Forest Productivity and Diversity: Using Ecological Theory and Landscape Models to Guide Sustainable Forest Management

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Abstract—Sustainable forest management requires maintaining or increasing ecosystem productivity, while preserving or restoring natural levels of biodiversity. Application of general concepts from ecological theory, along with use of mechanistic, landscape-based computer models, can contribute to the successful achievement of both of these objectives.

Ecological theories based on the energetics and dynamics of populations can be used to predict the general distribution of individual species, the diversity of different types of species, ecosystem process rates and pool sizes, and patterns of spatial and temporal heterogeneity over a broad range of environmental conditions. This approach requires subdivision of total biodiversity into "functional types" of organisms, primarily because different types of organisms respond very differently to the spatial and temporal variation of environmental conditions on landscapes. The diversity of species of the same functional type (particularly among plants) tends to be highest at relatively low levels of net primary productivity, while the total number of different functional types (particularly among animals) tends to be highest at high levels of productivity (e.g., site index or potential net primary productivity). In general, the diversity of animals at higher trophic levels (e.g., predators) reaches its maximum at much higher levels of productivity than the diversity of lower trophic levels (e.g., plants). This means that a single environment cannot support high diversity of all types of organisms.

Within the framework of the general patterns described above, the distributions, population dynamics, and diversity of organisms in specific regions can be predicted more precisely using a combination of computer simulation models and GIS data based on satellite information and ground surveys. Biophysical models that use information on soil properties, climate, and hydrology have been developed to predict how the abundance and spatial distribution of various plants and animals. These models can be used to predict the patterns of forest type and structure that develop in response to variation in productivity and disturbance across complex landscapes, as well as species diversity and the distribution and population fluctuations of threatened species in specific regions.

The dual constraints of cost and logistics mean that only a small subset of ecological properties and processes can be monitored on any landscape, and this monitoring can only be carried out at a few locations that represent a very small proportion of the total landscape. Given these limitations, how can ecological monitoring programs provide the largest amount of interpretable information for a given expenditure of funds?

Ecological theory can contribute to more effective monitoring and management of forest ecosystems by predicting the general types and patterns of biodiversity responses that are most likely under specific conditions, so resources can be focused on the most critical ecosystem properties and processes. Theory can also provide qualitative predictions of how specific ecosystems properties, such as species diversity, are expected to change in response to natural variability in environmental conditions, as well as to specific management actions, such as changes in harvest schedule or grazing regime. Predictions of expected responses are essential for guiding adaptive management, for interpretation of changes detected by long-term monitoring, and for improving early detection of potentially undesirable changes.

Landscape models allow the application of theoretical predictions to specific landscapes by providing quantitative estimates of the spatial and temporal variation of the environmental conditions (soil moisture, nutrients, temperature, streamflow, etc.) that influence the patterns of growth and survival of organisms on each particular landscape. These dynamic landscape models go far beyond typical habitat suitability models to predict how population size should change over time, as well as changes in the spatial distribution of the population. Dynamic landscape models allow more effective management and monitoring by predicting the specific patterns of response that should be expected on a specific landscape under specific conditions, so monitoring results can be quickly interpreted as either consistent or inconsistent with expected changes.

Classification of Landscapes for Planning Monitoring Programs

At a coarse level, it is obvious that forests require different monitoring methods than grasslands or wetlands. However, even within forests (or within grasslands or wetlands) there is sufficient variation in environmental conditions that a single "monitoring model" is not appropriate for all forests. Planning a monitoring program requires information on the expected spatial and temporal variability in critical ecosystem properties, as well some information on expected directions of change in response to natural environmental fluctuations or specific management actions.


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Even within a particular biome or ecoregion, landscapes and waterscapes vary sufficiently in major properties that a "one-size-fits-all" monitoring program or ecosystem model will not work, and could lead to serious errors in ecological assessments and natural resource management. Some of the most likely errors relate to predicted changes in species diversity, and the size and distribution of specific populations.

Universal Properties of Landscapes

All landscapes, no matter how large or small in area, include spatial variation in two essential attributes: 1) the disturbance regime (as characterized by disturbance type, frequency, intensity, and timing); and 2) the rate of biomass production (the potential primary productivity of plants and/or the potential productivity of animals). In addition to local heterogeneity in these two attributes, there are major regional differences in disturbance regime and productivity, as well as global patterns that result from differences in soils, topography, rainfall, and temperature.

These two landscape properties, disturbance regime and potential productivity, provide a framework for classifying landscapes. These factors influence a wide range of ecosystem properties that are directly related to forest management and biodiversity conservation. This framework, originally described as the "dynamic equilibrium model" of species diversity (Huston 1979, 1984), allows prediction of the balance between competitive exclusion (which reduces diversity under some conditions) and conditions that slow or interrupt the process of competitive exclusion. According to this model, species diversity can be reduced by either competitive exclusion under conditions of high potential productivity, or by mortality and the failure of populations to recover from mortality under conditions of high disturbance frequency/intensity or low productivity (Fig. 1). The basic "hump-backed" (unimodal) pattern of species diversity in relation to potential productivity that is predicted by this model is found in a wide variety of plant communities (Grime 1973, 1979; Huston 1979, 1980, 1994) (Fig. 2).

