patterns of covariance among interrelated biological patterns

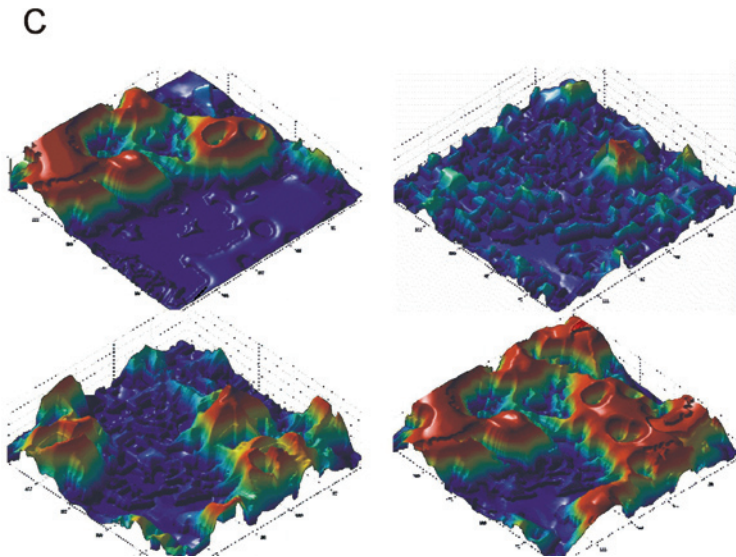
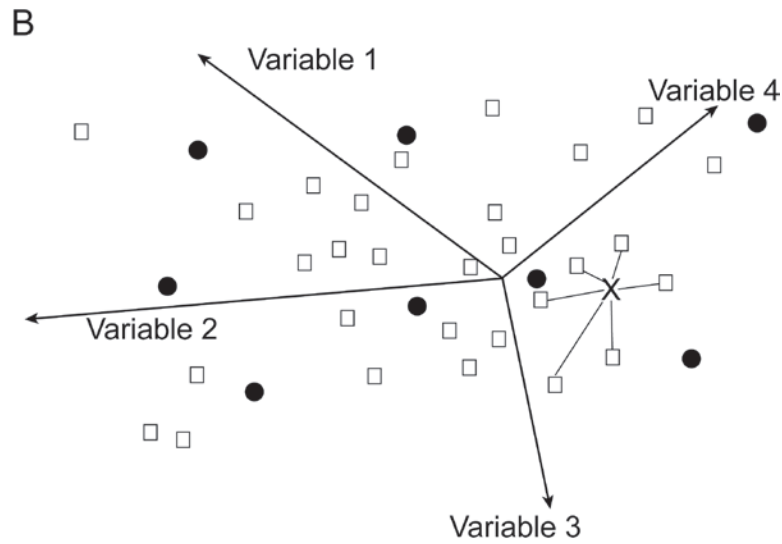
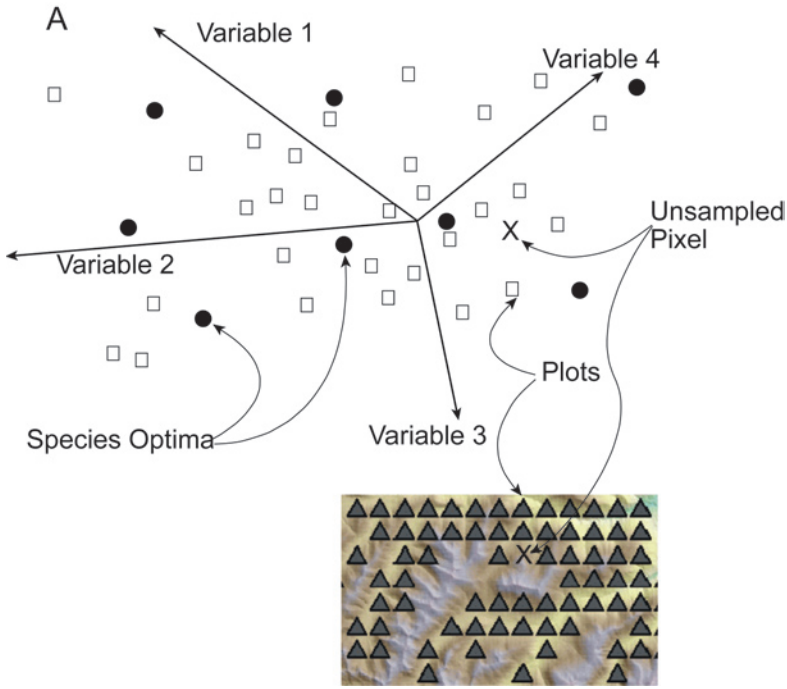


Figure 11. Gradient imputation of niche structure with scaled biophysical variables. (A) Independent variables at a range of spatial scales are used for a nonlinear gradient model of niche structure for each species. This example uses CCA (ter Braak and Prentice 1986). Axes are orthogonal dimensions of ecological space. Species optima locate the center of their environmental niche with respect to the measured predictor variables. (B) The niche model uses ecological space, but we can make inferences about suitability in geographic space using *gradient imputation* (Ohmann and Gregory 2002). Each unsampled location (cell) is projected iteratively into the environmental space defined by the niche model. By imputing the value of the species at the nearest sampled plot (or a weighted average of nearby plots) we estimate the suitability of the new location for that species. (C) Gradient imputation allows the explicit translation from quantitative models in environmental space to suitability maps in geographic space. Normalized values for multiple species at each location provide equilibrium estimates of relative competitive ability, useful for defining parameters in ecosystem dynamics (gap) models.

and processes to make their predictions. This yields models that are self-calibrating and do not suffer from compounding error rates across levels of estimation (McKenzie and others 1996). Second, the imputations are made at the native scale of the input predictor variables, avoiding the very troublesome issues of aggregation and extrapolation error (King 1991, Rastetter and others 1992). Gradient modeling also avoids the subjectivity and information losses associated with discrete classifications of inherently continuous and covarying ecological gradients (McGarigal and Cushman 2005) and facilitates optimal multi-scale analysis of multiple response surfaces.

Ohmann and Gregory (2002) used canonical ordination (CCA) and gradient nearest neighbor (GNN) imputation (Figure 11) to produce predictive maps of forest composition and structure in coastal Oregon. CCA is effective at predicting responses of multiple, continuous biotic response variables, is widely used by ecologists, and is robust to correlations among environmental variables and sparse data matrices (Palmer 1993, Guisan and Zimmerman 2000, Ohmann and Gregory 2002). Response variables were basal area by species and size class. Predictor variables were derived from LANDSAT TM bands, PRISM climatic data, geographic location, topographical indices, and geologic variables. They argued that the GNN method has several advantages over alternatives. First, each imputed pixel is attributed with a list of trees by species, size, and density (essentially the *tree list* required by vegetation simulators), so vegetation data are not transformed and thereby subject to information loss. Second, because GNN imputes from a single nearest-neighbor plot the covariance among predicted species and structures is not under-estimated. Third, the range of variability present in the sampled stands is maintained in predictions. Fourth, CCA models are interpretable in terms of species responses, connecting regional environmental gradients directly to forest vegetation.

Uncertainty in gradient imputation

As with any modeling, the choice of modeling approach, predictive variables, and scales of measurement have profound influences on imputation performance. The uncertainties associated with gradient imputation arise from the interplay of several factors.

- Spatial variables used to construct the models often do not reflect the factors to which the vegetation is responding. In the past, most imputation efforts have used what spatial data were available, rather than seeking out specific variables that represent driving mechanisms.

- The spatial data used to construct the models are often at inappropriate scales. Many data layers used to predict species responses at the scale of an FIA plot (0.4 ha) have a grain that is much larger. This scale mismatch greatly reduces the likelihood of observing strong relationships. For example, AVHRR data has a 1-km cell size. Vegetation structure at a finer spatial scale cannot be accurately resolved from AVHRR data regardless of the modeling method used. It will be informative to use GNN modeling approaches using higher resolution remotely sensed data sets, such as hyperspectral imagery, Quickbird, and NAIP imagery.
- The climate data often used in imputation modeling are derived from coarse-scale GIS layers or modeled extrapolations of low elevation, valley bottom climate from meteorological stations. Microclimate varies over much finer scales and is a strong influence on vegetation patterns. It is essential to obtain climatic data at a spatial scale that matches the scale of the plot-level response of vegetation. DAYMET (1 km) and PRISM (4 km) data are too coarse to meet this need. If, for example, gradient models used a grid of micro-weather stations placed across the range of biophysical conditions, the scales of predictors and response would match.
- Most models developed to predict vegetation use spectral, topographical, and mapped geological data at the immediate footprint of each plot. It is likely, however, that these predictor variables drive vegetation responses at a variety of spatial extents, and not necessarily most strongly at the scale of the plot's immediate footprint. Accordingly, using multi-scale ordination and *partial bivariate scaling* (Figure 9) may improve models by identifying the scales at which each variable has the strongest influence on plot-level vegetation response.
- In many cases, models built on fine-scale plot-level data make inferences to much larger spatial extents. For example, Moisen and Frescino (2002) produced predictions at a 1-km scale from single 0.4 ha plots nested within. This assumes that the sampled plot is representative of the vegetation condition throughout the 1-km cell. Given the high spatial variability of vegetation and biophysical gradients within a 1-km scale, this is an unsupported assumption. Such unsupported scale extrapolations produce highly equivocal predictions.
- Most past gradient imputation has ignored the issues of temporal nonequilibrium and time lags. However,

by including disturbance history and stand age as predictor variables in hierarchical gradient modeling we will be able to incorporate temporal dynamics in the models by in effect trading space for time.

- In the past, gradient imputation has ignored patterns of spatial autocorrelation. As these patterns are strong at the fine scales to which imputation modeling is defined, their influence can be profound.

Most of the sources of uncertainty listed above are directly addressable either through more sophisticated modeling, better data collection, or both. The interpretability of gradient models and their utility in making predictions at fine scales, in new landscapes, or in future conditions will be improved by building gradient models with theoretically understood limiting factors. Additionally, bivariate scaling and variance partitioning address important sources of uncertainty associated with imputation modeling. By linking gradient imputation to canonical ordination models developed using partial bivariate scaling and hierarchical variance partitioning of limiting factors we should be able to improve both predictions of current conditions and inferences about expected changes in occurrence, growth, and regeneration under possible future climate and disturbance regimes.

Intrinsic limits to gradient modeling

By linking the limiting factor niche modeling (McKenzie and others 2003), hierarchical partitioning (Cushman and McGarigal 2003), partial bivariate scaling (Thompson and McGarigal 2002), and gradient imputation (e.g., Ohmann and Gregory 2002), we can address most key issues of spatial and temporal scale, spatial autocorrelation, and temporal disequilibrium in models of species occurrence, growth, and regeneration. However, gradient models do not explicitly address a chain of causation. Gradient models are rooted in species-environment correlations, which do not always reflect causation. Also ecological mechanisms have *transient dynamics*. These temporal dynamics of biophysical conditions are difficult to represent in equilibrium gradient models. In contrast, process-based modeling with explicit time-steps can more directly relate organism responses to the action of specific mechanisms and address temporal disequilibria and transient dynamics (Neilson 1995, Keane and others 1996, Waring and Running 1998). We therefore suggest that understanding the causes and effects of pattern-process relationships in forest systems will benefit from linking empirical gradient models with mechanistic ecosystem models. Also, gradient models are limited in their ability to project landscape changes from large-scale and temporally punctuated disturbances

such as insects and wildfire, which are disturbances that will likely be the direct agents of ecosystem changes in response to global climate change (McKenzie and others 2004). Thus we suggest integrating landscape dynamics modeling of broad-scale disturbance with gradient and ecosystem dynamics models. The following sections review these two additional modeling paradigms in the context of integrated landscape modeling.

Ecosystem Dynamics Modeling

Time lags, nonequilibrium dynamics, and mismatch of temporal scale between responses and drivers reduce the effectiveness of equilibrium models. Gradient models can address time lags and non-equilibrium dynamics implicitly by incorporating dynamic climates, disturbance history, and species interactions within the hierarchical gradient modeling framework. In contrast, ecosystem dynamics models bring an explicit temporal dimension by simulating responses of vegetation to specific combinations of mechanisms across formal time-steps. Whereas gradient models in effect trade space for time (McGarigal and Cushman 2002), ecosystem dynamics models make predictions at successive time-steps, with each state depending on the previous one. This greatly improves the realism and flexibility with which time lags and temporal dynamics can be addressed.

Comprehensive reviews of ecosystem dynamics models are found in Waring and Running (1998) and Keane and Finney (2003). We focus on the characteristics of ecosystem dynamics models that would mesh with gradient and landscape dynamics modeling to synthesize analyses of forest vegetation responses to climate and disturbance regimes across spatial and temporal scale. Vegetation dynamics models use mechanistic approaches to simulate plant growth, regeneration, mortality, decomposition, and nutrient cycling (Landsberg and Gower 1997). Waring and Running (1998) distinguish between biogeochemical (BGC) models and “gap-phase” (gap) models. BGC-type models emphasize physiology and biogeochemistry, whereas gap models emphasize life-cycle dynamics.

Gap-phase models simulate relationships between species occurrence, growth, and regeneration and biophysical drivers over time. They are readily linked to multi-scale gradient models because both predict the same response variables (vegetation composition and structure) based on the same predictor variables (biophysical drivers at the level of each plot). Gap models track individual trees and distinguish vegetation responses at the species level, thereby factoring in competitive interactions via reciprocal influences of individual trees on each other’s microenvironment. Comprehensive reviews

of gap models are provided by Botkin and Schenk (1996) and Urban and Shugart (1992).

The FM model (Miller and Urban 2000, Miller 2003), an extension of ZELIG (Urban and others 1991), exemplifies how ecosystem modeling can support and extend gradient modeling. FM simulates the establishment, growth, and death of individual trees on a tree-sized plot, which is considered to be homogeneous. A key attribute of the FM model is that it simulates feedbacks. Trees are affected by the environment and in turn, trees affect the environment. Species tolerances to environmental conditions are formalized in the model as heuristic, unimodal response curves; species replacements during succession or with climate change are a function of their relative positions with respect to the centers of the response functions. Gap-phase models such as FM are not spatially explicit, in that they simulate the dynamics of individual stands at specific locations in a

landscape rather than the pattern of vegetation continuously across space. However, the FM model addresses spatial complexity by simulating arrays of individual plots in a rectangular grid across the landscape. The plots interact with one another via shading and seed sources. This relaxes the assumption of a homogeneous stand and allows for spatial interactions that modify the microenvironment within a stand (Smith and Urban 1988, Urban and others 1991).

