CHAPTER

Modeling Understory Vegetation and Its Response to Fire

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Donald McKenzie, Crystal L. Raymond, and Samuel A. Cushman

The understory is an oft-neglected element in landscape modeling. Most landscape models focus on the dominant vegetation and how it responds over successional time to climate, competitive interactions, and disturbance (Keane et al. 2004, Cary et al. 2006). Even forest stand-level models rarely consider understory components other than seedlings, saplings, and downed wood (Pacala et al. 1993, He and Mladenoff 1999, Gratzer et al. 2004), except in special cases such as the need for estimating surface fuels for fire modeling (Rebain 2006).

Understory vegetation has important ecological functions on many landscapes. For example, in many coniferous forests, which are relatively depauperate in tree species, the understory, including shrubs, forbs, grasses, and nonvascular plants, accounts for most plant diversity (Halpern and Spies 1995, Gilliam and Roberts 2003, Halpern et al. 2005). Habitat quality for both arboreal and ground-dwelling wildlife is often controlled by understory characteristics such as regeneration and subcanopy tree layers, shrub cover and density, dead and downed wood, and edible herbaceous species (Hansen et al. 1995, Block and Morrison 1998, Pearman 2001, MacFaden and Capen 2002, Manning and Edge 2004).

In contrast to canopy vegetation composition and structure, which can be quantified reasonably well from remotely sensed images in both forested or nonforested landscapes, understory vegetation is largely invisible to remote sensing. Our ability to characterize it accurately at broad spatial scales depends on inferences about its relationships with observable characteristics like overstory structure or species composition. In this chapter, we review understory models—qualitative or quantitative frameworks for estimating understory composition, diversity, structure, and spatial pattern. Understory models are valuable as a baseline for predicting and managing other ecosystem components that depend on vegetation, including wildlife and wildlife habitat, insects, specifically population dynamics of defoliators and beetles, fungi, and fire hazard and fire effects (Holt et al. 1995, Wisdom et al. 2002). We identify three types of models:

1. *Empirical models,* which predict understory characteristics from a set of independent variables, using statistical or expert-system approaches, or

both. A leading edge of research in this area studies hierarchical models that incorporate multiple contingencies;

2. *Process-based models,* which simulate understory development, usually within a mechanistic ecosystem-modeling paradigm that focuses on photosynthesis, element cycling, mortality, and decomposition; and

3. *Qualitative or knowledge-based models,* which infer understory characteristics indirectly using a combination of logic and expert opinion.

We concentrate on empirical modeling because of the relative wealth of literature on this paradigm compared to the others. We then discuss the need and available methods for extrapolating understory models across the large landscapes that are the focus of this book. Disturbance plays a key role in forest understory dynamics, and its effects are rarely included in understory models. Fire is the principal disturbance in western North America, which is also a focal area for wildlife conservation. In fire-adapted ecosystems such as dry forests, shrublands, and grasslands, surface fuels (i.e., understory) determine fire behavior and severity (Raymond and Peterson 2005, Vaillant et al. 2006, Wright and Prichard 2006). Some landscape models assign fire behavior fuel models (Deeming et al. 1978, Anderson 1982) to dominant vegetation types to predict fire behavior and fire effects, but these are derived heuristically from the dominant vegetation and do not provide details on understory vegetation. We therefore examine the fire-effects literature, as it can inform understory modeling by identifying key variables that control fire effects on understory vegetation.

Lastly, we look to the future of understory models and recommend areas in need of further research. We emphasize the inherent uncertainty associated with estimating understory characteristics, especially in the context of a rapidly changing climate (Bonan et al. 2003, Neilson et al. 2005), changes in disturbance regimes (McKenzie et al. 2004, Gedalof et al. 2005), and the ubiquity of invasive species that respond to those changes (Keeley 2003, 2006; Brooks et al. 2004; Emery and Gross 2005).

UNDERSTORY MODELING PARADIGMS

An ideal understory model should:

1. Capture the range of variability across space and time associated with a particular ecosystem type (Landres et al. 1999), and also, where possible, specify the error structure of quantitative models. For example, given a range in the percent canopy cover, what is the range of shrub cover expected? The ranges of variability of most statistics in natural resources are at least as useful, and generally less biased, than predicted means. Several types of intervals around the mean are important: confidence intervals for predicted mean values, prediction intervals for the estimates of individual

observations, and tolerance intervals for proportions of new observations that fall within a specific range (Vardeman 1992).

2. Be dynamic, as opposed to giving only a snapshot in time. Because ecosystems can change rapidly, ecological data from stand inventories to coarse-scale GIS layers can quickly become outdated.

3. Incorporate disturbance types associated with the ecosystem; for example, fire frequency, grazing, and invasive species in rangelands, or fire severity and frequency, insect outbreaks, and logging in forests.

4. Provide a means for robust validation of results and for extrapolation outside the range of conditions within which the model was built. It should also identify limits to extrapolation. For example, a statistical model to predict total shrub cover might be invalid outside the range of overstory densities used to build it, whereas a model to predict herb-layer composition might be more sensitive to overstory cover type. Crucial to this validation is accounting for various sources of uncertainty, such as errors in measurement, model specification, or parameter estimates, or an incomplete specification of the spatial and temporal domain of the model.

5. For specific applications, focus on key variables for management or for predicting other ecosystem components. For example, management for a particular wildlife species that needs a specific shrub for food or cover would need an accurate understory model for that species more than a model for total herbaceous cover, seedling density, or coarse woody debris.

In practice, each type of understory model (described next) falls short of these ideals in different ways.

EMPIRICAL MODELS

Most models that explicitly estimate understory characteristics are of the empirical model type. Predictive vegetation mapping (Franklin 1995) is an active area of research that has produced special issues of journals (Guisan et al. 2002, Moisen et al. 2006), comparisons of multiple methods (Bolliger et al. 2000, Elith et al. 2002, Moisen and Frescino 2002, Leathwick et al. 2006), and broad theoretical investigation (Oksanen and Minchin 2002, Austin et al. 2006). Forest understory models are the most problematic, particularly at broad spatial scales, because canopy cover interferes with direct remote sensing of the understory.

Modeling techniques abound, but they fall broadly into two types: (1) machine-learning or expert-system approaches and (2) gradient-based methods, whether parametric or nonparametric (Cushman et al. 2007). The former category includes artificial neural networks (Ripley 1996), genetic algorithms (Stockwell 1999, 2006), Bayesian classification (Termansen et al. 2006), and recursive partitioning, the best known of which is classification and regression trees (Breiman et al. 1984) and its offshoots such as adaptive regression splines (Friedman 1991) and random forests (Breiman 2001). The latter category includes both univariate and multivariate methods. The most widely used univariate methods are ordinary multiple regression, generalized linear models (GLMs; McCullagh and Nelder 1989), generalized additive models (GAMs; Hastie and Tibshirani 1990), and embellishments of these to include spatial dependence in the response variable. Of these latter, two important developments are generalized linear mixed models (GLMMs; Hooten et al. 2003, Gelfand et al. 2005), which are particularly applicable in a landscape context, and multivariate gradient models, which are either eigenvector-based (e.g., canonical correspondence analysis [CCA]; ter Braak 1986) or distance-based (e.g., multidimensional scaling [NMDS]; Faith et al. 1987), and can also incorporate spatial dependencies (Gelfand et al. 2005).

Cushman et al. (2007) identify strengths and weaknesses of machine learning versus gradient modeling for vegetation modeling. Machine-learning methods excel at pattern matching—separating signal from noise in a data set and thereby optimizing prediction accuracy. These methods often yield better classification accuracy than gradient modeling (Moisen and Frescino 2002). In contrast, gradient modeling invokes driver-response mechanisms more directly, making it more robust to ecological interpretation and to extrapolation beyond conditions associated with the model database. Typical predictors for both methods are either surrogate variables for ecological mechanisms, such as elevation, geographic coordinates, and satellite spectra, or more direct drivers such as climate or climate-derived variables (e.g., snowpack depth or soil moisture), and biotic variables such as stand structure or composition (Fig. 15-1). For forest understories, overstory variables (Fig. 15-1) are often the strongest predictors because they modify the direct effects of environmental factors (Alaback 1982, Riegel et al. 1995, Klinka et al. 1996, McKenzie et al. 2000).

Given the vast literature on predictive vegetation models that use empirical approaches, we provide a few illustrative examples of understory shrub models from western North America. A comprehensive review is found in Guisan and Zimmerman (2000).

Binary Data

Data on the presence-absence of a species, life form, plant association, etc., should be analyzed with models that restrict predicted values to (0,1), either probabilistically or by allowing only presence or absence to be predicted. Generalized linear models or generalized additive models of the binomial family are typical gradient-based methods, whereas classification trees and Genetic Algorithms for Rule-set Prediction (GARP; Stockwell 2006) are standard machine-learning methods. Franklin (1998) used GLMs, GAMs, and classification trees to predict presence-absence of 20 chaparral and coastal sage shrub species in southwestern California, USA, from climate and terrain variables.

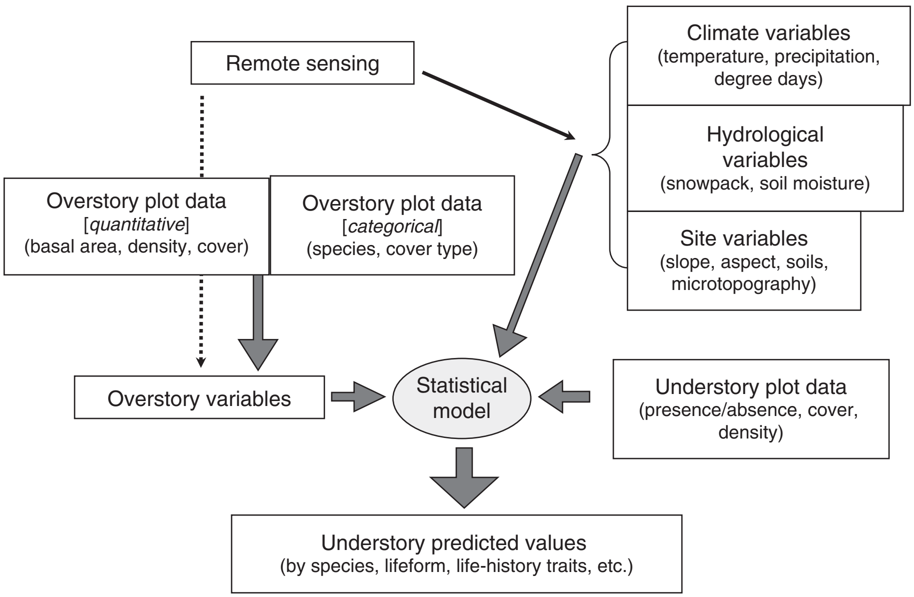


FIG. 15-1

Key elements of empirical models for predicting understory vegetation. Climate, hydrological, and site variables may or may not be predicted from remote sensing. Overstory plot data are preferred for generating overstory predictors, but remote sensing is also used to generate these directly when plot data are lacking.