Gap models such as FM are an ideal means by which to strengthen and extend the predictions of gradient modeling (Figure 12) because they simulate feedbacks between vegetation and the environment. Species are ranked by tolerances to environmental conditions, explicitly linking the simulation to niche characterization. Gap models simulate regeneration, growth, and death of trees based on the interaction between the optima and tolerances with respect to environmental conditions present

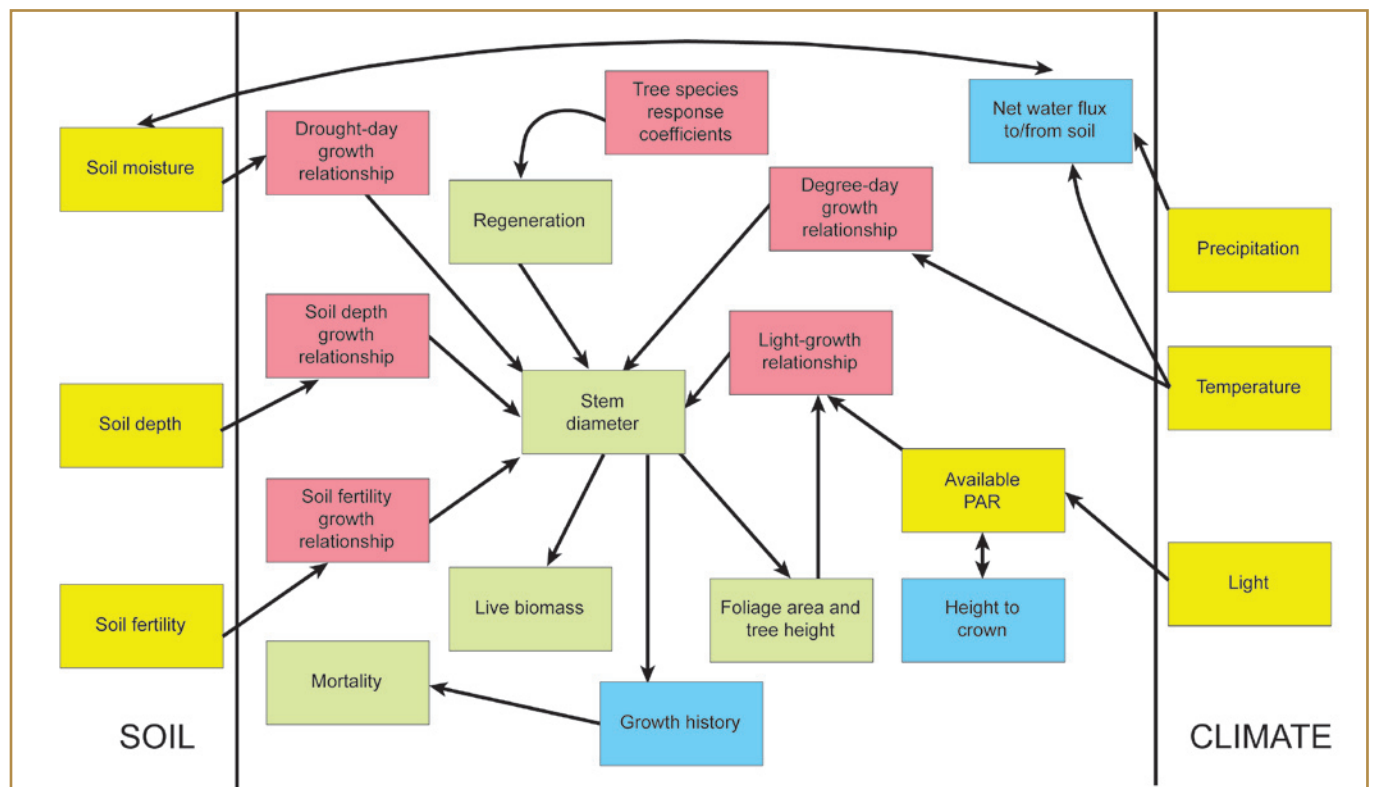


Figure 12. Gap-phase ecosystem dynamics models simulate growth, death, regeneration, and stand structure based on initial vegetation and biophysical conditions. They are based on mechanistic relationships between biological response variables and environmental drivers. In the conceptual model here, biotic responses (green boxes) are predicted as functions (pink boxes) of climate and soil characteristics (yellow boxes). The climate and soil characteristics at each simulated plot can be measured in the field. Gap models require a statement of initial vegetation conditions for initialization, which can be measured on a sample of plots. Extending predictions across space requires estimates of initial vegetation and biophysical conditions for unsampled plots. Imputation of multi-scale biophysical models is perhaps the best means of gaining these estimates of driving variables across space. Ecosystem models also require explicit information about the functional nature of vegetation response to each driving variable. These functional relationships must be based on empirical data from the system of interest. Extensive samples of vegetation across biophysical gradients, coupled with gradient modeling, provide information needed to quantify mechanistic relationships between specific environmental drivers and vegetation response.

at the site and changes in those conditions through time due to biotic interactions, climate change, or disturbance. These attributes of gap models can circumvent some limitations of gradient modeling, most notably the difficulty of dealing with temporal disequilibrium between current vegetation and the environment.

Conversely, gradient modeling offers solutions to the major challenges facing implementation of gap models across complex landscapes (Figure 12). Gap models rely on a quantitative understanding of the optima, tolerance, and performance of each species along biophysical gradients. Specifically, gap models use relationships between soil moisture, precipitation, snow pack, solar radiation and growth, mortality, and regeneration. Gradient modeling provides critical parameters by estimating the optima and tolerances of each species for growth, regeneration, and occurrence along each biophysical gradient. Large, representative samples taken across the full span of biophysical gradients, followed by multi-scale gradient modeling, are the best means to minimize the uncertainty associated with these critical relationships.

Gap-phase models have been implemented within landscape applications (Shugart and Seagle 1985, Urban and others 1991, Mladenoff and Baker 1999) but have used aggregation techniques that involve information loss and error propagation (Rastetter and others 1992, King 1991). The uncertainties in aggregation to a landscape mosaic can be partially obviated by using multi-scale gradient imputation models (Cushman and McGarigal 2003, Ohmann and Gregory 2002). Gap-phase models can produce expected future stand structure and composition for grids of forest plots. Gradient imputation on the simulated future plot values provided by the gap models can then be used to infer future vegetation composition and structure as a function of spatial location and biophysical gradients at each plot-sized cell in a landscape. Thus, by combining gap-phase futuring of permanent forest plots with gradient imputation, it is possible to simulate vegetation dynamics continuously across complex landscapes (e.g., Spies and others 2002).

Landscape-Level Disturbance Modeling

A major limitation of ecosystem modeling is the difficulty of addressing large-scale disturbance. Ecosystem dynamics models excel at predicting the effects of processes acting at the gap and stand scale, but they have difficulty addressing broad-scale, contagious spatial processes such as wildfire. Although some gap-phase models simulate disturbance (e.g., Shugart and Noble 1981, Bonan and Shugart 1989, Miller and Urban 2000), they do not simulate the propagation of fire across

landscapes (Miller 2003). Instead, disturbance is represented in ecosystem models by linking multiple plots within a spatial network and using aggregate results (Urban and others 1991, Acevedo and others 1996). Interaction among cells, a key to successful simulation of contagious processes, is limited. Attempts to fully incorporate spatial interactions in a mechanistic framework encounter not only logistical problems associated with limits on data and computing resources, but also a host of inherent problems that may be intractable.

Limitations of mechanistic fire modeling

Keane and Finney (2003) describe in detail the components that a mechanistic fire effects simulation model (FESM) would need in order to predict fire occurrence, spread, and intensity across large landscapes and incorporate both succession after fire and repeated fire events. The program outlined is ambitious and suggests that robust mechanistic simulation of landscape-level fire effects is still out of reach. Drawing on Keane and Finney's (2003) exposition, we recognize the following impediments to broad-scale mechanistic fire modeling:

1. Fully physical fire models that mechanistically represent the three-dimensional fire environment do not run in real time even on small patches (Linn and others 2005). Thus, we are a long way from having computing resources adequate for landscape physical modeling. Current fire-behavior and fire-spread models rely on empirical approximations of crown and surface fire behavior (e.g., Finney 2003), and they have a maximum resolution of 30 m—too coarse to accurately capture the combustion process and the spatial heterogeneity of fuels.
2. Even if these resource limitations were to be overcome, two other problems might be intractable.
 - a) There will likely always be a lack of good data at the scale of the landscape application. Keane and Finney (2003) suggest that five major processes should be included in a mechanistic landscape model: climate, fire, insect, disease, seed dispersal, and hydrology. Just looking at climate data, top down approaches usually couple coarse predictions from global circulation models to mesoscale gridded mechanistic climate models, such as RegCM2 (Giorgi and others 1993, Luce and others 1999), MM5 (Grell and others 1994), or RAMS (Pielke and others 1992). The predictions of these gridded weather estimates are then used to compute site-specific weather through interpolation (Luce and others 1999) or finer-scale mechanistic modeling (Running and others 1987). However, with up to four orders of estimation in this process, the

site-level error rates are likely to be unacceptably high, particularly in complex mountainous topography.

- b) Even with data as accurate as reasonably possible, sensitive dependence on initial conditions (Ruelle 1991) may rapidly degrade the accuracy of such a mechanistic model with multiple non-linear dependencies. For example, both fireline intensity and fire spread depend nonlinearly on the packing ratio of combustible fuels and its variability at fine scales (Rothermel 1972). In turn, fireline intensity is a key predictor of crown-fire initiation and spread, which can influence ecosystem properties for decades into the future. Data are lacking as to how serious this problem is, but ongoing experiments suggest that ecosystem-scale fire effects are very sensitive to small adjustments in fire-behavior parameters (Stocks and others 2004, Linn and others 2005).
3. Extreme events, which are the principal drivers of ecosystem change, are associated with coarse-scale controls. Even given error-free fine-scale modeling, there is a scale mismatch between driver and response. Extreme weather events, characterized by low relative humidity, high temperature, and high winds, trigger and maintain large high-severity fires (Johnson and Wowchuk 1993, Agee 1997, Skinner and others 1999, Baker 2003, Gedalof and others 2005). Some success in prediction of total area burned has been achieved with fire behavior simulated at coarse resolution, assuming a homogeneous fuel environment at a scale matching climatic controls (Lenihan and others 2003), but these authors did not simulate fire spread nor did they incorporate the sub-cell heterogeneity associated with mountain landscapes.
4. Successful ignition, represented as fire starts, is a limiting factor whose accurate implementation is beyond the capacity of current mechanistic modeling. Broad-scale atmospheric conditions conducive to dry lightning have been identified (Rorig and Ferguson 1999), but individual fire starts have not been directly linked to them. Thus, ignition is usually simulated with stochastic methods (Keane and others 1996, Keane and Long 1998).
5. Mechanistic fire modeling across large landscapes may be inherently intractable, as it encounters the “middle-number” problem (Allen and Hoekstra 1992). Allen and Hoekstra (1992) compare landscape modeling to statistical thermodynamics, wherein the number of individual molecules that interact is astronomical, therefore impossible to model individually,

but accessible using aggregate statistics. Analogously, aggregating ecosystem and landscape attributes to coarse scales (resolutions of multiple km) enables broad-scale modeling (e.g., Keane and Long 1998, Lenihan and others 1998) but cannot reproduce landscape variation at meaningful scales for contagious processes such as fire.

Because all of these limitations cannot be solved without major scientific advances, we submit that a stochastic paradigm, using aggregate properties of fire regimes and ensemble modeling, though eschewing the direct representation of fire behavior and fire spread, provides the best approach to landscape fire modeling.

Stochastic landscape dynamics simulators

Stochastic models exploit aggregate statistical properties of disturbance processes, rather than attempting to predict individual events and their behavior mechanistically. Fire, in particular, is appropriately modeled as a stochastic process, of which each fire history, whether from field observations or simulations, is just one realization (Lertzman and others 1998, Falk 2004, McKenzie and others 2005). Landscape dynamics simulators do not simulate fire behavior *per se*. Instead they use empirical models to estimate fire frequency, size, spread behavior, and intensity along biophysical gradients. These statistical relationships are used to populate landscapes with fire events that match expected patterns and frequency. Via “ensemble” simulations (see above), they are able to simulate properties of *fire regimes* accurately and can incorporate seasonal to multi-decadal climatic variability in the form of altered fire patterns. Rather than attempting to use coarse climatic predictions to mechanistically produce fires, these predictions are used to infer changes in fire regime.

Dynamic landscape simulation models have been used to explore synergistic effects of long-term climatic change and fire on landscape-level patterns of vegetation (Baker and others 1991, Keane and others 1996, Gardner and others 1999, He and Mladenoff 1999a, Hargrove and others 2000). A thorough review of landscape dynamics simulation models is found in Mladenoff and Baker (1999). The LANDIS (Mladenoff and others 1996), SIMPPLLE (Chew and others 2004) and RMLANDS (<http://www.umass.edu/landeco/research/rmlands/rmlands.html>) models simulate fire, wind throw, and “harvest” on landscape pattern and structure. LANDSIM (Roberts 1996) uses life history and vital attributes to drive succession in polygons. DISPATCH (Baker 1992, 1993) uses stochastic simulation of fire occurrence and spread based on dynamically simulated weather, fuel loadings, and topographic setting, and then

simulates forest succession in change of cover type and stand age. Fire-BGC (Keane and others 1996) aggregates stand-level output of the ecosystem dynamics model Forest-BGC and applies disturbance stochastically using random ignitions. This model comes closest of any to date in linking mechanistic stand-level ecosystem dynamics to landscape disturbance; a revision is now complete and being applied across the northwestern United States (personal communication, Robert Keane, Rocky Mountain Research Station).

Fire regimes are defined in terms of probability distributions of size, frequency, and severity. Statistical models can be used to estimate expected values of fire-regime parameters (McKenzie and others 2004, Duffy and others 2005, Gedalof and others 2005, Littell and others, submitted) as functions of climatic variability, using historical records. They can be extrapolated with some confidence to predict future fire-size and frequency distributions under changing climatic regimes, and to a certain extent past fire regimes can inform likely changes associated with potential future climates. If, for instance, hot dry years are associated with increases in fire size, frequency, or both, then a warmer and dryer future climate can be expected to produce similar results. Alternatively, instead of being constrained in advance, fire-size distributions may arise from deterministic or stochastic rules applied during the simulation of a fire event. For example, in grid-based cellular automata models, fire susceptibility in a cell adjacent to a burning cell may be “on” or “off,” or probabilistic. An interesting hybrid model is MC1 (Bachelet and others 2001a, Lenihan and others 2003), in which the flammable proportion of a cell is determined by biomass and fuel

moisture thresholds during the event but constrained at the upper end by natural fire rotation.

An ideal landscape dynamics model would preserve the empirical detail provided by gradient models and the mechanism/response paradigm associated with the ecosystem dynamics models. However, as we noted above, the aggregate properties of a landscape subject to physical and ecological mechanisms are best captured with a stochastic approach, because of the logistical and technical limitations of mechanistic modeling at broad spatial scales. Stochastic landscape dynamics models, however, simulate the patch dynamics associated with each disturbance regime, a different organizational level than species-level responses to biophysical gradients. Stochastic landscape dynamics models address different entities (patches instead of organisms) at different scales (patches vs. plots), creating an obstacle to model integration, as discussed in more detail in the following section. Also, most landscape dynamics models under-represent variability in fire severity through space, because most are patch-based and force fire to spread along polygon boundaries or from cell to cell, ignoring spatial variability in biophysical gradients. Within-cell heterogeneity in fire severity can have significant effects on stand- and community-level succession (Turner and others 2003), and vegetation succession provides important constraints on future fire. Unlike some other sources of error, the biases associated with this underestimation of variance are not correctable with the ensemble approach to modeling. In the next section, we propose an approach to integrate gradient, ecosystem dynamics, and landscape dynamics models to overcome these difficulties.

The Challenge of Integration

The overall goal of the integrated modeling program described in this document is to obtain fine-scale predictions of ecosystem attributes across large geographical areas and project them over time under changing climate and disturbance regimes. The effort aims to extend plot-level measurements of vegetation composition and structure across space with gradient imputation, and through time with mechanistic ecosystem and stochastic landscape dynamics models. The challenge is to integrate these three different modeling approaches to account for non-equilibrium relationships between current vegetation and biophysical drivers, spatial complexity across broad landscapes, and the large differences in scale of processes that drive local vegetation response to biophysical conditions and disturbance processes such as timber harvest and wildfire. The integration will depend on the adequacy of three major components, discussed in the sections below. This research agenda is ambitious and full implementation under a single funding source is highly unlikely. However, the agenda consists of a series of interrelated tasks that could be addressed incrementally under a series of independently funded research projects. For example, the base empirical data required to anchor the analysis may be collected as parts of existing or future broad-scale vegetation monitoring programs, such as FIA and CVS. Numerous researchers are actively engaged in addressing many of the issues we identified in gradient modeling, ecosystem dynamics modeling, and landscape simulation. Progress in these areas is approaching the point where one or several formal integration efforts will be able to combine methods between these components to achieve reliable predictions of forest vegetation across complex landscapes and over time under altered climate and disturbance regimes.

The Empirical Anchor

The most fundamental requirement for successful integration is the adequacy of empirical data relating species distribution, growth, and regeneration to biophysical drivers and disturbance history. This empirical data anchor has three components.