Error misclassification rates, more appropriate for a binary response than deviance explained, were between 5–30% for GLMs, 2–27% for GAMs, and 3–25% for classification trees. Franklin (1998) notes that the gradient models (GLMs, GAMs) were easier to interpret ecologically than the tree-based models, an observation supported by the analysis of Cushman et al. (2007).

Abundance Data

Data on plant cover or density require models that predict a nonnegative response, either continuous or discrete. Generalized linear models or GAMs of the gamma and Poisson families, respectively, are gradient-based methods (note that standard linear regression is ill advised because it can predict negative values). Regression trees are a standard machine-learning method for abundance data, whereas multinomial models (count data) can be fit via feed-forward neural networks (Venables and Ripley 2002). Kerns and Ohmann (2004) used regression-tree models to predict shrub cover at a regional scale in managed coastal forests of Oregon, USA, after initially trying multiple linear regression. Forest structural variables were the best predictors, and shrub cover was lowest

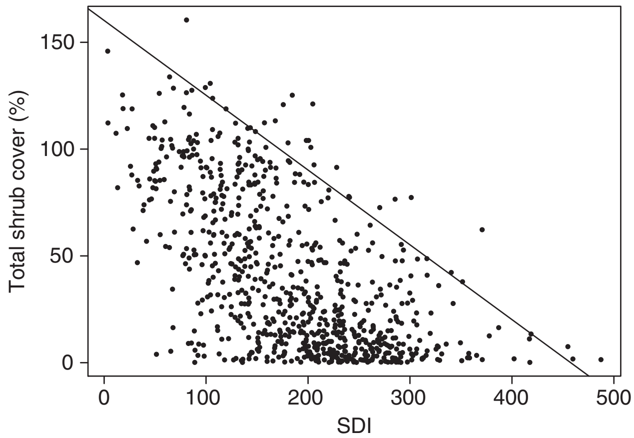


FIG. 15-2

Response of total shrub cover to stand density index (sqrt(basal_area * trees_per_ha)). Models of the mean response are noisy; models of maximum response produce a much better fit. Adapted from McKenzie et al. (2000).

during periods associated with stem exclusion, but explanatory power was compromised by the influence of human-caused disturbance.

McKenzie et al. (2000) examined the response of shrub cover to stand variables graphically (Fig. 15-2) and with regression-tree analysis and then elected to look at methods for estimating maximum abundance as a function of limiting factors (Guo et al. 1998, Scharf et al. 1998). This method is distinct from quantile regression (Cade et al. 1999, 2005; Cade and Guo 2000; Koenker and Hallock 2001) in that it uses a semiqualitative procedure to identify a constraint line as a surrogate for a limiting factor, rather than developing a full statistical model with associated error structure with confidence and prediction intervals. Proportion of deviance explained from nonlinear maximum-abundance models was 0.84–0.92 for shrub and herb response variables, as opposed to 0.49–0.80 from regression-tree models for estimating mean abundance (McKenzie et al. 2000). Maximum-abundance models clearly facilitate ecological interpretation but are not applicable to the prediction of mean values, nor is the error structure well defined in current implementations (Scharf et al. 1998, McKenzie et al. 2000).

Quantile regression is a feasible alternative to GLMs or regression trees for estimating means (i.e., 50% quantiles) or other quantiles (e.g., 5% and 95% quantiles, which can be surrogates for minimum and maximum response). It also provides a more rigorous means of quantifying confidence intervals, error structure, and goodness of fit (Koenker and Hallock 2001) than other maximum-response techniques. Extensions of quantile regression can accommodate asymmetrical distributions, nonlinear parametric models, and nonparametric models such as GAMs.

Multivariate Data

The presence-absence or abundance, or rarely for vegetation modeling, compositional data (proportions that sum to 1) for multiple species can be fit by gradient modeling. We are unaware of any examples of multivariate vegetation data modeled via neural networks or other machine-learning methods. Ohmann and Spies (1998) used gradient modeling (CCA) at the regional scale to predict the abundance and spatial pattern of woody plant species, including understory shrubs, across forests of Oregon, USA. Explanatory power was relatively low, not surprisingly, given that predictor variables (climate being the best) likely affected plant abundance at different scales and interacted in complex ways.