First, it is essential to base the modeling efforts on large and representative samples of vegetation composition and structure along gradients of biophysical condition and disturbance history. These data should include species, size, and condition of each individual tree in the plot, including seedlings, the density and

volume of woody debris in several size classes, and the cover of shrubs, forbs, and grasses by species and non-vegetation cover by type (e.g., rock, soil, water). Rates of growth for each species should be measured by computing annual increment from cores and diameters of canopy dominant trees. Grid-based efforts such as FIA (Rudis 2003) sample biophysical conditions across broad spatial and ecological gradients, via massive replication of vegetation plots. These plots would be distributed on a grid across large geographical areas. Sample sizes in the hundreds to thousands would be ideal to cover the range of biophysical conditions and temporal disequilibria of vegetation. This magnitude of data collection is realistic, as the FIA system includes tens of thousands of vegetation plots on which much of the required data have already been collected. Alternatively, in areas where gridded plots are incomplete or to augment the grid to obtain data for specific areas of interest, one could design a sample *a priori* to capture key biophysical gradients. For example, Littell and others (2005) used digital terrain models and GIS-based modeling of environmental gradients to locate plots that filled the hyperspace of biophysical gradients expected to be key predictors of the response (in this case annual growth of montane Douglas-fir).

The second essential component is the adequacy of biophysical data. Plot-level biophysical variables would include soil depth and texture, slope, elevation, aspect, parent material, and microclimate records from portable weather stations (e.g., Hobo <http://www.microdaq.com/occ/hws/index.php>). The microclimate data would include photosynthetically active radiation, daily precipitation, maximum temperature, minimum temperature, relative humidity, soil moisture, and April 1 snow-water equivalent. Gradient modeling and geostatistics can then be used to infer microclimate characteristics continuously across complex landscapes at a fine spatial scale. This obviates major scaling and extrapolation problems with downscaling regional climate models to landscape scales. There is no need to extrapolate across scale; rather the task is to model microclimate based on biophysical gradients and then impute it at its native scale to unsampled locations within the spatial domain of the sampling network. Also, plot-level biophysical data is not a sufficient predictor set, as biophysical factors from a range of scales simultaneously influence vegetation response. In addition, synoptic biophysical data is required to impute vegetation composition and structure to unsampled

locations across the landscape. Thus, indices derived at multiple spatial scales from remotely sensed multi-spectral imagery and DEM will be essential for gradient modeling and imputation.

Accurate and spatially comprehensive information about disturbance history is the final component of essential empirical information. Disturbance history should include the dates of previous disturbances and their types, severities, and extents across the landscape. The availability of these data is currently limited for most landscapes and this is among the most substantial challenges facing this integrated modeling effort. Spatially comprehensive disturbance history is difficult to obtain. Most methods of estimating disturbance history, such as fire scars and charcoal analysis, do not produce spatially complete inferences of the disturbance histories of specific landscapes. These efforts are usually based on sparse samples across broad spatial extents and do not readily produce spatially synoptic estimates of fire history in terms of dates, extents and severities of past fires. Geostatistical modeling of fire scar chronologies is technically possible but logistically prohibitive in most landscapes. Stand age as a surrogate for disturbance history is more promising in areas of high intensity fire regime. However, in mixed- and low-severity fire regimes stand age is not a reliable surrogate for time since last disturbance. In addition, in complex mountainous landscapes, fire regime is expected to vary substantially based on topography, microclimate, barriers, and refugia, making the utility of stand age questionable as a surrogate for disturbance history. In many forested landscapes management history has had a major influence on the development of current vegetation. It is essential to obtain accurate maps of past management activities. Spatial databases describing management history should include the date, type, and perimeter of past management activities. Most public land management agencies have reasonably complete and accurate records of this kind. The integrated research agenda outlined in the final section of this document describes steps to improve the sufficiency of each component of the empirical data that is the core of this modeling paradigm.

Gradient Modeling and Ecosystem Modeling on Grids

Linking multi-scale gradient modeling with gap dynamics models is the second major component of the integrated modeling effort. Once the range of environmental hyperspace has been sampled, gradient models relating responses of interest (e.g., species distribution, growth, and establishment) to biophysical drivers and disturbance history can be built at multiple geographic

scales. With sufficient sampling across gradient space, imputation can provide unbiased estimates across the landscape at a fine spatial resolution (Ohmann and Gregory 2002). Simultaneously, the gradient models can provide species-specific parameters for ecosystem dynamics models. Ecosystem dynamics models then can project plot-level vegetation on the sampled grid into the future, accounting for growth, mortality, and succession. These future plot-level vegetation data then provide the training set to build gradient models for imputing future vegetation condition across the full landscape. This integration offers a means to extend non-equilibrium predictions across space and through time, wherein gradient models provide species response parameters, ecosystem models project future conditions on the sampled plots, and imputation provides spatial prediction of current and expected future vegetation composition and structure at a fine spatial scale (Figure 13). Importantly, climate change can be incorporated directly in the gradient and ecosystem dynamics models (Figure 13). This integration facilitates prediction of expected changes in vegetation composition and structure across complex landscapes under changing climatic conditions at a fine spatial scale.

Linking Gradient, Ecosystem, and Landscape Models

The final component of the integration is the linkage of stochastic landscape-dynamics models with gradient models of vegetation response to biophysical conditions and disturbance history. Multi-scale gradient modeling and imputation, linked to gap-phase ecosystem dynamics, can predict species distributions, growth, regeneration, succession, and fuels at a fine spatial scale and then can impute these variables with known error characteristics across large landscapes. However, neither approach is sufficient to address large-scale disturbance processes. Large-scale disturbances, such as wildfire and timber harvest, are the dominant proximate drivers of landscape-level vegetation dynamics in the western United States. However, they are not predictable based on the fine-scale relationships between vegetation and biophysical conditions at specific locations on the landscape, and thus beyond the scope of gradient and gap dynamics models. These disturbances are largely related to processes acting at much broader spatial and temporal scales. For example, timber harvest may be determined by a complex political and economic process that may or may not relate to the biophysical drivers and current vegetation condition of a given harvested stand. The size, frequency, and severity of wildfire is often related to extreme fire weather events within the constraints of

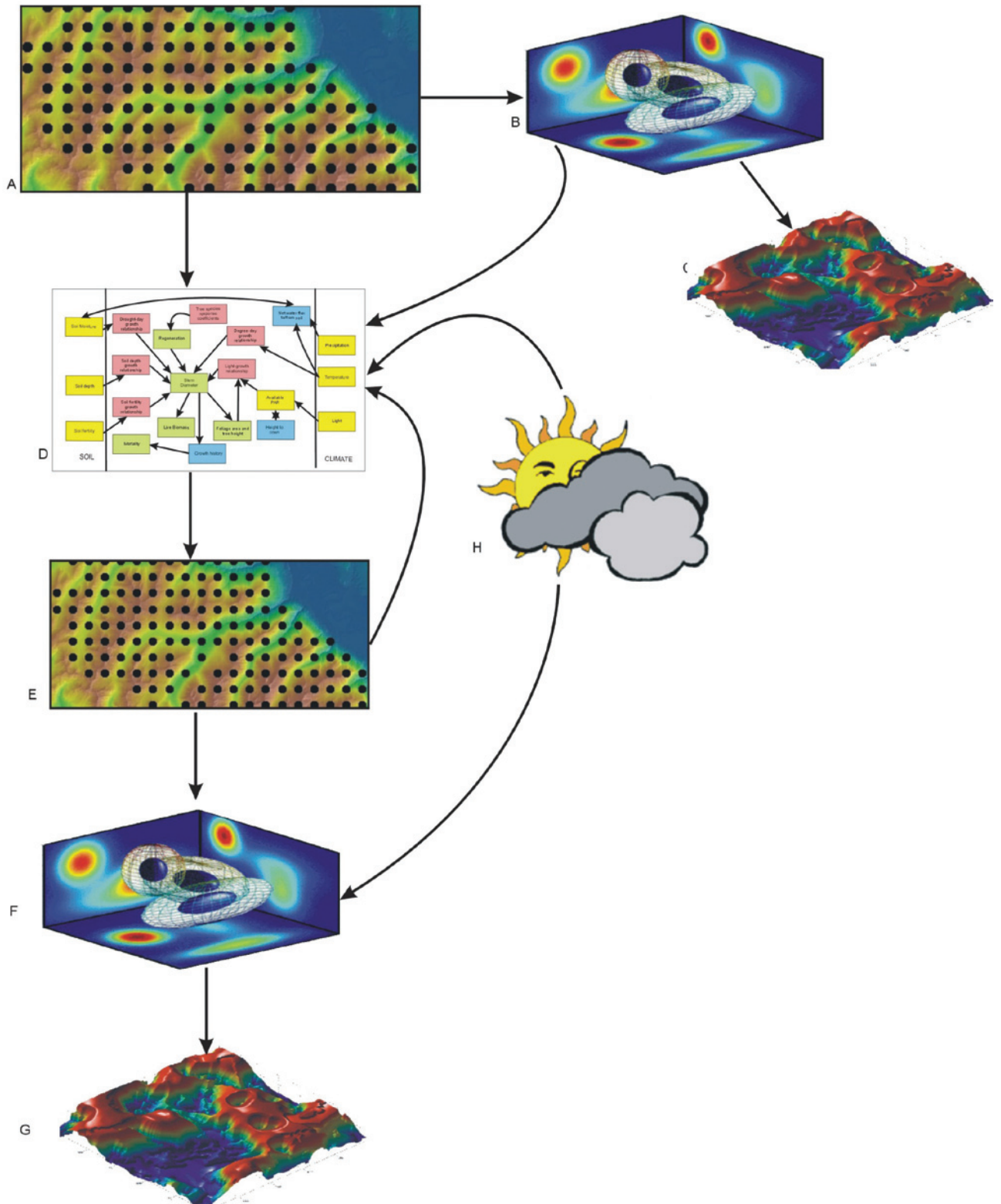


Figure 13. Integrating gap-phase ecosystem dynamics models with gradient modeling and simulation. We begin with a large sample of vegetation plots distributed across a landscape (A). Gradient models (B) are then used to quantify relationships between growth and mortality of trees by species and size by biophysical condition. Current vegetation and composition across the landscape are then mapped (C) with gradient imputation. The gap dynamics model (D) is used to project the future condition of vegetation (E) based on growth, mortality and succession in each of these plots. Gradient modeling (F) is then used to associate vegetation composition and structure with biophysical gradients, and gradient imputation (G) is used to infer expected composition and structure of vegetation across the full landscape. Changes in climate across time-steps (H) can be inserted into the ecosystem dynamics model and gradient model to project how changes in microclimate at each plot affects expected future patterns of vegetation in the imputed landscape.

biophysical context, past disturbance history, and current vegetation and fuels. Fire is also spatially contagious. Thus the occurrence of fire at a given location at a given time is not predictable based on the biophysical and vegetational characteristics of that specific location.

As discussed in the landscape dynamics modeling section above, we believe that stochastic models that simulate area, frequency, shape, and intensity of wildfires under alternative climatic scenarios provide the most reliable means to project effects of changing climate regimes on wildfire. By linking these landscape-level disturbance simulations with gradient modeling and gap-phase ecosystem modeling, it may be possible to obtain a broad integration of the processes that drive the relationships between forests, climate and fire, and the ability to produce expectations about the effects of future changes in climate and disturbance regime on forest ecosystems across space and through time.

The challenge lies in the fact that stochastic landscape dynamics models simulate patches, while ecosystem and gradient models predict vegetation composition

and structure within stands. This disjunction in organizational level is the major challenge in uniting these models to predict the effects of altered climate and fire regimes on vegetation composition and structure across broad landscapes. It is essential to translate the patch-dynamics predictions of stochastic landscape dynamics models back down to stand level vegetation and composition. As discussed in the integrated research agenda below, this may be accomplished by using appropriate transfer functions. The stochastic landscape models produce perimeters of disturbance polygons (e.g., timber harvest, insects, wildfire). Disturbance effects on vegetation can be inferred using empirically derived transfer functions, developed from large samples of plots across biophysical context and disturbance history, or appropriate submodels, such as FOFEM (Peterson and Ryan 1986, <http://fire.org>). Through these transfer functions the local effects of broad-scale disturbance on vegetation composition and structure can be inferred. Figure 14 illustrates the approach we suggest for integrating landscape, ecosystem, and gradient models.

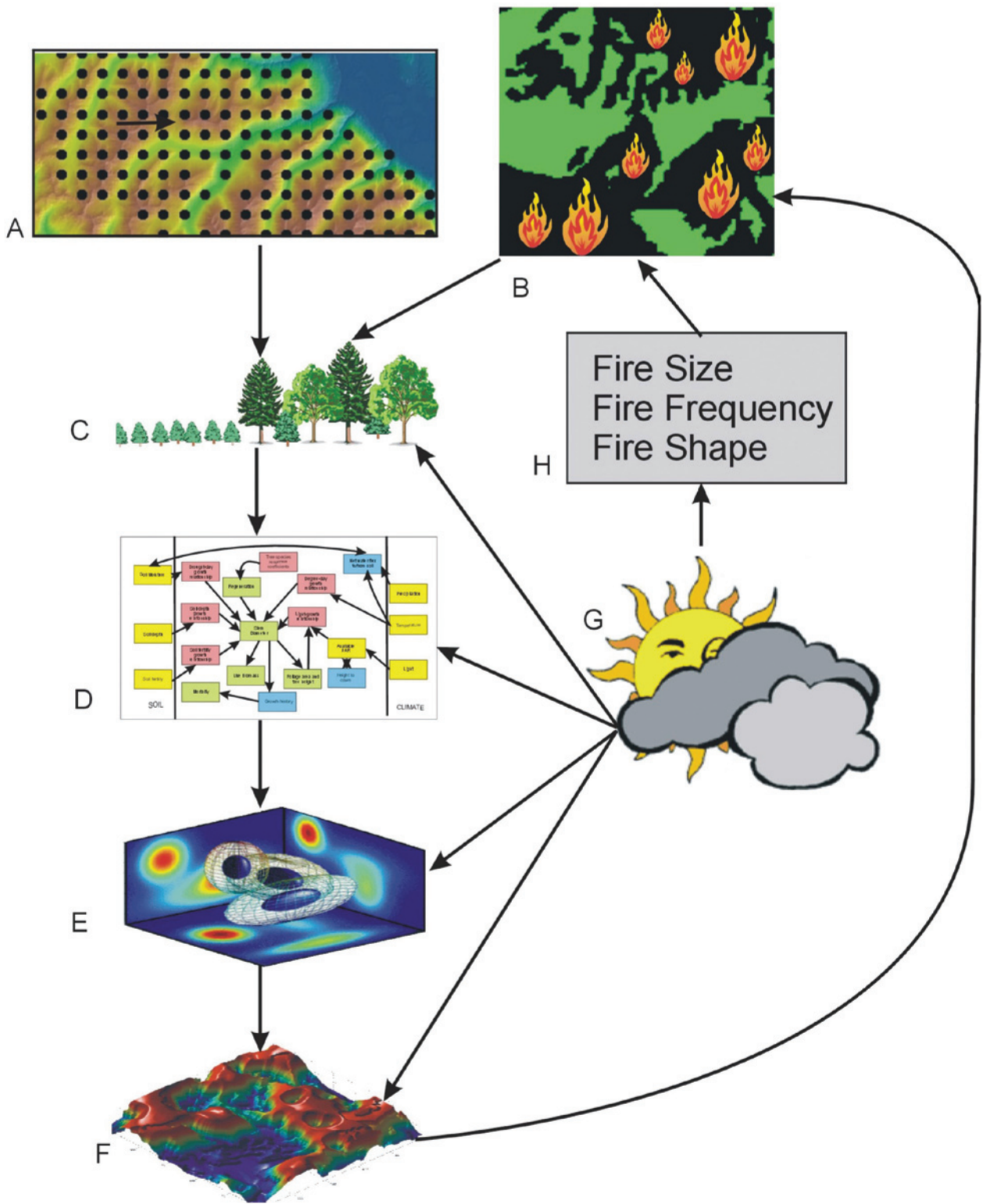


Figure 14. Integrating stochastic landscape dynamics with gradient and gap models. The approach is the same as outlined in Figure 13, with the addition of climate affects on fire regime (H), stochastic simulation of landscape disturbance, including fire and timber harvest (B), and transfer functions or submodels (C) to translate from the patch mosaic produced by the landscape model to vegetation composition and structure within stands. At each time-step the sequence of steps is: (A) begin with a large sample of vegetation plots distributed across a landscape, (B) simulate disturbances with the landscape model, (C) infer effects of these disturbances on existing vegetation in sampled plots, (D) grow sampled plots with ecosystem dynamics model, (E) apply gradient models to predict vegetation composition, structure, and growth based on biophysical and disturbance factors, and (F) impute gradient models to produce spatially explicit predictions of vegetation composition and structure across the landscape. This imputed landscape is then the initial condition for the next time-step and the process continues iteratively. Changes in climate across time-steps (G) influences fire regime parameters (H), transfer functions (C), ecosystem dynamics models (D), biophysical gradient models (E), and imputation across the landscape (F), as described more fully in the integrated research agenda section below.