Data Requirements and Limitation

Measurement error is the initial uncertainty associated with any modeling effort. Obviously, every effort should be made to assure data quality (as with any research). Some additional desirable attributes of data for empirical models are (1) capture as much of each associated ecological gradient as possible in data collection, for the response and predictor variables; (2) avoid surrogate variables where possible (for example, elevation and latitude-longitude often turn out to be good predictors for ecological responses but represent ecological mechanisms poorly, if at all); and (3) in only apparent contrast to #2, try to collect at least a surrogate variable for each expected limiting factor in an ecological process being modeled. For example, energy and water are universal requirements for vegetation, understory or other. A model of understory response will likely miss much explanatory power if it does not represent both these elements, with variables such as soil temperature, degree days, or solar radiation (energy), or soil moisture, precipitation, or snowpack (water).

ECOSYSTEM DYNAMICS MODELS

In contrast to empirical models, which begin by assembling data, models in this paradigm begin by specifying key ecological mechanisms to be simulated (Fig. 15-3). Ecosystem dynamics models use mechanistic approaches to simulate plant growth, regeneration, and mortality, decomposition, and nutrient cycling (Neilson and Running 1996, 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 models simulate growth, death, regeneration, and stand structure based on initial vegetation and biophysical conditions, and can in theory simulate explicit understory attributes such as shrub and herbaceous cover, density, and composition. In practice, however, they focus almost exclusively on forests

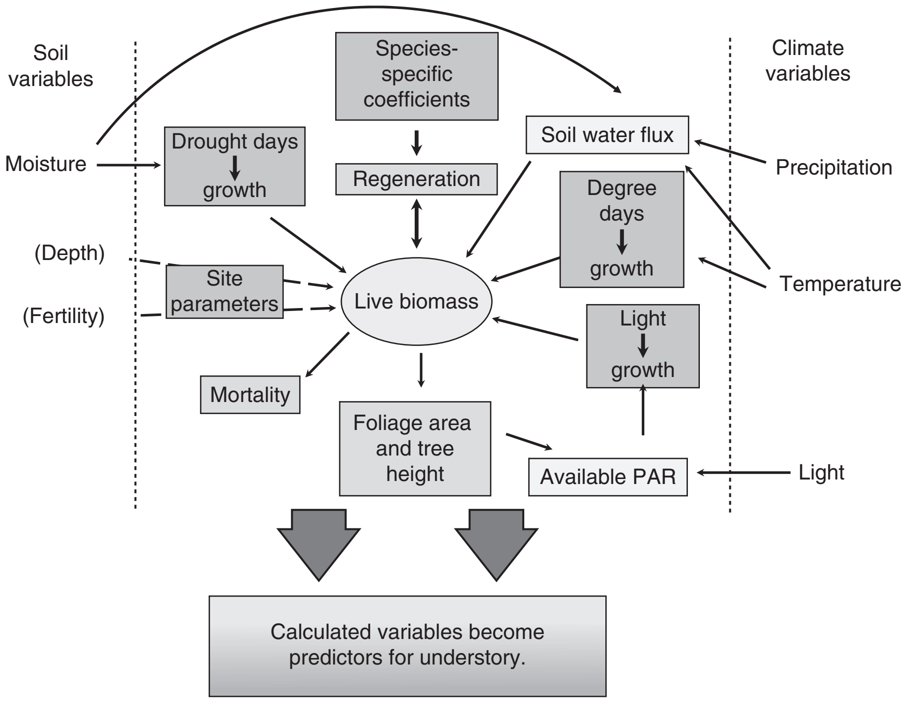


FIG. 15-3

Key elements of ecosystem models for predicting understory vegetation. At each time step, tree regeneration is simulated explicitly and other understory vegetation is predicted from intermediate calculations. Adapted from Cushman et al. (2007).

and the tree layer, with tree regeneration being the only understory component simulated (Urban and Shugart 1992, Pacala et al. 1993, Bugmann 1996). We know of no simulation model to date within the gap-phase mechanistic paradigm that includes nontree understory components (Bugmann 2001). However, shrubs could be modeled as trees in models such as LANDIS (He et al., this volume) which considers attributes such as species shade tolerance and longevity.

The Forest Vegetation Simulator (FVS; Dixon 2002) provides an example of how nontree understory attributes could be extracted from a gap-phase model. It is based on empirical growth equations rather than mechanistic modeling, updating a "tree list" at each time step with respect to growth, mortality, and regeneration. The FVS has two add-on modules: COVER (Laursen 1984, Moeur 1985), which calculates shrub cover based on empirical equations, and

FVS-FFE (Fire and Fuels Extension; Reinhardt and Crookston 2003, Rebain 2006), which calculates understory fuels. The allometry of these calculations is based on empirical models like those we discussed previously. Much as ecosystem dynamics models include stochastic routines for regeneration and mortality, they could include empirical models for understory components until such time as an explicit mechanistic framework is developed.

Data Requirements and Limitations

As with empirical-statistical models, the weak link in process-based models is often the lack of databases for initializing and calibrating model algorithms. An oft-neglected limitation of these models is the reliability of the sources of the "physical" processes modeled. For example, as noted previously, the FVS model is based on empirical growth equations throughout. More subtly, however, many process-based simulators have empirical equations at their core. It is the specific use of these equations to represent processes as mechanistically as possible, rather than some embedded association with ecological mechanisms, that justifies their being part of process-based modeling.