An Integrated Research Agenda

Step 1—Multi-scale Gradient Modeling

Questions

1. What are the multi-scale relationships between topography and microclimatic variability (e.g., temperature, humidity, soil moisture, and snow pack)?
2. How does microclimatic variability affect the distribution of individual tree species, the composition of plant communities, growth at the species and community levels, and regeneration?
3. To what extent is current vegetation prediction affected by disturbance history?
4. How do fine and coarse fuel loads and their rates of accumulation depend on energy, temperature, humidity, water, snow-pack, soils, and topography in interaction with vegetation condition and age?
5. What is the relative importance of spatial dependence vs. non-spatial biophysical variables for predicting the response of individual tree species and the plant community?
6. What is the relative predictive power of coarser-scale predictors, such as DAYMET, PRISM, and MTCLIM, compared to plot-derived measurements of energy, temperature, humidity, water, snowpack, soils, and topography?
7. Can we successfully aggregate predictions from plot-level measurements to the scale of coarser (DAYMET, etc.) grids?

Data

1. Plot-level measurements of topography, vegetation composition and structure, annual growth, microclimate, seedling establishment, snow-water equivalent, and soils.
2. Topographical variables for each plot DEM include slope, aspect, elevation, profile curvature, tangent curvature, topographical wetness index, and others at a range of radii (approximately 100, 200...1,000 m), that spans the plausible range of influence of local topography on microclimate and vegetation.
3. Disturbance history data such as fire perimeter and cutting history maps, plot level evidence of past fire dates and intensities, beetle infestations, and timber harvest.
4. A large sample of plots, distributed representatively across the full combination of biophysical gradients.

Existing re-measure plot grids should be utilized to gain the benefit of prior investment and data collection. FIA and related sample grids such as the National Vegetation Pilot provide sufficient replication and geographic coverage, and they are ideal as a base for these analyses. Plot structures should be augmented to better capture spatial autocorrelation factors critical to successful imputation.

5. We suggest developing these approaches on one or several pilot grids, e.g., the National Vegetation Pilot grid located in the Idaho Panhandle National Forests. These grids should be augmented to ensure that rare types and disturbance histories are adequately sampled.
6. The following climatological/ecological variables on each plot, weekly, monthly, seasonally, annually, for five years:
 - a) ambient temperature
 - b) solar radiation (incident, diffuse)
 - c) humidity
 - d) precipitation
 - e) snow pack
 - f) soil depth and texture
7. At the end of the five-year period vegetation conditions on the plots should be remeasured, including measurement of annual increment of canopy dominant trees, seedlings, and coarse and fine fuels.

Analysis

1. Gradient modeling appropriate for identifying driver-response relationships (Table 1) for example CCA, GLM, GAM.
2. A combination of multiple scale variables, partial bivariate scaling (Thompson and McGarigal 2002), and hierarchical variance partitioning (Cushman and McGarigal 2003) to optimize scaling relationships across independent variables and incorporate the influence of spatial dependence.
3. Data splitting or Monte Carlo resampling methods to evaluate the predictive power of the models, and formal accuracy assessment involving ROC, Kappa, and other appropriate tests.

Expected products

1. Multi-scale gradient models predicting microclimate from topographical data.

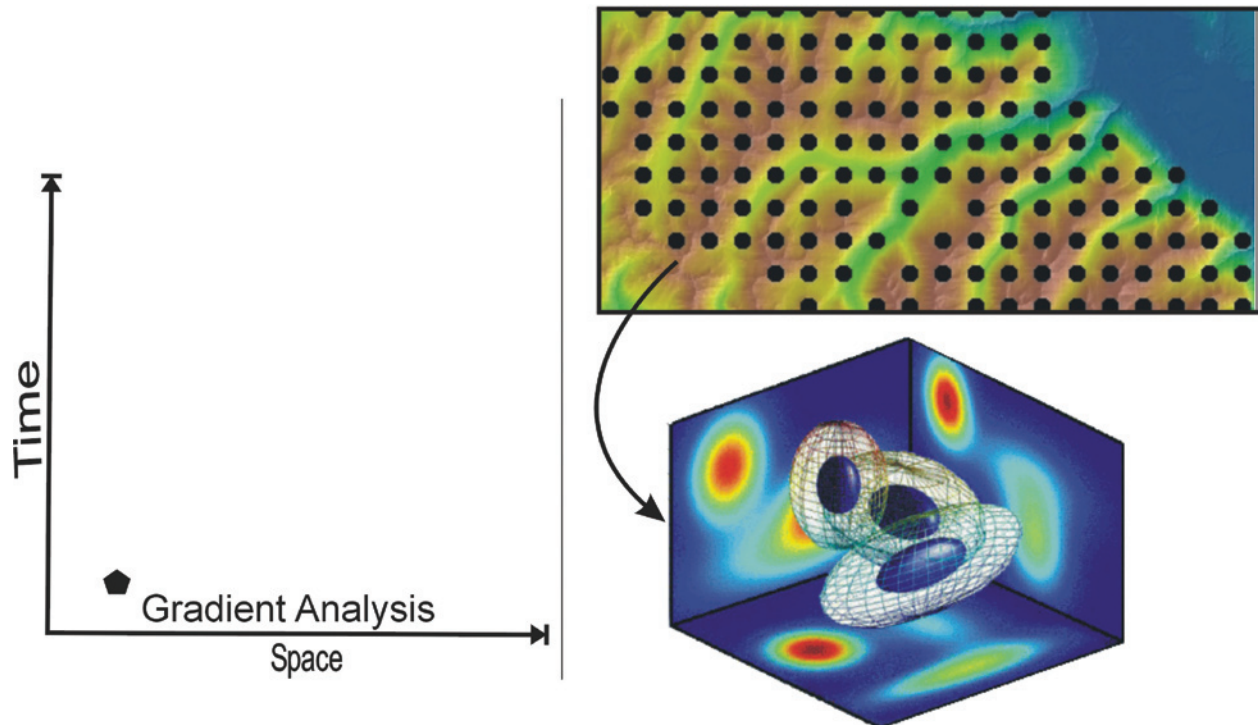


Figure 15. Gradient modeling produces statistical models of relationships between species distributions, community structure, growth, and other dependent variables and gradients of biophysical driving variables and disturbance history. These gradient models are non-spatial and limited to the single instance in time at which their data was gathered. Temporal factors such as disturbance history are included as explanatory variables. These are reasonable time-proxies, giving gradient models temporal depth looking backward in time, but with limited ability to project change into the future. Thus, looking forward in time, the gradient method produces predictions that have zero dimension in the Time-by-Space scale space (a point in the two-dimensional space on the left).

2. Multi-scale gradient models predicting species occurrence, growth and regeneration, forest structure, and fuels.

Importance

1. These models in themselves will be useful to managers by providing quantitative predictions of relationships between biophysical gradients and the responses of forest ecosystems.
2. Gradient models are the basis for gradient imputation, in which the expected condition of vegetation is mapped at a fine spatial resolution across landscapes.
3. Gradient models will provide species-specific parameters for ecosystem dynamics models. Specifically, they will provide growth, mortality, and regeneration curves for each species across each dimension of the biophysical niche.

Step 2—Gradient Imputation

Questions

1. What is the spatial structure of microclimatic gradients across complex landscapes?
2. What is the spatial pattern of vegetation composition and structure, growth, and regeneration across complex landscapes?
3. What is the accuracy of these imputed maps of microclimate and forest structure for each dependent variable?

Data

1. Multi-scale data derived from DEM including slope, aspect, elevation, profile curvature, tangent curvature, topographical wetness index, and others at a range of radii. These will be produced by moving window algorithms for each variable at the same radii as used in Step 1.
2. Remotely sensed data and GIS data:
 - a) Spectral data from TM imagery and, ideally, recent images from spring and summer.
 - b) Spectral data from Quickbird if available and NAIP color imagery. These provide much higher spatial resolution than TM imagery, which could be critical in producing powerful imputation models.
 - c) GIS layers showing stand histories, past disturbances, soil, geology, and hydrology.

Analysis

1. Gradient imputation to derive expected values for each dependent variable at each location in the landscape based on the multi-scale gradient models. The

models used for imputation will include both the biophysical driving variables used in Step 1 and the synoptic scale GIS and remote sensing variables collected for this Step, including disturbance history.

2. The imputation methods will include gradient nearest neighbor and k-nearest neighbor for canonical ordination, or analogous methods for GLM and GAM.
3. Quantify spatial patterns of each dependent variable across the landscape using landscape pattern analysis software such as FRAGSTATS.

Expected products

1. Predicted values of each dependent variable mapped across complex landscapes.
2. These variables will include microclimate and vegetation. Predicted microclimate variables include growing degree days, spring snow-water equivalent, expected temperature, and soil moisture regime. Predicted vegetation variables will include occurrence probability and basal area by tree species, stand age, canopy closure, cover by shrub species, and coarse and fine fuels.

Importance

1. These spatially explicit, fine-scale, broad-extent predictions of forest composition, structure, growth, and regeneration will provide managers more detail about the condition of forest resources across complex landscapes than has been possible in the past.
2. Such information is essential to quantify the site-level and cumulative effects of management actions and natural disturbances.

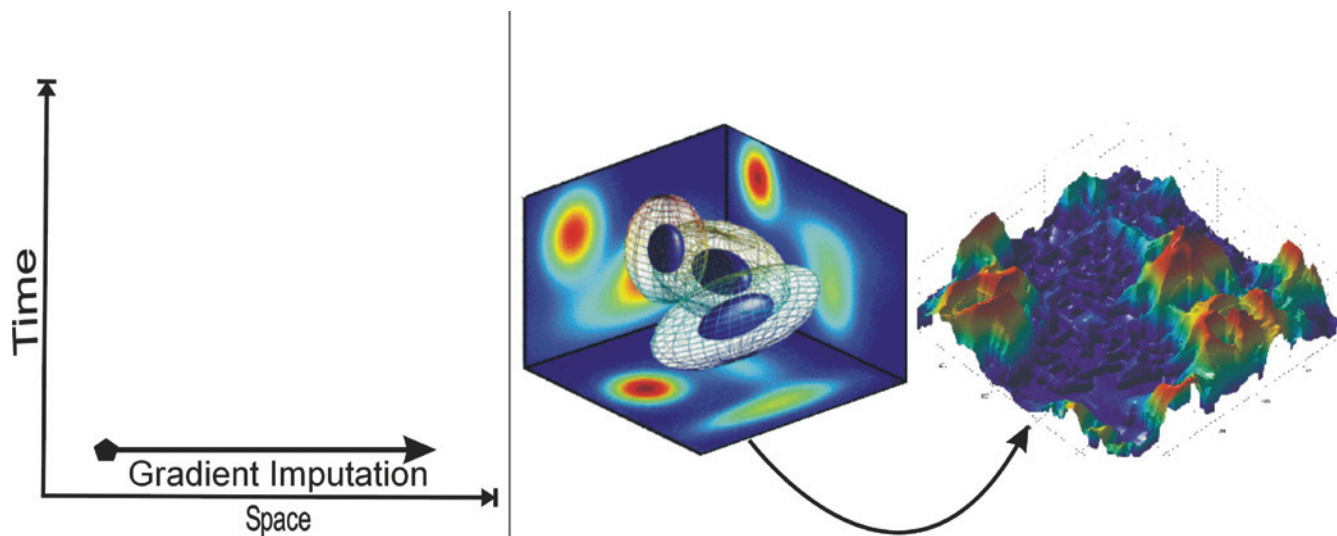


Figure 16. Gradient models predict the value of a dependent variable as a function of n-dimensional environmental data. These models are multi-scale and multi-dimensional in ecological space (Figure 15). Gradient imputation links the model in ecological space to the structure of biophysical gradients across the landscape, thereby extending the gradient approach in the spatial dimension. Output maps provide quantitative estimates of the distribution of each variable across the landscape, providing spatially explicit information about resource conditions at multiple spatial scales.

Step 3—Linking ecosystem dynamics to gradient imputation

Questions

1. How can parameters for stand-level, plant-based ecosystem dynamics models (growth, mortality, regeneration, competition, soil, climate) be developed using multi-scale gradient models?
2. What are the initial conditions for each cell on complex landscapes?
3. How reliably can we integrate predictions of future vegetation on plots with gradient imputation to predict future vegetation across complex landscapes?
4. How will altered climate affect the response of vegetation across the simulated landscape?

Data

1. Initial vegetation condition among sampled plots.
2. Initial microclimate and biophysical characteristics of each plot.
3. Empirical models of growth, death, and regeneration responses by species, age, and competitive position, across biophysical gradient space. This is provided by Step 1.
4. Empirical models of microclimate across biophysical gradient space. This is provided by Step 1.
5. Expected initial condition of cell across the simulated landscape, in terms of species composition, age, biophysical context, and microclimate, provided from Step 2.

Analysis

1. Use gradient models of growth, mortality, and regeneration by species, age, and competitive position, across biophysical gradient space to quantify response functions in a forest dynamics model, such as FM.
2. Use imputation results from Step 2 to provide the biophysical context and microclimate for each cell across the landscape.

3. Simulate changes in forest composition and structure in sampled plots under an equilibrium climate.
4. Simulate changes in forest composition and structure under four alternative climate change scenarios: 1) warmer/wetter, 2) warmer/drier, 3) colder/wetter, 4) colder/drier.
5. Use the results of 3 and 4 as input into gradient models to produce imputed expectations of the composition and structure of vegetation across the full landscape under each scenario.
6. Quantify expected changes in vegetation composition and structure under current and altered climate regimes in the absence of exogenous disturbance. Quantify changes in the spatial configuration of the vegetation mosaic using landscape pattern analysis tools such as FRAGSTATS.

Expected products

1. Predictions of future vegetation on measured plots accounting for succession and climatic change.
2. Prediction of future vegetation across complex landscapes under alternative climate regimes in the absence of disturbance.

Importance

1. The forest dynamics model will explicitly address nonequilibrium dynamics of existing vegetation due to succession and interspecific interactions.
2. The linkage of the forest dynamics model with gradient imputation will allow projection of growth, mortality, and succession across landscapes at fine spatial scale.
3. Simulation under current and altered climate regimes will provide an estimate of impact possible from altered climate due to autogenous community-level processes.
4. Mapping expected future fine-scale vegetation across complex landscapes will provide managers with improved information about expected condition of forest resources in the coming decades.

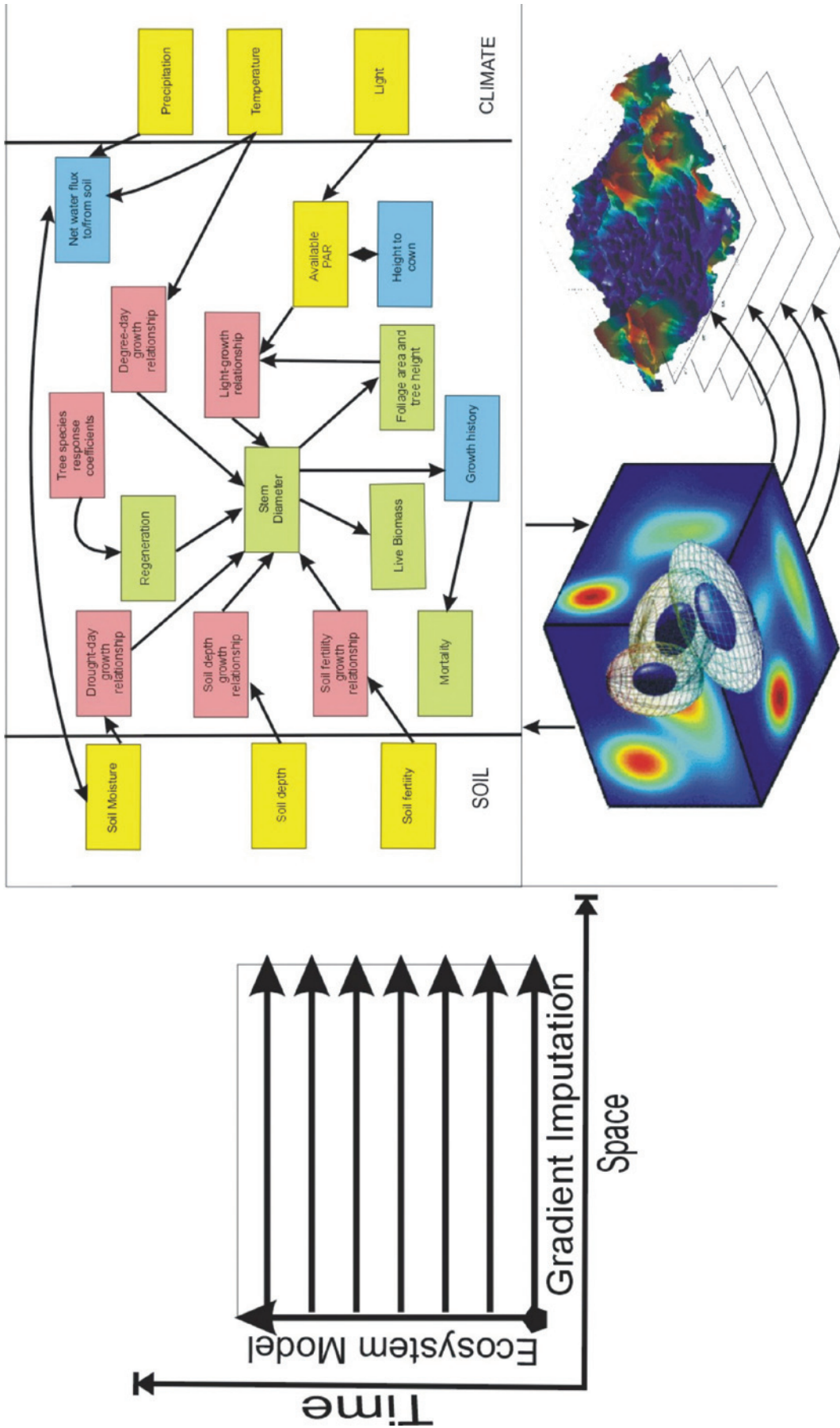


Figure 17. The gradient models provide parameter values and functional forms for the ecosystem dynamics models (pink boxes above). This anchors the ecosystem dynamics models with empirically derived growth, regeneration, and mortality parameters. Gradient imputation provides the initial conditions of driving variables (yellow boxes) on each cell. Ecosystem dynamics models are then run across all measured vegetation plots, providing expected future vegetation. Altered climatic scenarios can be readily implemented by changing climate inputs. At each time-step, the results of the ecosystem dynamics model are returned as the training data for the gradient models and a map of vegetation composition and structure at that time-step is created through gradient imputation. By linking ecosystem dynamics models to gradient models with imputation, it is possible to span the space x time scale space, integrating spatial and temporal complexity in forest responses to biophysical drivers.

Step 4—Linking landscape dynamics simulation to ecosystem and gradient models

4a implementing alternative disturbance regimes in a landscape dynamics model

Questions

1. What is the relationship between climate, weather, microclimate, vegetation, topography, and fire regime in terms of frequency, size, and severity of fires?
2. How do insect outbreaks and expected future land use confound these relationships?
3. How can these relationships be translated into input for landscape dynamics models such that uncertainties and error propagation are minimized?
4. How will expected fire regimes, management, and insect outbreaks under different climate affect forest ecosystems on complex landscapes?

Data

1. Predictive models of the responses of fire regimes to climate.
2. Extent and pattern of expected land use change.
3. Method for estimating insect disturbance (quantitative or heuristic).
4. Initial vegetation conditions (imputed from gradient models) and ecosystem model outputs at appropriate time-steps.

Analysis

1. Use a landscape dynamics simulation model, such as RMLands, to simulate current and alternative disturbance regimes.
2. Define current disturbance regime based on frequency, extent, pattern, and severity of each disturbance type by biophysical context.
3. Define alternative disturbance regimes based on expected changes to frequency, extent, severity, and pattern of each disturbance type across biophysical gradients.
4. Alternative scenarios should include the warm/wet, warm/dry, cold/wet, cold/dry scenarios used in Step 3.

5. Apply estimated parameters of disturbance regimes to the landscape dynamics simulation model for current and alternative scenarios.
6. Initialize each scenario with current vegetation and biophysical conditions.
7. Simulate each scenario with multiple runs (minimum of 100 over 500+ years), at a relatively short time-step (5-20 years).
8. Characterize change in landscape pattern of cover types and successional stages under each scenario using landscape pattern analysis software such as FRAGSTATS and multivariate landscape trajectory analysis (Cushman and McGarigal 2007, in press).

Expected products

1. Quantification of range of variation in patch mosaic consisting of cover types and successional stages under the current climate.
2. Range of variation of vegetation mosaic under alternative future climates.
3. Predicted effects of altered disturbance regimes on the area and configuration of cover types and successional stages, enabling managers to infer the effects of alternative management at the stand level.

Importance

1. Information about the range of variation of cover type and successional stage mosaic under current climatic conditions will provide critical information for evaluating the current condition with respect to historic ranges and desired future conditions.
2. Information about expected ranges of variation of cover types and successional stages under possible future climatic regimes will provide managers critical information about the possible extent and nature of changes in forest ecosystems resulting from altered climate and disturbance regimes.
3. This information will enable managers to anticipate changes in disturbance regimes and to take proactive measures to appropriately manage resources under changing ecological conditions.

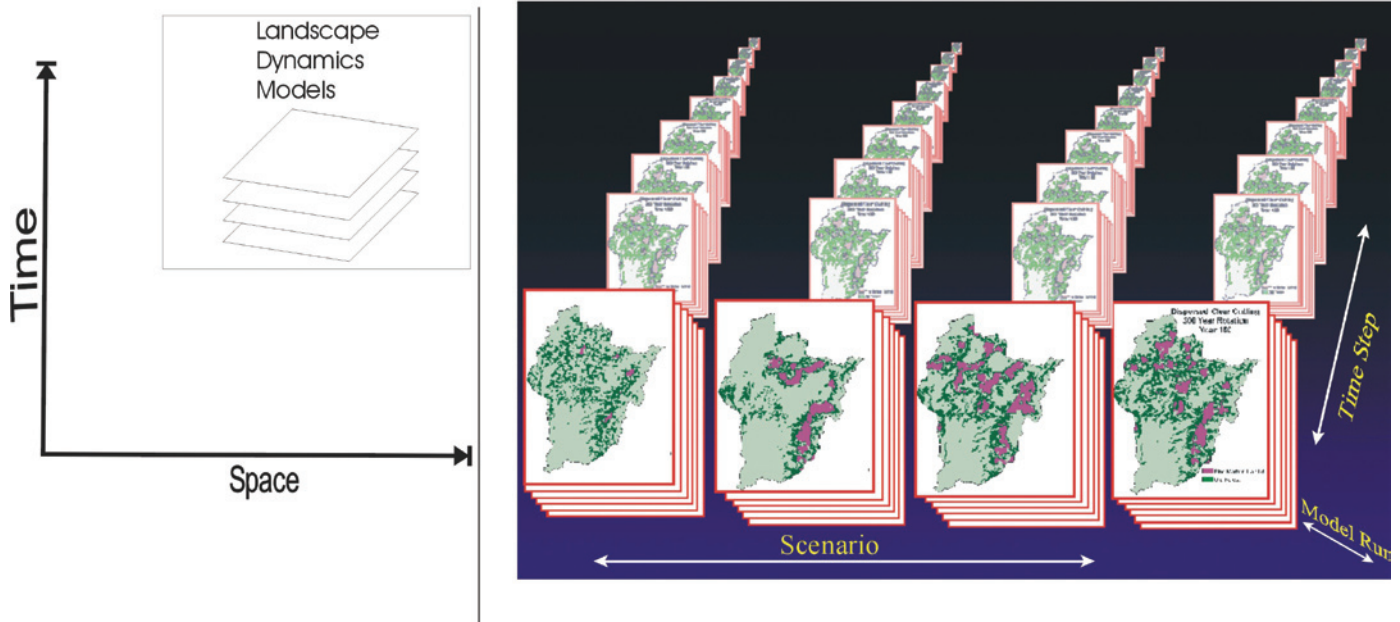


Figure 18. Stochastic landscape simulation models provide a means to simulate how disturbance regimes affect the area and configuration of cover types and successional stages across complex landscapes and through time. The predictions are probabilistic and patch-based. Thus although they explicitly model broad-scale disturbance, they do so with different entities (patches instead of organisms) than the ecosystem and gradient models. A significant remaining challenge is to link patch level predictions of fire size, shape, and severity with the responses of organisms across complex biophysical gradients.

4b linking extent, frequency, and severity of fires to vegetation response at a fine spatial scale, continuously across the landscape

Questions

1. What are the relationships between type, extent, frequency, and severity of disturbance and fine-scale vegetation composition and structure across broad landscapes?
2. What are the uncertainties in predicting site-level changes in vegetation composition, structure, growth, mortality, and regeneration from the output of patch-based landscape dynamics models?
3. Does the integration of gradient models, ecosystem dynamic models, and landscape disturbance models improve our ability to predict the effects of changing biophysical conditions and disturbance regimes on forest vegetation, at a fine-spatial scale, across large spatial extents, and through time?

Data

1. Empirical measurements of fire impacts on vegetation. Requires measurement of vegetation response on a large number of fires of varying age, size, and severity across biophysical gradients.
2. Requires a large and representative sample of re-measure plots before and after disturbance within the perimeter of each fire.
3. These plots must cover the full combination of biophysical gradients and disturbance size, severity, and age in order to derive robust models.
4. A large investment to collect samples prior to fires, to populate the landscape with “pre-treatment” measurements.

5. A large investment in post-fire remeasurements on these permanent plots to quantify fire impacts in the context of initial vegetation condition, biophysical context, and disturbance characteristics.

Analysis

1. Use gradient modeling to infer relationships between species response and type, size, intensity, biophysical context, and time since fire.
2. Apply these models to predict effects of simulated fires on vegetation condition across complex landscapes.
3. Predict post-fire vegetation response and recovery. This is done for each cell post-fire in the succeeding time-step. Within scenarios, this provides expected response of fine-scale vegetation across the full landscape to one realization of a disturbance regime. Across scenarios, this provides aggregate statistics of vegetation response to altered climate and fire regime.

Expected products

1. Spatially explicit predictions of expected future vegetation across complex landscapes under alternative climatic and disturbance regimes.

Importance

1. Effectively translating from the patch-mosaic dynamics of landscape simulation models back to fine-scale vegetation dynamics is the key to integrating biophysical modeling of individualistic vegetation response with large-scale disturbances.
2. This integration is essential if we are to successfully understand and predict the effects of climate change and disturbance regime change on forest ecosystems.

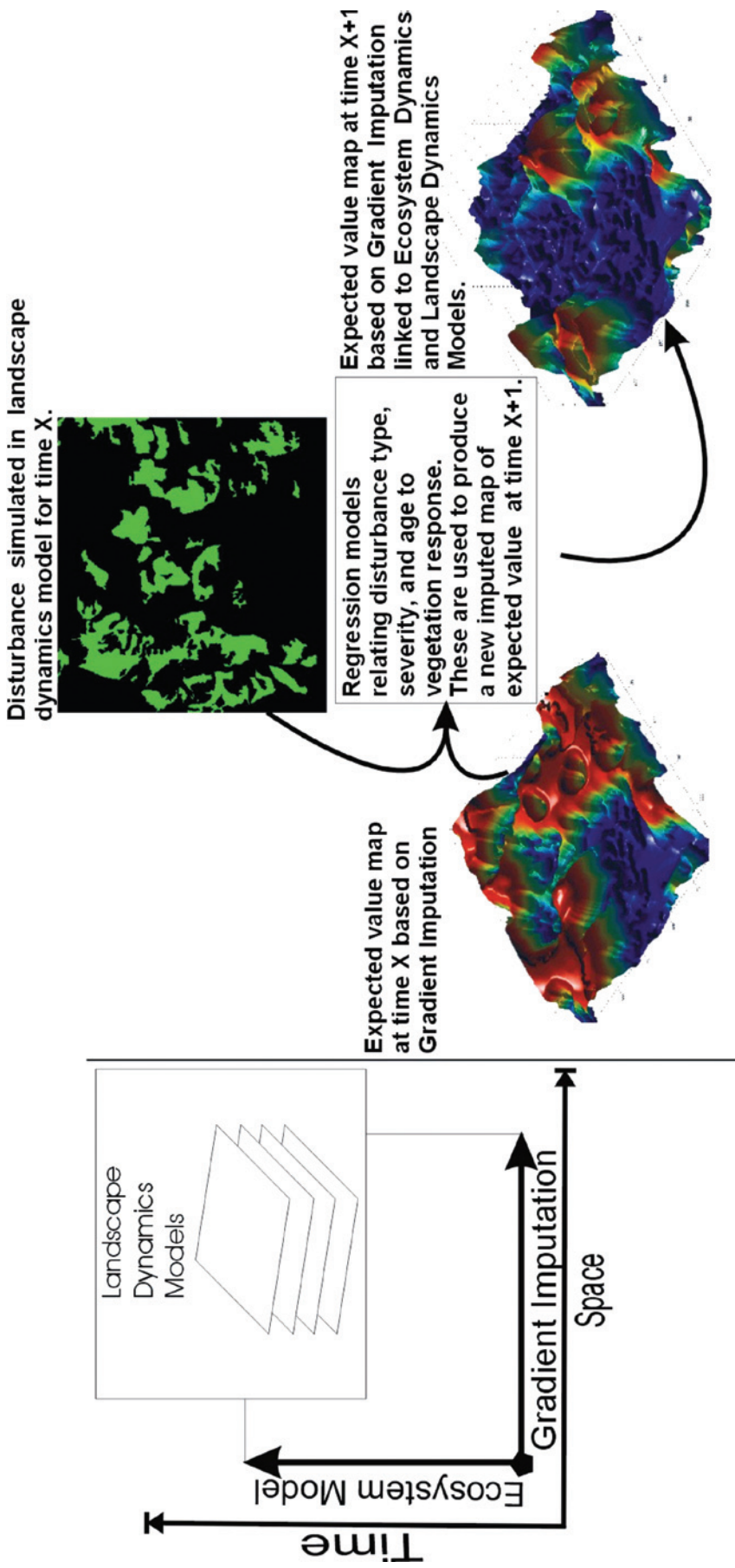


Figure 19. Reliable predictions of the effects of management, climate, and disturbance regimes require the integration of broad-scale disturbance with ecological responses across biophysical gradients and over time. This can be done by linking gradient modeling, ecosystem dynamics modeling, and landscape dynamics modeling. However, this integration is challenging due to the qualitative difference between the entities being addressed (Figure 18). We therefore return full-cycle to the gradient modeling paradigm. With large samples of remeasure plots in areas that have received fire we can develop quantitative link functions (via regression, GLMs, and CCA) between fire size, shape, and biophysical context and the response of vegetation and other ecological factors at the site-level. The key ingredient for this analysis is pre-disturbance and post-disturbance sampling.