QUALITATIVE MODELING

When data to inform empirical or process-based models are of poor quality, at the wrong scale, or simply lacking, qualitative reasoning, based on logic, expert opinion, or both provide an alternative paradigm. Knowledge-based systems are often used successfully in natural resource applications (Puccia and Levins 1985, Robertson et al. 1991, Schmoldt and Rauscher 1996 and references therein). For example, successional pathways provide an experiential logic for estimating changes in overstory and understory structure and composition over time (Cattellino et al. 1979, Beukema et al. 2003, Kipfmueller and Kupfer 2005). They can stand alone as predictive models or be embedded in simulation systems or larger qualitative frameworks (Keane and Long 1998, Hemstrom et al. 2001). However, much care is warranted in applying qualitative models, as they are by definition a formalization of assumptions and are neither derived from nor usually tested with empirical data. In some cases, including expert opinion as explanatory factors in empirical models has produced worse performance and lower predictive success (Seoane et al. 2005).

As with process-based simulations, few successional-pathway models provide an explicit description, let alone quantification, of the understory apart from tree regeneration. Understory composition and structure generally are inferred indirectly. For example, Raymond et al. (2006) developed a classification of fuels, in both overstory and understory, by combining overstory structure and composition with successional changes, a comprehensive inventory database, and expert opinion of local fire managers.

Data Requirements and Limitations

Data requirements can be just as substantial as for empirical-statistical models or process-based models. Qualitative inferences do not necessarily imply a lack of available data, although it is often the case. When the statistical properties of the data are not evident or weakly specified, that is where qualitative inference often comes in. The main limitation of this approach is the lack of a rigorous quantitative framework to guide inferences and extrapolations to different landscapes or future conditions. In general, extrapolations will depend on a new set of qualitative inferences, rather than evolving out of the model structures themselves.

CAN WE BUILD THE IDEAL UNDERSTORY MODEL?

At best, empirical models can satisfy four of our five requirements for an ideal understory model. Because each model is a snapshot of data collected at specific places and times, it does not capture the transient dynamics associated with ecological mechanisms. Time lags, nonequilibrium dynamics, and mismatch of temporal scale between responses and drivers reduce the effectiveness of equilibrium 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 et al. 1996, Waring and Running 1998). The ideal understory model will use robust empirical models to inform parameter choices in process-based simulations (green-shaded components in Fig. 15-3), while incorporating temporal dynamics, either via successional pathways or more quantitatively—for example, with state-transition components to a gap model (Acevedo et al. 1996). It should also account for stochastic perturbations (disturbances, human-caused or natural).

Which model paradigm is best? We suggest that this comparison is valid only within the context of particular studies, and that none is best globally. In general, however, the more clearly defined the statistical properties of the model database, the more empirical-statistical models should be favored over qualitative models. Similarly, the better understood the temporal dynamics of the system, the better the argument for using process-based simulations. For dynamic landscape modeling of understory vegetation, we suggest linking empirical and process-based models so that each can do what it does best.

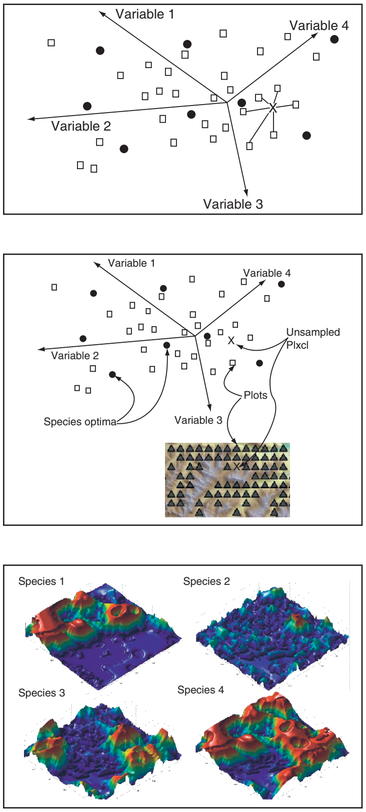
PREDICTING UNDERSTORY CHARACTERISTICS OF LARGE LANDSCAPES

We suggested previously that process-based simulations, with due attention to choices of parameters, can project empirical relationships through time, particularly those from gradient models. For management of large landscapes, we would also like to project these relationships across space. With a representative sample of inventory plots and robust statistical relationships across scales between explanatory and response variables (Fig. 15-1), predicted values for response variables can be assigned to new observational units, often cells or polygons rather than plots. This process, termed "imputation," is distinct from specifying distributions for missing data at the same scale as existing observations, and has received much recent attention because of increasing emphasis on large-scale management of vegetation and disturbance. Nearest-neighbor algorithms (University of Minnesota 2006), which impute values at a new location from those at one or more nearby locations (either in geographic or parameter space), preserve much of the explicit covariance structure of the empirical data in imputed responses, and are therefore superior to strict interpolation methods such as Kriging (Isaaks and Srivastava 1989) or inverse-distance weighting (Hessl et al. 2007). Unlike interpolation, however, imputation methods require explanatory variables to be available, usually as GIS layers, at the spatial scale and resolution for which predictions are to be made. For an understory model, overstory plot data may have to be imputed from coarser-scale predictors before the understory response is specified.