Conclusion

The response of forest ecosystems and fire regimes to global climate change will depend on factors at multiple scales and complex interactions among climate, fire, and vegetation. Altered fire regimes may have larger impacts on species distribution, migration, substitution, and extinction than the direct effects of climate change itself (Weber and Flannigan 1997, McKenzie and others 2004). An integrated approach is needed that addresses the nonequilibrium and often discontinuous dynamics of mechanisms and responses at biologically meaningful scales, including the critical scale of direct interactions between organisms and the environment. Our agenda links multi-scale gradient modeling, ecosystem dynamics modeling, and landscape simulation, to predict the changes to forest ecosystems from a changing biophysical environment and disturbance regimes.

Complete model integration brings us back full-cycle to the relationships between forest vegetation and biophysical gradients. Without a linkage to fine-scale vegetation and the biophysical limiting factors that govern its response, landscape disturbance models cannot reliably predict changes in species distributions,

community structure, stand structure, and other critical attributes of forest ecosystems. Conversely, without addressing landscape dynamics, predictions of relationships between biophysical limiting factors and vegetation are confounded by disturbance. Wildfire is likely to be the proximate cause of ecosystem change in the context of climate change, and meaningful understanding must involve linking vegetation response to biophysical gradients with the effects of large-scale disturbance.

Synthesis of existing data sets will be helpful in guiding this effort but will not be sufficient. Successful integration of forest ecosystem dynamics, climate change, and disturbance regimes will require investment in sampling efforts to gather empirical data on species distributions, growth, regeneration, and fire histories across broad scales and over extensive biophysical gradients. As the effort will necessarily be large and involve integration of several major fields of research, it will also require collaboration among many partners. No one scientist, institution, or research discipline has the expertise required for this integration. Broad and magnanimous collaboration will be essential.

References

- Acevedo, M. F., Urban, D. L., and Shugart, H. H. 1996. Models of forest dynamics based on roles of tree species. *Ecological Modeling* 87(1-3): 267-284.
- Agee, J. K. 1997. Severe fire weather: too hot to handle? *Northwest Science* 71: 153-156.
- Aide, T. M. and Cavelier, J. 1994. Barriers to lowland tropical forest restoration in the Sierra Nevada de Santa Marta, Colombia. *Restoration Ecology* 2: 219-229.
- Aitchison, J. 1986. The statistical analysis of compositional data. New York, NY: Chapman and Hall.
- Allen, T. F. H. and Hoekstra, T. W. 1992. Toward a unified ecology. New York, NY: Columbia University Press.
- Anderson, R. P., Lew, D., and Peterson, A. T. 2003. Evaluating predictive models of species' distributions: criteria for selecting optimal models. *Ecological Modeling* 162: 211-232.
- Austin, M. P. 1985. Continuum concept, ordination methods, and niche theory. *Annual Review of Ecology and Systematics* 16: 39-61.
- Austin, M. P. 1987. Models for the analysis of species' response to environmental gradients. *Vegetatio* 69: 35-45.
- Austin, M. P. 1999. A silent clash of paradigms: some inconsistencies in community ecology. *Oikos* 86: 170-178.
- Austin, M. P. 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modeling. *Ecological Modeling* 157: 101-118.
- Austin, M. P. and Cunningham, R. B. 1981. Observational analysis of environmental gradients. *Proceedings of the Ecological Society of Australia* 11: 109-119.
- Austin, M. P., Nicholls, A. O., Doherty, M. D., and Meyers, J. A. 1994. Determining species response functions to environmental gradient by means of a B-function. *Journal of Vegetation Science* 5: 215-228.
- Bachelet, D., Lenihan, J. M., Daly, C., Neilson, R. P., Ojima, D. S., and Parton, W. J. 2001b. MC1: a dynamic vegetation model for estimating the distribution of vegetation and associated ecosystem fluxes of carbon, nutrients, and water. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station; General Technical Report PNW-GTR-508.
- Bachelet, D., Neilson, R. P., Lenihan, J. M., and Drapek, R. J. 2001a. Climate change effects on vegetation distribution and carbon budget in the United States. *Ecosystems* 4: 164-185.
- Baker, W. L. 1989. Effect of scale and spatial heterogeneity on fire-interval distributions. *Canadian Journal of Forest Research* 19: 700-706.
- Baker, W. L. 1992. The landscape ecology of large disturbances in the design and management of nature reserves. *Landscape Ecology* 7: 181-194.
- Baker, W. L. 1993. Spatially heterogeneous multi-scale response of landscapes to fire suppression. *Oikos* 66: 66-71.
- Baker, W. L. 1995. Longterm response of disturbance landscapes to human intervention and global change. *Landscape Ecology* 10: 143-159.
- Baker, W. L. 2003. Fires and climate in forested landscapes of the U.S. Rocky Mountains. In: Veblen, T. T., Baker, W. L., Montenegro, G., and Swetnam, T. W., eds. Fire and climate change in temperate ecosystems of the western Americas. New York, NY: Springer-Verlag. pp. 120-157.
- Baker, W. L., Egbert, S. L., and Frazier, G. F. 1991. A spatial model for studying the effects of climatic change on the structure of landscapes subject to large disturbances. *Ecological Modeling* 56: 109-125.
- Ball, G. L. and Gimblett, H. R. 1992. Spatial dynamic emergent hierarchies simulation and assessment system. *Ecological Modeling* 62: 107-121.
- Barnosky, C. W., Anderson, P. M., and Bartlein, P. J. 1987. The northwestern U.S. during deglaciation; vegetational history and paleoclimatic implications. In: Ruddiman, W. F., and Wright H. E., Jr., eds. North America and adjacent oceans during the last deglaciation. Boulder, CO: Geological Society of America. pp. 289-321.
- Bartlein, P. J., Whitlock, C., and Shafer, S. 1997. Future climate in the Yellowstone National Park region and its potential impact on vegetation. *Conservation Biology* 11: 782-792.
- Bassow, S., Ford, E. D., and Kiester, A. R. 1990. A critique of carbon-based tree growth models. In: Dixon, R. K., Meldahl, R. S., Ruark, G. A., and Warren, W. G., eds. Process modeling of forest growth responses to environmental stress. Portland, OR: Timber Press. pp. 50-57.
- Battaglia, M. and Sands, P. 1998. Process-based forest productivity models and their application in forest management. *Forest Ecology and Management* 102: 13-32.
- Billheimer, D., Guttorp, P., and Fagan, W. F. 2001. Statistical interpretation of species composition. *Journal of the American Statistical Association* 96: 1205-1214.
- Bolliger, J., Kienast, F., and Bugmann, H. 2000a. Comparing models for tree distributions: concept, structures, and behavior. *Ecological Modeling* 134: 89-102.
- Bolliger, J., Kienast, F., and Bugmann, H. 2000b. Risks of global warming on montane and subalpine forests in Switzerland—a modeling study. *Register of Environmental Change* 1: 99-111.
- Bonan, G. B. and Shugart, H. H. 1989. Environmental factors and ecological processes in boreal forests. *Annual Review of Ecology and Systematics* 20: 1-28.
- Boose, E. R., Foster, D. R., and Fluet, M. 1994. Hurricanes impacts to tropical and temperate forest landscapes. *Ecological Monographs* 64: 369-400.
- Booth, G. D., Niccolucci, M. J., and Schuster, E. G. 1994. Identifying proxy sets in multiple linear regression: an aid to better coefficient interpretation. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station; Research Paper INT-470.
- Borcard, D. and Legendre, P. 1994. Environmental control and spatial structure in ecological communities: an example using oribatid mites (*Acari, Oribatei*). *Environmental and Ecological Statistics* 1: 37-53.

- Borcard, D., Legendre, P., and Drapeau, P. 1992. Partialling out the spatial component of ecological variation. *Ecology* 73: 1045-1055.
- Botkin, D. B. and Schenk, H. J. 1996. History and rationales of the JABOWA model of forest growth. In: Review and analysis of JABOWA and related forest models and their use in climate change studies. Research Triangle Park, NC: National Council of the Paper Industry for Air and Stream Improvement, Inc. pp. 11-162.
- Breiman, L., Friedman, J. H., Olshen, R., and Stone, C. J. 1984. Classification and regression trees. Belmont, CA: Wadsworth International Group. 358 p.
- Bunn, A. G., Goetz, S. J., and Fiske, G. J. 2005a. Observed and predicted responses of plant growth to climate across Canada. *Geophysical Research Letters* 32(L16710).
- Bunn, A. G., Graumlich, L. J., and Urban, D. L. 2005b. Trends in twentieth-century tree growth at high elevations in the Sierra Nevada and White Mountains, USA. *Holocene* 15: 481-488.
- Bunn, A. G., Lawrence, R. L., Bellante, G. J., Waggoner, L. A., and Graumlich, L. J. 2003. Spatial variation in distribution and growth patterns of old growth strip-bark pines. *Arctic, Antarctic and Alpine Research* 35: 323-330.
- Campbell, I. D. and McAndrews, J. H. 1993. Forest disequilibrium caused by rapid Little Ice Age cooling. *Nature* 366: 336-338.
- Chew, J. D., Stalling, C., and Moeller, K. 2004. Integrating knowledge for simulation vegetation change at landscape scales. *Western Journal of Applied Forestry* 19(2): 102-108.
- Christensen, N. L. 1988. Succession and natural disturbance: paradigms, problems, and preservation of natural ecosystems. In: Agee, J. K. and Johnson, D. R., eds. *Ecosystem management for parks and wilderness*. Seattle, WA: University of Washington Press. pp. 62-81.
- Clark, J. S. 1990a. Fire and climate change during the last 750 years in northwestern Minnesota. *Ecological Monographs* 60: 135-159.
- Clark, J. S. 1990b. Integration of ecological levels: individual plant growth, population mortality, and ecosystem dynamics. *Journal of Ecology* 78: 275-299.
- Clark, J. S. 1993. Fire, climate, and forest processes during the last 2000 years. In: Dean, W. E. and Bradbury, J. P., eds. *Ecology and Paleocology of Elk Lake*. Boulder, CO: Geological Society of America. pp. 295-308.
- Clark, J. S. 1993. Sensitivity of forest communities to global climate change. Kareiva, P., Kingsolver, J. G., and Huey, R. B., eds. *Biotic Interactions and Global Change*. Sunderland, MA: Sinauer Associates. pp. 315-332.
- Clark, L. A. and Pregibon, D. 1992. Tree-based models. In: Chamber, J. M. and Hastie, T. J., eds. *Statistical models*. Pacific Grove, CA: Wadsworth and Brooks/Cole. pp. 377-419.
- Cohen, W. B., Maierperger, T. L., Spies, T. A., and Oetter, D. R. 2001. Modeling forest cover attributes as continuous variables in a regional context with Thematic Mapper data. *International Journal of Remote Sensing* 22: 2279-2310.
- Collins, S. L., Knapp, A. K., Briggs, J. M., Blair, J. M., and Steinauer, E. M. 1998. Modulation of diversity by grazing and mowing in native tallgrass prairie. *Science* 280: 745-747.
- Connell, J. H. and Slatyer, R. O. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist* 111: 1119-1144.
- Cooper, W. S. 1913. The climax forest of Isle Royale, Lake Superior, and its development. *Botanical Gazette* 55: 1-235.
- Cumming, S. G. 2001. Forest type and wildfire in the Alberta boreal mixedwood: what do fires burn? *Ecological Applications* 11: 97-110.
- Cushman, S. A. and McGarigal, K. 2003. Hierarchical, multi-scale decomposition of species-environment relationships. *Landscape Ecology* 17: 637-646.
- Cushman, S. A. and McGarigal, K. 2004. Hierarchical analysis of forest bird species-environment relationships in the Oregon Coast Range. *Ecological Applications* 14(4): 1090-1105.
- Cushman, S. A. and McGarigal, K. In press. Multi-variate landscape trajectory analysis: an example using simulation modeling of American marten habitat change under three disturbance regimes. In: Bissonette, J. A. and Storch, I. *Temporal explicitness in landscape ecology: wildlife responses to changes in time*. New York, NY: Springer
- Cushman, S. A. and Wallin, D. O. 2002. Separating the influences of spatial, environmental, and disturbance factors in forests of the Russian Far East. *Forest Ecology and Management* 168(1-3): 201-215.
- Cwynar, L. C. 1987. Fire and the forest history of the North Cascade Range. *Ecology* 68: 791-802.
- Dale, V. H., Joyce, L. A., McNulty, S., Neilson, R. P., Ayres M. P., Flannigan, M. D., Hanson, P. J., Irland, L. C., Lugo, A. E., Peterson, C. J., Simberloff, D., Swanson, F. J., Stocks, B. J., and Wotton, B. M. 2001. Climate change and forest disturbances. *BioScience* 51: 723-734.
- da Silva, J. M., Uhl, C., and Murray, G. 1996. Plant succession, landscape management, and the ecology of frugivorous birds in abandoned Amazonian pastures. *Conservation Biology* 10: 491-503.
- Davis, M. B. 1986. Climatic instability, time tags, and community disequilibrium. In: Diamond, J. and Case, T., eds. *Community ecology*. New York: Harper and Row. pp. 269-284.
- Davis, M. B. 1989. Insights from paleoecology on global change. *Ecological Society of America Bulletin* 70(4): 222-228.
- Delcourt, H. R., Delcourt, P. A., and Webb, T. 1983. Dynamic plant ecology: the spectrum of vegetational change in space and time. *Quaternary Science Reviews* 1: 153-175.
- Denslow, J. S. 1980. Gap partitioning among tropical rainforest trees. *Biotropica* 12(Suppl): 47-55.
- Doebell, M. and Dieckmann, U. 2003. Speciation along environmental gradients. *Nature* 421: 259-264.
- Duffy, P. A., Walsh, J. E., Graham, J. M., Mann, D. H., and Rupp, T. S. 2005. Impacts of large-scale atmospheric-ocean variability on Alaskan fire season severity. *Ecological Applications* 15(4): 1317-1330.
- Dunwiddie, P. W. 1986. A 6000-year record of forest history on Mount Rainier, Washington. *Ecology* 67: 58-68.
- Eis, S. and Craigdallie, D. 1983. Reproduction of conifers. A handbook for cone crop assessment. Canadian Forest Service Technical Report 31: 12-27.
- Ettl, G. J. and Peterson, D. L. 1995. Growth response of subalpine fir (*Abies lasiocarpa*) to climate in the Olympic Mountains, Washington, USA. *Global Change Biology* 1: 213-230.

- Falk, D. A. 2004. Scale dependence of probability models for fire intervals in a ponderosa pine ecosystem. Dissertation. Tucson, AZ: University of Arizona.
- Finegan, B. 1984. Forest Succession. *Nature* 312: 109-114.
- Finney, M. A. 2003. Calculation of fire spread rates across random landscapes. *International Journal of Wildland Fire* 12: 167-174.
- Forsythe, W. L. and Loucks, O. L. 1972. A transformation for species response to habitat factors. *Ecology* 53: 1112-1119.
- Foster, D. R. 1983. The history and pattern of fire in the boreal forest of southeastern Labrador. *Canadian Journal of Botany* 61: 2459-2471.
- Foster, D. R. and Boose, E. R. 1992. Patterns of forest damage resulting from catastrophic wind in central New England, USA. *Journal of Ecology* 80: 79-98.
- Foster, D. R. and Boose, E. R. 1995. Hurricane disturbance regimes in temperate and tropical forest ecosystems. In: Coutts, M. and Grace, J., eds. *Wind and trees*. Cambridge, UK: Cambridge University Press. pp. 305-339.
- Foster, D. R. and King, G. A. 1986. Vegetation pattern and diversity in S.E. Labrador, Canada: *Betula papyrifera* (birch) forest development in relation to fire history and physiography. *Journal of Ecology* 74: 465-483.
- Franklin, J. 1995. Predictive vegetation mapping: geographic modeling of biospatial patterns in relation to environmental gradients. *Progress in Physical Geography* 19: 479-499.
- Franklin, J. 1998. Predicting the distribution of shrub species in southern California from climate and terrain-derived variables. *Journal of Vegetation Science* 9: 733-748.
- Frescino, T. S., Edwards, T. C., and Moisen, G. G. 2001. Modelling spatially explicit forest structural attributes using generalized additive models. *Journal of Vegetation Science* 12: 15-26.
- Friedman, J. H. 1991. Multivariate adaptive regression splines (with discussion). *Annals of Statistics* 19: 1-141.
- Gardner, R. H., Romme, W. H., and Turner, M. G. 1999. Predicting forest fire effects at landscape scales. In: Mladenoff, D. J. and Baker, W. L., eds. *Spatial modeling of forest landscape change: approaches and applications*. Cambridge, UK: Cambridge University Press. pp. 163-185.
- Gedalof, Z., Peterson, D. L., and Mantua, N. J. 2005. Atmospheric, climatic, and ecological controls on extreme wildfire years in the northwestern United States. *Ecological Applications* 15: 154-174.
- Giorgi, F., Marinucci, M. R., Bates, G. T., and DeCanio, G. 1993. Development of a second-generation regional climate model (RegCM2). *Monthly Weather Review* 121: 2814-2832.
- Givnish, T. J. 1981. Serotiny, geography, and fire in the Pine Barrens of New Jersey. *Evolution* 35(1): 101-123.
- Gleason, H. 1926. The individualistic concept of the plant association. *Bulletin of the Botany Club* 53: 1-20.
- Glenn, S. M. and Collins, S. L. 1992. Effects of scale and disturbance on rates of immigration and extinction of species in prairies. *Oikos* 63: 273-280.
- Gottfried, M., Pauli, H., and Grabherr, G. 1998. Prediction of vegetation patterns at the limits of plant life: a new view of the alpine-nival ecotone. *Arctic and Alpine Research* 30(3): 207-221.
- Grand, J., Buonaccorsi, J., Cushman, S. A., Mello, M., and Griffin, C. R. 2004. A comparison of predicted and observed bird and moth rarity hotspots in a threatened pitch pine-scrub oak (*Pinus regida*—*Quercus ilicifolia*) community. *Conservation Biology* 18(4): 1063-1077.
- Graumlich, L. 1991. Subalpine tree growth, climate and increasing CO₂: an assessment of recent growth trends. *Ecology* 72: 1-11.
- Green, D. F. and Johnson, E. A. 1996. Wind dispersal of seeds from a forest into a clearing. *Ecology* 82: 595-609.
- Grell, G. A., Dudhia, J., and Stauffer, D. R. 1994. A description of the fifth-generation Penn State/NCAR Mesoscale Model (MM5). Boulder, CO: Mesoscale and Microscale Meteorology Division, National Center for Atmospheric Research; NCAR Technical Note, NCAR/TN-398+STR.
- Guisan, A., Edwards, T. C., and Hastie, T. 2002. Generalised linear and generalised additive models in studies of species distributions: setting the scene. *Ecological Modelling* 157: 89-100.
- Guisan, A., Weiss, S. B., and Weiss, A. D. 1999. GLM versus CCA spatial modeling of plant species distribution. *Plant Ecology* 143: 107-112.
- Guisan, A. and Zimmerman, N. E. 2000. Predictive habitat distribution models in ecology. *Arctic and Alpine Research* 30: 207-221.
- Halpern, C. B. 1988. Early successional pathways and the resistance and resilience of forest communities. *Ecology* 69: 1703-1715.
- Hargrove, W. W., Gardner, R. H., Turner, M. G., Romme, W. H., and Despain, D. G. 2000. Simulating fire patterns in heterogeneous landscapes. *Ecological Modelling* 135: 243-263.
- Hartshorn, G. S. 1980. Neotropical forest dynamics. *Biotropica* (Supl): 23-30.
- Hastie, T. and Tibshirani, R. 1986. Generalized additive models. *Statistical Science* 1(3): 297-318.
- Hawkins, B. A., Field, R., Cornell, H. V., Currie, D. J., Guegan, J. F., Kaufman, D. M., Kerr, J. T., Mittelback, G. G., Oberdorff, T., O'Brien, E. M., Porter, E. E., and Turner, J. R. G. 2003. Energy, water, and broad-scale geographic patterns of species richness. *Ecology* 84: 3105-3117.
- He, H. S. and Mladenoff, D. J. 1999a. Spatially explicit and stochastic simulation of forest landscape fire disturbance and succession. *Ecology* 80: 81-99.
- He, H. S. and Mladenoff, D. J. 1999b. Effects of seed dispersal in the simulation of long-term forest landscape change. *Ecosystems* 2: 308-319.
- He, H. S., Mladenoff, D. J., and Gustafson, E. J. 2002. Simulating landscape change under forest harvesting and climate warming-induced fire disturbance. *Forest Ecology & Management* 155: 257-270.
- Host, G. E. and Isebrands, J. G. 1994. An interregional validation of ECOPHYS, a growth process model of juvenile poplar clones. *Tree Physiology* 14: 933-945.
- Host, G. E., Pregitzer, K. S., Ramm, C. W., Hart, J. B., and Cleland, D. T. 1987. Landform-mediated differences in successional pathways among upland forest ecosystems in northwestern Lower Michigan. *Forest Science* 33: 445-457.
- Host, G. E., Pregitzer, K. S., Ramm, C. W., Lusch, D. P., and Cleland, D. T. 1988. Variation in overstory biomass among glacial landforms and ecological land units in northwestern Lower Michigan. *Canadian Journal of Forest Research* 18: 659-668.

- Houghton, J. T., Ding, Y., Griggs, D. J., Nogue, M., van der Linden, P. J., and Xiaosu, D., eds. 2001. *Climate change 2001: the scientific basis: contributions of working group I to the third assessment report of the Intergovernmental Panel on Climate Change*. Cambridge, UK: Cambridge University Press.
- Houghton, J. T., Meira Filho, L. G., Callender, B. A., Harris, N., Kattenberg, A., Maskell, A., and Maskell, K. 1995. *The science of climate change: contribution of working group I to the second assessment of the Intergovernmental Panel on Climate Change*. Cambridge, U.K.: Cambridge University Press.
- Hunsaker, C., Goodchild, M., Friedl, M., and Case, T. 2001. *Spatial uncertainty in ecology*. New York, NY: Springer-Verlag.
- Hutchinson, G. E. 1957. Concluding remarks. *Cold Spring Harbour Symposium on Quantitative Biology* 22: 415-427.
- Isaaks, E. H. and Srivastava, R. M. 1989. *An introduction to applied geostatistics*. New York, NY: Oxford University Press. 561 p.
- Johnson, E. A. 1992. *Fire and vegetation dynamics: studies from the North American boreal forest*. Cambridge, U.K.: Cambridge University Press.
- Johnson, E. A. and Wowchuck, D. R. 1993. Wildfires in the southern Canadian Rocky Mountains and their relationship to mid-tropospheric anomalies. *Canadian Journal of Forest Research* 23: 1213-1222.
- Johnson, W. C., Sharpe, D. M., DeAngelis, D. L., Fields, D. E., and Olson, R. J. 1981. Modelling seed dispersal and forest island dynamics. In: Burgess, R. L. and Sharpe, D. M., eds. *Forest island dynamics in man-dominated landscapes*. New York, NY: Springer Verlag. pp. 215-329.
- Keane, R. E. and Finney, M. A. 2003. The simulation of landscape fire, climate, and ecosystem dynamics. In: Veblen, T. T., Baker, W. L., Montenegro, G., and Swetnam, T. W., eds. *Fire and climatic change in temperate ecosystems of the western Americas*. New York, NY: Springer Verlag. pp. 32-68.
- Keane, R. E. and Long, D. G. 1998. A comparison of coarse scale fire effects simulation strategies. *Northwest Science* 72: 76-90.
- Keane, R. E., Morgan, P., and Running, S. W. 1996. FIRE-BGC—a mechanistic ecological process model for simulating fire succession on coniferous forest landscapes of the Northern Rocky Mountains. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Intermountain Research Station; Research Paper INT-484.
- Keane, R. E., Morgan, P., and White, J. D. 1999. Temporal patterns of ecosystem processes on simulated landscapes in Glacier National Park, Montana, USA. *Landscape Ecology* 14: 311-329.
- King, A. W. 1991. Translating models across scales in the landscape. In: Turner, M. G. and Gardner, R. H., eds. *Quantitative methods in landscape ecology*. Ecological Studies ed. Springer, N.Y. pp. 479-518.
- Kulakowski, D. and Veblen, T. T. 2002. Influences of fire history and topography on the pattern of a severe wind blowdown in a Colorado subalpine forest. *Journal of Ecology* 90(5): 806-819.
- Landsberg, J. J. and Gower, S. T. 1997. *Applications of physiological ecology to forest management*. San Diego, CA: Academic Press. 354 p.
- Legendre, P. 1993. Spatial autocorrelation: trouble or new paradigm? *Ecology* 74: 1659-1673.
- Lenihan, J. M. 1993. Ecological response surfaces for North American boreal tree species and their use in forest classification. *Journal of Vegetation Science* 4: 667-680.
- Lenihan, J. M., Daly, C., Bachelet, D., and Neilson, R. P. 1998. Simulation of broad-scale fire severity in a dynamic global vegetation model. *Northwest Science* 72: 91-103.
- Lenihan, J. M., Drapek, R. J., Bachelet, D., and Neilson, R. P. 2003. Climate change effects on vegetation distribution, carbon and fire in California. *Ecological Applications* 13: 1667-1681.
- Leopold, A. 1933. *Game management*. New York, NY: Charles Scribner and Sons.
- Lertzman, K. P. and Fall, J. 1998. From forest stand to landscape: the impacts of disturbance. In: Peterson, D. and Parker, V. T., eds. *Scale issues in ecology*. New York, NY: Columbia University Press. pp. 339-367.
- Lertzman, K. P., Fall, J., and Dorner, B. 1998. Three kinds of heterogeneity in fire regimes: at the crossroads of fire history and landscape ecology. *Northwest Science* 72: 4-23.
- Levin, S. A. 1992. The problem of pattern and scale in ecology. *Ecology* 73: 1943-1967.
- Linn, R., Winterkamp, J., Colman, J. J., Edminster, C., and Bailey, J. D. 2005. Modeling interactions between fire and atmosphere in discrete element fuel beds. *International Journal of Wildland Fire* 14: 37-48.
- Littell, J. S., McKenzie, D., Peterson, D. L., and Westerling, A. In review. Climate and area burned by fire in ecoprovinces of the western U.S. *Ecological Applications*.
- Littell, J. S. and Peterson, D. L. 2005. A method for estimating vulnerability of Douglas-fir growth to climate change in the northwestern U.S. *Forestry Chronicle* 81: 369-374.
- Littell, J. S., Peterson, D. L., and Tjoelker, M. Submitted. Douglas-fir growth in mountain ecosystems: water limits tree growth from stand to region.
- Logan, J. A. and Powell, J. A. 2001. Ghost forests, global warming, and the mountain pine beetle. *American Entomologist* 47(3): 160-173.
- Luce, C. H., Tarboton, D. G., and Cooley, K. R. 1999. Sub-grid parameterization of snow distribution for an energy and mass balance snow cover model. *Hydrological Processes* 13: 1921-1933.
- Malanson, G. F. 1984. Fire history and patterns of Venturan subassociations of Californian coastal sage scrub. *Vegetatio* 57: 121-128.
- McCullagh, P. and Nelder, J. A., 1989. *Generalized linear models*. London, UK: Chapman and Hall. 511 p.
- McGarigal, K. and Cushman, S. A. 2002. Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. *Ecological Applications* 12(2): 335-345.
- McGarigal, K. and Cushman, S. A. 2005. The gradient concept of landscape structure. In: Wiens, J. A. and Moss, M. R., eds. *Issues and perspectives in landscape ecology*. Cambridge University Press. pp. 112-120.
- McKenzie, D., Gedalof, Z., Peterson, D. L., and Mote, P. 2004. Climatic change, wildfire, and conservation. *Conservation Biology* 18: 890-902.
- McKenzie, D., O'Neill, S. M., Larkin, N., and Norheim, R. A. 2005. Integrating models to predict regional haze from wildland fire. *Ecological Modelling*.

- McKenzie, D., Peterson, D. L., and Alvarado, E. 1996. Predicting the effect of fire on large-scale vegetation patterns in North America. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station; Research Paper PNW-489.
- McKenzie, D., Peterson, D. W., Peterson, D. L., and Thornton, P. E. 2003. Climatic and biophysical controls on conifer species distributions in mountain forests of Washington State, USA. *Journal of Biogeography* 30: 1093-1108.
- McLachlan, J. S. and Brubaker, L. B. 1995. Local and regional vegetation change on the northeastern Olympic Peninsula during the Holocene. *Canadian Journal of Botany* 73: 1618-1627.
- Mearns, L. O., Katz, R. W., and Schneider, S. H. 1984. Extreme high-temperature events: changes in their probabilities with changes in mean temperature. *Journal of Climate and Applied Meteorology* 23: 1601-1613.
- Miller, C. 2003. Simulation of effects of climatic change on fire regimes. In: Veblen, T. T., Baker, W. L., Baker, W. L., Montenegro, G., and Swetnam, T. W. *Fire and climatic change in temperate ecosystems of the western Americas*. NY: Springer. pp. 69-94.
- Miller, C. and Urban, D. L. 2000. Modeling the effects of fire management alternatives on mixed-conifer forests in the Sierra Nevada. *Ecological Applications* 10: 85-94.
- Miller, J. and Franklin, J. 2002. Modeling the distribution of four vegetation alliances using generalized linear models and classification trees with spatial dependence. *Ecological Modelling* 157: 227-247.
- Miller, T. E. 1982. Community diversity and interactions between size and frequency of disturbances. *American Naturalist* 120: 533-536.
- Milne, B. T., Gupta, V. K., and Restrepo, C. 2002. A scale invariant coupling of plants, water, energy, and terrain. *Ecoscience* 9(2): 191-199.
- Mladenoff, D. J. and Baker, W. L., 1999. *Advances in spatial modeling of forest landscape change: approaches and applications*. Cambridge, UK: Cambridge University Press.
- Mladenoff, D. J., Host, G. E., Boeder, J., and Crow, T. R. 1996. LANDIS: a spatial model of forest landscape disturbance, succession, and management. In: Goodchild, M. F., Steyaert, L. T., Parks, B. O., Johnston, D., Maidment, D., Crane, M., and Glendinning, S., eds. *GIS and environmental modeling*. Fort Collins, CO: GIS World Books. pp. 175-179.
- Moer, M. and Stage, A. R. 1995. Most similar neighbor: an improved sampling inference procedure for natural resource planning. *Forest Science* 41: 337-359.
- Moisen, G. G. and Edwards, T. C., Jr. 1999. Use of generalized linear models and digital data in a forest inventory of northern Utah. *Journal of Agricultural, Biological and Environmental Statistics* 4: 164-182.
- Moisen, G. G. and Frescino, T. S. 2002. Comparing five modeling techniques for predicting forest characteristics. *Ecological Modelling* 157: 209-225.
- Mooney, H. A. and Godron, M., Editors. 1983. *Disturbance and ecosystems*. New York: Springer-Verlag. 292 p.
- Morgan, J. N. and Sonquist, J. A. 1963. Problems in the analysis of survey data, and a proposal. *Journal of the American Statistical Association* 58: 415-435.
- Mueller-Dombois, D. and Ellenberg, H. 1974. *Aims and methods of vegetation ecology*. New York, NY: John Wiley and Sons.
- Neilson, R. P. 1995. A model for predicting continental-scale vegetation distribution and water balance. *Ecological Applications* 5: 362-385.
- Neilson, R. P. and Drapek, R. J. 1998. Potentially complex biosphere responses to transient global warming. *Global Change Biology* 4: 505-521.
- Nepstad, D., Uhl, C., and Serrao, E. A. 1990. Surmounting barriers to forest regeneration in abandoned, highly degraded pastures: A case study from Paragominas, Para, Brazil. In: Anderson, A. B., ed. *Alternatives to deforestation: steps toward sustainable use of the Amazon rain forest*. New York, NY: Columbia University Press. pp. 215-229.
- Noble, I. R. and Slatyer, R. O. 1980. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. *Vegetatio* 43: 5-21.
- O'Neill, R. R., De Angelis, D. L., Waide, J. B., and Allen, T. F. H. 1986. *A hierarchical concept of ecosystems*. Princeton, NJ: Princeton University Press.
- Oberhauser, K. and Peterson, A. T. 2003. Modeling current and future potential wintering distributions of eastern North American monarch butterflies. *Proceedings of the National Academy of Sciences* 100: 14063-14068.
- Ohmann, J. L. and Gregory, M. J. 2002. Predictive mapping of forest composition and structure with direct gradient analysis and nearest-neighbor imputation in coastal Oregon, USA. *Canadian Journal of Forest Resources* 32: 725-741.
- Ohmann, J. L. and Spies, T. A. 1998. Regional gradient analysis and spatial pattern of woody plant communities of Oregon forests. *Ecological Monographs* 68: 151-182.
- Olden, J. D. and Jackson, D. A. 2000. Torturing data for the sake of generality: how valid are our regression models? *Ecoscience* 7: 501-510.
- Olden, J. D. and Jackson, D. A. 2002. A comparison of statistical approaches for modelling fish species distributions. *Freshwater Biology* 47: 1976-1995.
- Overpeck, J., Hughen, K., Hardy, D., Bradley, R., Case, R., Douglas, M., Finney, B., Gajewski, K., Jacoby, G., Jennings, A., Lamoureux, S., Lasca, A., MacDonald, G., Moore, J., Retelle, M., Smith, S., Wolfe, A., and Zielinski, G. 1997. Arctic environmental change of the last four centuries. *Science* 278: 1251-1256.
- Overpeck, J. T., Rind, D., and Goldberg, R. 1990. Climate-induced changes in forest disturbance and vegetation. *Nature* 343: 51-53.
- Palmer, M. W. 1993. Putting things in even better order: the advantages of canonical correspondence analysis. *Ecology* 74: 2215-2230.
- Peet, R. K. and Christensen, N. L. 1980. Succession: a population process. *Vegetatio* 43: 131-140.
- Peet, R. K. and Loucks, O. L. 1977. A gradient analysis of southern Wisconsin forests. *Ecology* 58(3): 485-499.
- Peters, R. L. and Lovejoy, T. L., 1992. *Global warming and biological diversity*. New Haven, CT: Yale University Press. 386 p.
- Peterson, A. T., Soberon, G., and Sanchez-Cordero, V. 1999. Conservatism of ecological niches in evolutionary time. *Science* 285: 1265-1267.
- Peterson, C. J. and Carson, W. P. 1996. Generalizing forest regeneration models: the dependence of propagule availability on disturbance history and stand size. *Canadian Journal of Forest Research* 26: 45-52.