There are three standard approaches to nearest-neighbor imputation in vegetation analysis. Most-similar-neighbor (MSN; Moeur and Stage 1995) is the simplest conceptually. A distance measure of choice, usually multivariate, is applied to the GIS layer(s) of explanatory variables. The response variables at each unsampled location are then assigned the values at the sampled location for which the multivariate distance to the unsampled location is smallest. In its simplest form, MSN is simple to use and draws on the full range of values from sampled locations but cannot assign any new values to unsampled locations.

K-nearest-neighbor imputation (KNN; Dale 2002) draws on multiple ("k") nearest neighbors and applies a weighting scheme of choice to impute new values of the response variable at unsampled locations. As k increases, however, the averaging process decreases the variance among locations compared to that from the original samples (Pierce and Ohmann 2006). KNN algorithms are based in machine-learning and can be computationally intensive, so approximate techniques are useful (Finley et al. 2006).

Gradient-nearest-neighbor (GNN; Ohmann and Gregory 2002; Fig. 15-4) takes advantage of nonlinearities in species-environment relationships and is particularly useful across large landscapes in which gradients are long, species turnover is high, and there are many zeros in response variables (e.g., understory species presence-absence). The relationship between GNN and KNN is analogous to that between gradient-based and machine-learning methods in empirical modeling. Gradients in the ordination space of GNN models (Fig. 15-4) are interpretable in the same way as gradients in the empirical models that are the basis for imputation, and can reinforce our understanding of driver-response relationships and limiting factors that affect understory composition, structure, and



(1) 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. Axes are orthogonal dimensions of ecological space. Species optima locate the center of their environmental niche with respect to the measured predictor variables.

(2) The niche model uses ecological space, but we can make inferences about suitability in geographic space using *GNN.* 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.

(3) 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.

FIG. 15-4

Gradient imputation example using canonical correspondence analysis (ter Braak 1986) and gradient-nearest-neighbor (Ohmann and Gregory 2002). Adapted from Cushman et al. (2007).

abundance (Cushman et al. 2007). In contrast, machine-learning methods (e.g., combining regression-tree models with KNN imputation) are more difficult to interpret in terms of ecological mechanisms.

On landscapes affected by warming temperatures, changing disturbance regimes, invasive species, and accelerated land-use change, the most robust models will be those that can be interpreted in terms of ecological fundamentals even under new environmental conditions. We suggest that gradient-based imputation techniques such as GNN, perhaps with hierarchical elements to account for processes at multiple scales (Cushman and McGarigal 2003, Gehringer 2006), are in general the best choice for extrapolating understory models to large landscapes.

FIRE AND UNDERSTORY MODELS

Fire is a key disturbance worldwide and universally affects understory vegetation, whether fire regimes are of low or high severity. To inform our understanding of understory composition, structure, and dynamics, we briefly review fire effects because information on understory response to fire can refine variables used in understory models and enable better representation of disturbances and their effects on succession.

Fire, and disturbance in general, can reset or drastically alter successional pathways, especially in the presence of invasive species. Understory vegetation drives forest succession in the boreal forest by influencing tree seedling regeneration and below-ground nutrient cycling processes, and wildfire is the main determinant of understory vegetation in this ecosystem (Nilsson and Wardle 2005). Frequent burning favors invasive species, and time-since-fire is an important predictor of invasive species presence in mixed-conifer forests, blue oak savannahs, and chaparral ecosystems (Keeley 2003). Sagebrush ecosystems are particularly sensitive to invasive species like cheatgrass (*Bromus tectorum*) because grasses increase fuel cover and continuity, thereby increasing the risk of large frequent fires that destroy habitat for the endangered sage grouse (*Centrocercus urophasianus;* Miller and Rose 1999).

Fire is often a key to wildlife habitat quality. Some species are fire-dependent, whereas others are fire-sensitive. Sometimes a change in fire regime, particularly increased fire severity, can change habitat quality (e.g., nesting, forage, protection from predators). In many ecosystems of the United States (and worldwide), fire management is central to ecosystem resilience, restoration, and maintenance. Land management in western North America is increasingly focused on wildfire mitigation and fuel reduction, including mechanical removal of biomass and reintroduction of fire. These treatments alter understory structure and composition, which can affect wildlife habitat and forage. Understory models can be useful tools for predicting the effects of management, and conversely, empirical data from management activities can be used to refine simulation and empirical models and contribute knowledge to qualitative models.

About half (17 of 35) of the fire effects studies we reviewed were conducted in pine forests, pine/oak woodlands, or pine grasslands; four were in boreal forests and the remainder included mixed conifer, woodlands, and sagebrush ecosystems. Studies of fire effects typically evaluate initial and short-term responses (less than 5 years); only six are long-term studies in which fire effects were studied for >5 years postdisturbance. Understory response to fire varies with species, fire, and site characteristics, but in the majority of studies reviewed, fire significantly increased understory diversity (Griffis et al. 2001, Wang and Kemball 2005), richness (Griffis et al. 2001, Huisinga et al. 2005), abundance (Sparks et al. 1998, Lloret et al. 2003), and cover (Keeley 2003, Huisinga et al. 2005). In some cases, fire had no or minimal effect on understory (Rego et al. 1991, Fulé et al.

2005) or initially decreased abundance (Schwartz and Heim 1996), diversity (Wang and Kemball 2005), and richness (Metlen et al. 2004).

The following factors influence fire effects on species structure and composition and represent a set of variables that may be relevant for understory models that include a disturbance component. Fire effects can vary with hillslope position (ridge, mid, valley). In a burned pine/oak forest of eastern North America, species diversity in the understory layer increased on ridges, decreased on the mid-slope, and did not change on the low slope (Elliot et al. 1999). Season of burned in mixed-oak forests, dormant or growing, can also alter the effects of burning and may be a key management choice for achieving desired effects on understory composition (Hutchinson et al. 2005). Variability in fire intensity, frequency, and severity affects overstory basal area, creating an indirect pathway by which fire affects understory vegetation through an inverse relationship between overstory basal area and understory production and composition (Bataineh et al. 2006) and richness (Beckage and Stout 2000). Fire severity can also directly affect understory vegetation and alter the relevant abundance of vegetative forms. For example, severe fire in the boreal forest initially decreases species diversity and richness and favors herbaceous and nonvascular plants over woody plants (Wang and Kemball 2005). Fire frequency can directly affect understory vegetation because the relative abundance of invading and residual species changes with time since disturbance (Halpern 1989).

Fire effects on understory can, in part, be predicted by known conditions prior to disturbance. Understory species respond to fire in a way consistent with life history traits (Halpern 1989, Lloret et al. 2003). For example, in mixed oak/pine forests, more frequent fires increase the abundance of sprouting grasses, shrubs, and hardwoods, whereas seeding species reach greatest abundance with intermediate fire frequencies (Lloret et al. 2003). Incorporating life history traits into process-based models should therefore improve predictions of understory vegetation response to disturbance. Site conditions such as prefire overstory structure and fuel loads (Fulé et al. 2005) and water table depths (Blank et al. 2003) can mitigate the effects of fire and explain the variability in species richness and diversity that is observed postfire. Climate can alter fire effects because vegetation response following fire is driven in part by inter-annual climatic variability in ecosystems susceptible to drought stress (Fulé et al. 2005).

Fire extent, frequency, and severity are likely to increase in a warming climate (Flannigan et al. 1998, McKenzie et al. 2004, Gedalof et al. 2005, Westerling et al. 2006), increasing the influence of fire on understory composition, structure, and succession. Our ideal understory model (described previously) clearly should incorporate fire effects dynamically. A less desirable alternative, though certainly easier to implement, would be to represent fire as a “snapshot” variable, e.g., time-since-fire. State transition (successional pathway) models use fire events to reset succession and vegetation development (Keane and Long 1998, Hemstrom et al. 2001), and empirical models use time-since-fire as a predictor for understory richness and diversity (Chipman and Johnson 2002, Laughlin and Grace 2006).

Ecosystem dynamics (gap phase) models can incorporate fire dynamically. For example, Miller and Urban (1999, 2000) and Miller (2003) integrated fire into a gap model to examine landscape patterns and the effects of climatic change, but the understory was only represented in terms of fuel loadings and fuel-bed connectivity. A dynamic fire-succession model with an understory component is still in the future, but clearly within the range of current modeling paradigms.

FUTURE DIRECTIONS

We see four research tasks ahead to improve our ability to model and manage the understory component of large landscapes.

Incorporate the Range of Variability of Understory Vegetation into Models

Even the best statistical models of understory vegetation are noisy (Franklin 1998, Ohmann and Spies 1998, McKenzie and Halpern 1999, McKenzie et al. 2000), reflecting the considerable range of variability in understories even under strong abiotic and biotic controls. Imputation to large landscapes should take advantage of the ability of statistical models to quantify uncertainty, rather than treat variation as noise to be overcome by more precise models driven by more advanced algorithms. For example, suppose we are imputing the results from 1,000 sampled locations (plots) to 20,000 unsampled locations (cells in a GIS layer). The algorithms MSN, GNN, or KNN populating those cells will assign each either a fitted value from a model (MSN, GNN) or a weighted average (KNN), but iteration of this process disguises the uncertainties associated with the original models. Instead, imputation procedures could draw on the full distributions associated with predicted values, depending on the model type (e.g., binomial for presence-absence data, Poisson for count data, etc.).

For example, suppose a binomial GLM were built to estimate the probability of presence of an understory species given environmental conditions. Estimates would have standard errors associated with them, so imputed values could be drawn from the associated binomial distribution, not just assigned the means (fitted values). Alternatively, a hierarchical Bayesian model might be used to quantify the variance structure at different scales (Hooten et al. 2003), providing a direct approach to probabilistic imputation. As spatial scales of inference broaden, procedures like these are more appropriate than they would be for inferences at single points, whether for mean values or single observations, and more representative of landscape variability.

Integrate Space with Time in the Modeling Domain

Empirical gradient models, imputation to landscapes, and (process-based) ecosystem dynamics models need to be integrated to combine spatial patterns and temporal dynamics. Cushman et al. (2007) propose a framework for doing this, which we outline here:

1. Environmental data and stand inventories are used to build empirical gradient models;
2. Gradient imputation is used to populate landscapes with predicted values from gradient models;
3. Gradient models can supply parameters to ecosystem models; for example, unimodal response functions of organisms, both mature trees and understory vegetation, to climate variables (Miller and Urban 1999, 2000; McKenzie et al. 2003); and
4. Ecosystem models simulate succession over time at each cell.