- Peterson, D. L. and Ryan, K. C. 1986. Modeling postfire mortality for long-range planning. *Environmental Management* 10: 797-808.
- Peterson, D. W. and Peterson, D. L. 2001. Mountain hemlock growth responds to climatic variability at annual and decadal time scales. *Ecology* 82: 3330-3345.
- Pickett, S. T. A. 1980. Non-equilibrium coexistence of plants. *Bulletin of the Torrey Botanical Club* 107: 238-248.
- Pickett, S. T. A., Collins, S. L., and Armesto, J. J. 1987. A hierarchical consideration of causes and mechanisms of succession. *Vegetatio* 69: 109-114.
- Pickett, S. T. A., Kolasa, J., and Jones, C. G. 1994. *Ecological understanding: the nature of theory and the theory of nature*. San Diego, CA: Academic Press.
- Pielke, R. A., Cotton, W. R., Walko, R. L., Tremback, C. J., Lyons, W. A., Grasso, L. D., Nicholls, M. E., Moran, M. D., Wesley, D. A., Lee, T. J., and Copeland, J. H. 1992. A comprehensive meteorological modeling system—RAMS. *Meteorological and Atmospheric Physics* 49: 69-91.
- Pierce, K. B., Jr. and Ohmann, J. 2005. Gradient nearest neighbor imputation for mapping forest attributes and variability. In: Marsden, M., Downing, M., and Riffe, M., compilers. *Quantitative techniques for deriving national-scale data*; Westminster, CO. Fort Collins, CO: Forest Health Technology Enterprise Team FHTET-2005-12: 145-172.
- Prichard, S. J. 2003. Spatial and temporal dynamics of fire and forest succession in a mountain watershed, North Cascades National Park. Dissertation. Seattle, WA: University of Washington.
- Rastetter, E. B., King, A. W., Cosby, B. J., Hornberger, G. M., O'Neill, R. V., and Hobbie, J. E. 1992. Aggregating fine-scale ecological knowledge to model coarser-resolution attributes of ecosystems. *Ecological Applications* 2: 55-70.
- Reiners, W. A. and Lang, G. E. 1979. Vegetational patterns and processes in the balsam fir zone, White Mountains, New Hampshire. *Ecology* 60: 403-417.
- Roberts, D. W. 1996. Modeling forest dynamics with vital attributes and fuzzy systems theory. *Ecological Modeling* 90: 161-173.
- Romme, W. H. and Knight, D. H. 1981. Fire frequency and subalpine forest succession along a topographical gradient in Wyoming. *Ecology* 62: 319-326.
- Rorig, M. L. and Ferguson, S. A. 1999. Characteristics of lightning and wildland fire ignition in the Pacific Northwest. *Journal of Applied Meteorology* 38: 1565-1575.
- Rothermel, R. C. 1972. A mathematical model for predicting fire spread in wildland fuels. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station; Research Paper INT-115. 40 p.
- Rowe, J. S. 1981. Concepts of fire effects on plant individuals and species. In: Weinand, R. W. and Maclean, D. A., eds. *The role of fire in northern circumpolar ecosystems*. New York, NY: Wiley and Sons. pp. 135-154.
- Rudis, V. A. 2003. Comprehensive regional resource assessments and multipurpose uses of forest inventory and analysis data, 1976 to 2001: a review. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station; General Technical Report SRS-70. 129 p.
- Ruelle, D. 1991. *Chance and chaos*. Princeton, N.J.: Princeton University Press.
- Running, S. W., Nemani, R. R., and Hungerford, R. D. 1987. Extrapolation of synoptic meteorological data in mountainous terrain and its use for simulating forest evapotranspiration and photosynthesis. *Canadian Journal of Forest Research* 17: 472-483.
- Schneider, D. C. 1994. *Quantitative ecology: spatial and temporal scaling*. San Diego, CA: Academic Press.
- Schwerdtfeger, F. 1977. *Ökologie der Tiere: autökologie*. Hamburg, Germany: Verlag Paul Parey. 460 p.
- Shelford, V. E. 1931. Some concepts of bioecology. *Ecology* 12: 455-467.
- Shugart, H. H. and Noble, I. R. 1981. A computer model of succession and fire response of the high-altitude Eucalyptus forest of the Brindabella Range, Australian Capital Territory, Australia. *Australian Journal of Ecology* 6: 149-164.
- Shugart, H. H. and West, D. C. 1977. Development of an Appalachian deciduous forest succession model and its application to assessment of the impact of the chestnut blight. *Journal of Environmental Management* 5: 161-170.
- Shugart, H. H., Jr. and Seagle, S. W. 1985. Modeling forest landscapes and the role of disturbance in ecosystems and communities. In: Pickett, S. T. A. and White, P. S., eds. *The ecology of natural disturbance and patch dynamics*. Orlando, FL: Academic Press. pp. 253-368.
- Skinner, W. B., Stocks, B. J., Martell, B., Bonsal, and Shabbar, A. 1999. The association between circulation anomalies and the mid-troposphere and area burned by wildland fire in Canada. *Theoretical and Applied Climatology* 63: 89-105.
- Smith, T. M. and Urban, D. L. 1988. Scale and resolution of forest structural pattern. *Vegetatio* 74: 143-150.
- Solomon, A. M. and Leemans, R. 1997. Boreal forest carbon stocks and wood supply: past, present, and future responses to changing climate, agriculture, and species availability. *Agricultural and Forest Meteorology* 84: 137-151.
- Sousa, W. P. 1984. The role of disturbance in natural communities. *Annual Review of Ecology and Systematics* 15: 353-391.
- Spies, T. A., Reeves, G. H., Burnett, K. M., McComb, W. C., Johnson, K. N., Grant, G., Ohmann, J. L., Garman, S. L., and Bettinger, P. 2002. Assessing the ecological consequences of forest policies in a multi-ownership province in Oregon. In: Liu, J. and Taylor, W. W., eds. *Integrating landscape ecology into natural resource management*. Cambridge, UK: Cambridge University Press.
- Spomer, G. G. 1973. The concepts of "interaction" and "operational environment" in environmental analysis. *Ecology* 54: 200-204.
- Stephenson, N. L. 1990. Climatic control of vegetation distribution: the role of the water balance. *American Naturalist* 135: 649-670.
- Stephenson, N. L. 1998. Actual evapotranspiration and deficit: biologically meaningful correlates of vegetation distribution across spatial scales. *Journal of Biogeography* 25: 855-870.
- Stocks, B. J., Alexander, M. E., Wotton, B. M., Steffner, C. N., Flannigan, M. D., Taylor, S. W., Lavoie, N., Mason, J. A., Hartley, G. R., Maffey, M. E., Dalrymple, G. N., Blake, T. W., Cruz, M. G., and Lanoville, R. A. 2004. Crown fire behaviour in a northern jack pine-black spruce forest. *Canadian Journal of Forest Research* 34: 1548-1560.

- Stockwell, D. R. B. and Noble, I. R. 1992. Induction of sets of rules from animal distribution data: a robust and informative method of data analysis. *Mathematics and Computers in Simulation* 33: 385-390.
- Stockwell, D. R. B. and Peters, D. P. 1999. The GARP modelling system: problems and solutions to automated spatial prediction. *International Journal of Geographic Information Systems* 13: 143-158.
- Swanson, F. J., Johnson, S. L., Gregory, S. V., and Acker, S. A. 1998. Landform effects on ecosystem patterns and processes. *BioScience* 38: 92-98.
- ter Braak, C. J. F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67: 1167-1179.
- ter Braak, C. J. F. 1987. Unimodal models to relate species to environment. Doctoral thesis. Wageningen, the Netherlands: University of Wageningen. 152 p.
- ter Braak, C. J. F. and Prentice, I. C. 1988. A theory of gradient analysis. *Advances in Ecological Research* 18: 271-313.
- Thompson, C. M. and McGarigal, K. 2002. The influence of research scale on bald eagle habitat selection along the lower Hudson River, New York. *Landscape Ecology* 17: 569-586.
- Thompson, R. S., Hostetler, S. W., Bartlein, P. J., and Anderson, K. H. 1998. A strategy for assessing potential future changes in climate, hydrology, and vegetation in the western United States. U.S. Department of the Interior; U.S. Geological Survey Circular 1153.
- Tilman, D. 1982. Resource competition and community structure. Princeton, NJ: Princeton University Press.
- Tilman, D. 1990. Mechanisms of plant competition for nutrients: the elements of a predictive theory of competition. In: Grace, J. B. and Tilman, D., eds. *Perspectives on Plant Competition*. New York, NY: Academic Press. pp. 117-142.
- Turner, M. G. 1989. Landscape ecology: the effect of pattern on process. *Annual Review of Ecology and Systematics* 20: 171-197.
- Turner, M. G., Gardner, R. H., and O'Neill, R. V. 2003. *Landscape ecology in theory and practice*. New York, NY: Springer-Verlag. 401 p.
- Urban, D. L., Bonan, G. B., Smith, T. M., and Shugart, H. H. 1991. Spatial applications of gap models. *Forest Ecology and Management* 42: 95-110.
- Urban, D. L., Harmon, M. E., and Halpern, C. B. 1993. Potential response of Pacific Northwestern forests to climatic change: effects of stand age and initial composition. *Climatic Change* 23: 247-266.
- Urban, D. L. and Shugart, H. H. 1992. Individual-based models of forest succession. In: Glenn-Lewin, D. C., Peet, R. K., and Veblen, T. T., eds. *Plant succession: theory and prediction*. London, UK: Chapman and Hall. pp. 249-292.
- Van Der Pijl, L. 1982. *Principles of dispersal in higher plants*. Berlin, Germany: Springer-Verlag.
- Van Deusen, P. C. 1997. Annual forest inventory statistical concepts with emphasis on multiple imputation. *Canadian Journal of Forest Resources* 27: 379-384.
- Veblen, T. T., Baker, W. L., Montenegro, G., and Swetnam, T. W. 2003. Fires and climate in forested landscapes of the U.S. Rocky Mountains. In: *Fire and climate change in temperate ecosystems of the western Americas*. New York, NY: Springer-Verlag.
- Venables, W. N. and Ripley, B. D. 2002. *Modern applied statistics with S*, fourth edn. New York, NY: Springer. 495 p.
- Wagner, H. H. 2004. Direct multiscale ordination with canonical correspondence analysis. *Ecology* 85: 342-351.
- Waring, R. H. and Running, S. W. 1998. *Forest ecosystems*. San Diego, CA: Academic Press.
- Waring, R. H. and Schlesinger, W. H. 1985. *Forest ecosystems: concepts and management*. Orlando, FL: Academic Press. 340 p.
- Watt, A. S. 1947. Pattern and process in the plant community. *Journal of Ecology* 35: 1-22.
- Weber, M. G. and Flannigan, M. D. 1997. Canadian boreal forest ecosystem structure and function in a changing climate: impact on fire regimes. *Environmental Review* 5: 145-166.
- White, P. S. 1979. Pattern, process and natural disturbance in vegetation. *Botanical Review* 45: 229-299.
- Whittaker, R. H. 1956. Vegetation of the Great Smoky Mountains. *Ecological Monographs* 26: 1-80.
- Whittaker, R. H. 1967. Gradient analysis of vegetation. *Biological Review* 49: 207-264.
- Wiens, J. A. 1989. Spatial scaling in ecology. *Functional Ecology* 3(4): 385-397.
- Wimberley, M. C. and Spies, T. A. 2001a. Influences of environment and disturbance on forest patterns in coastal Oregon watersheds. *Ecology* 82: 1443-1459.
- Wimberley, M. C. and Spies, T. A. 2001b. Modeling landscape patterns of understory tree regeneration in the Pacific Northwest, USA. *Applied Vegetation Science* 4: 277-286.
- Wimberly, M. C. and Ohmann, J. L. 2004. A multi-scale assessment of human and environmental constraints on forest land cover change on the Oregon (USA) coast range. *Landscape Ecology* 19: 631-646.
- Wolter, P. T., Mladenoff, D. J., Host, G. E., and Crow, T. R. 1995. Improved forest classification in the northern lake states using multi-temporal Landsat imagery. *Photogrammetric Engineering and Remote Sensing* 61: 1129-1143.
- Woodcock, C. E., Collins, J., Gopal, S., Jakabhazy V., Li, X., Macomber, S., Ryherd, S., Wu, Y., Harward, V. J., Levithan, J., and Warbington, R. 1993. Mapping forest vegetation using Landsat TM imagery and a canopy reflectance model. *Remote Sensing of Environment* 50: 240-254.
- Woodcock, C. E., Gopal, S., Macomber, S. A., and Jakabhazy, V. D. 1994. Accuracy assessment of the vegetation map of the Plumas National Forest. Technical report, center for remote sensing, Boston University. Boston, MA: Boston University. 19 p.
- Woodward, F. I. Temperature and the distribution of plant species and vegetation. In: Long, S. P. and Woodward, F. I., eds. *Plants and temperature*. Cambridge, UK: The Company of Biologists Limited. pp. 59-75.
- Woodward, F. I. 1987. *Climate and plant distribution*. Cambridge, UK: Cambridge University Press.
- Woodward, F. I., Lomas, M. R., and Kelly, C. K. 2004. Global climate and the distribution of plant biomes. *Philosophical Transactions of the Royal Society Series B* 359: 1465-1476.

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Rocky Mountain Research Station
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