Incorporate Disturbance Quantitatively into Understory Models

We have seen in our brief review of fire effects that in many ecosystems, fire is a pervasive influence on understory composition, structure, and dynamics. Fire has been incorporated into mechanistic vegetation models (Keane et al. 1999, Miller and Urban 1999) and broader-scale stochastic vegetation models (LANDIS; He, this volume), but to our knowledge the successional-pathway approach is the only instance of including fire in temporal dynamics of the understory (other than tree regeneration). However, given the ubiquity of inventory databases, satellite-based models, and fire observations, at least on public lands in the United States (Hicke et al. 2002, Jenkins et al. 2003, National Interagency Fire Center 2006), there is now an opportunity to better quantify the response of understory nontree vegetation to fire in both statistical and simulation models.

Integrate over Multiple Scales

Aggregating information to broader spatial scales produces multiple uncertainties and can propagate and magnify errors in unknown ways (Rastetter et al. 1992, McKenzie et al. 1996). We have proposed gradient imputation as a means of preserving much of the range of variability across landscapes as represented in inventory data. Controls on understory vegetation operate at multiple scales, however, from biome-scale (e.g., climate) down to biotic interactions between individual organisms. Ideally, understory models could reflect multiple-scale controls. For example, Cushman and McGarigal (2003, 2004) built hierarchical models of avian species-environment relationships in the Oregon Coast Range, USA, and these methods could be transferred to understory vegetation. Wagner (2004) developed methods for multiscale ordination with CCA, and in theory, this technique could be used in GNN (Ohmann and Gregory 2002) or other forms of gradient imputation. Gehringer (2006) showed how nearest-neighbor imputation could be applied hierarchically. In general, hierarchical methods partition variance into scale-specific components, improving our ability to preserve the range of variability of individual data points when extrapolating to large landscapes.

As a possible alternative to these (non-Bayesian) hierarchical methods, Wikle (2003) developed a more mathematically unified, though less detailed, approach to combining spatial and temporal processes in ecological models. The temporal process, in this case movement of birds across the eastern United States, was specified as a diffusion process and nested in a hierarchy of conditional probabilities to be estimated by Markov Chain Monte Carlo procedures. If made accessible to working ecologists, and shown to account for cross-scale interactions (Wagner 2004, Gehringer 2006), this procedure could complement the Cushman et al. (2007) approach, particularly in cases where more rigorous statistical inferences were desired.

CONCLUSIONS

Understory modeling presents unique problems. Particularly in forests, understories are opaque to remote sensing, so inferences about understories must be made either from fine-scale plot data or indirectly through models. Indirect methods are also required to extrapolate fine-scale data to large landscapes; these methods propagate the considerable uncertainties associated with most fine-scale understory models and add more of their own. By incorporating these uncertainties directly into broad-scale predictions, focusing on the range of variability in understory response and on aggregate measures appropriate to broad scales, we can minimize biases that lead to poor management decisions.

We also propose that natural disturbance, particularly fire, be incorporated dynamically into understory models. Because understory succession is often rapid, on a scale of years rather than decades, understanding disturbance regimes *per se* (e.g., frequency, severity, and extent), will lead to better models of understory dynamics. Lastly, we look to active research in scaling and hierarchical models, whether incorporating scale explicitly (Cushman and McGarigal 2003, 2004; Wagner 2004; Li and Wu 2006) or of the Bayesian variety (Wikle 2003, Clark 2007), and integrating space with time in vegetation models (Cushman et al. 2007), to provide new insights and methods for modeling understories across large landscapes.

SUMMARY

Canopy vegetation composition and structure, whether in forested or nonforested landscapes, can be quantified reasonably well from remotely sensed images. In contrast, understory vegetation is largely invisible to remote sensing. Our ability to characterize it accurately at broad spatial scales depends on inferences about relationships to observable characteristics like overstory structure. We reviewed three modeling approaches to predicting understory vegetation from observable quantities: environmental variables, canopy vegetation, or disturbance history. Empirical models predict understory characteristics such as species composition or abundance from statistical relationships with predictors. Process-based simulation models use ecophysiological or biogeochemical algorithms to predict ecosystem properties such as rates of biomass accumulation or decomposition. Knowledge-based or expert-system approaches use qualitative reasoning, often when there is a dearth of empirical data for modeling. The optimal approach to understory modeling depends on both availability of data and the state of knowledge. Where a good understanding of ecological mechanisms exists, process-based models may be superior, whereas rich inventory data sets suggest the empirical approach. In all cases, understory models need to be scalable to be applied to large landscapes. We reviewed methods of extrapolation, focusing on gradient imputation, which preserves the covariance structure of models at their original scale. Fire is a ubiquitous disturbance across North America and an important control on understory structure. Conversely, live understory vegetation and dead woody fuels are the principal determinants of the severity and effects of understory fire. We reviewed the literature on fire effects on understories and suggested how fire might be incorporated into understory modeling. We concluded by offering recommendations for choosing the optimal method(s) for understory modeling of particular landscapes and pointed to directions for future research.

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