The two axes of this landscape classification can be quantified using a variety of sources of information. Direct measurements of site index or potential net primary productivity will not be available in most situations. However, a number of environmental factors that are correlated with NPP (such as climate, soil nutrient availability, soil moisture conditions) are available at a wide range of spatial resolutions for areas ranging from single watersheds to all of North America. Maps of soil types and topography can be combined with climatic data to predict variation in factors related to forest productivity at resolutions as fine as a few meters (e.g., Garten et al. 1994; Huston and Fontaine 1994). Appropriate analyses of remote sensing data can contribute to mapping of spatial and temporal patterns of primary productivity, and can potentially be used to identify the effects (frequency, intensity, extent) of many types of natural and anthropogenic disturbances that alter vegetation structure.

The Four Primary Landscape Types

The dynamic equilibrium model (Huston 1979, 1994) predicts the variation in spatial heterogeneity of vegetation structure and diversity that results from an interaction between disturbances that cause mortality (e.g., formation of disturbed patches) and the rate at which populations and ecosystem processes recover from the disturbances (e.g., population growth rates and the rate of successional change) (Fig. 3).

Although significant spatial heterogeneity exists on almost all landscapes, the broad consistency in regional patterns of climate, geology, and soils (e.g., biomes or ecoregions), allows the classification of landscapes on the basis of factors related to productivity and disturbance for spatial areas ranging from the entire earth (e.g., the Holdridge Lifezone Systems, Holdridge, 1947) to single watersheds (e.g., Garten et al. 1994; British Columbia Ministry of Forests 1990).

The four extreme combinations of disturbance and productivity described below represent four very different types of environments that have different dynamics of species diversity and require different approaches for natural resource monitoring and management. Although these landscape types represent the extremes of productivity and disturbance dynamics, they clearly intergrade along the natural continua of productivity and disturbance regimes.

**High Productivity - Low Disturbance Landscapes**

This combination of conditions is the one that is most...
Figure 2. — Patterns of plant species diversity in relation to factors related to potential productivity in different vegetation types. (A) - (C) are oldfields and grasslands, values are number of plant species per square meter; (D) - (F) are tropical forests, values are number of tree species per 0.1 ha, number of vascular plants per 0.1 ha, and number of tree species per ha, respectively. Note that in all cases the number of plant species declines at the highest levels of fertility or other factors correlated with productivity, while the maximum number of species is found at intermediate to low levels of the same factors (from Huston, 1993, 1994).
favorable for human uses and for many components of biodiversity. Unfortunately, this type of landscape has been pre-empted for human agricultural use around the world (Huston, 1993) and is one of the most endangered landscape types from the perspective of conservation and ecosystem services. Human activities typically shift this type of landscape into the high productivity - high disturbance category (see next section), with a very different set of processes and issues.

In the absence of human impacts, the combination of high productivity and low disturbance frequency and/or intensity allows most of the landscape to be covered with mature, high biomass communities. The rapid recovery of high levels of biomass following disturbance results in a relatively uniform landscape, where most of the spatial heterogeneity is caused by underlying topographic and geological variation, rather than by processes such as patch formation and succession. While scattered patches of mature forest can be found by chance even on landscapes with relatively high disturbance frequencies, on low disturbance landscapes, these mature, high biomass conditions dominate over the entire landscape (Fig. 3d).

Mature, "old-growth" forest in productive regions is typically low in tree diversity, and low in spatial heterogeneity. The classic examples of this type of landscape are the coastal evergreen forests of the Pacific Northwest of North America. Other examples might include bottomland hardwoods or certain swamp forests in the Southeastern United States. Low tree species diversity (and diversity of other types of plants as well) over a range of spatial scales in these systems is typically not overcome by the presence of early successional or "pioneer" species.

Low tree diversity may lead to a relatively low diversity of animals that are highly specialized or host-specific. However, the overall high productivity of the environment can support a high diversity of animals, particularly at higher trophic levels, including detritivores and decomposers, as well as predators (Lattin, 1990; Huston 1994). Population densities of animals can be quite high as a result of the high primary productivity.

Aquatic systems in productive environments are also likely to be highly productive, either as a result of algal growth supported by high nutrient and light availability, or high levels of organic matter input from the terrestrial system. Under these conditions, the diversity and productivity of aquatic invertebrates and fish may be quite high, particularly in streams, which typically have higher disturbance frequencies and intensities than lakes. High productivity in aquatic systems can also be caused by anthropogenic eutrophication, which often leads to low species diversity as a result of anoxia (caused by decomposition of large amounts of organic matter), toxics from certain species of algae, and competitive exclusion, particularly among the primary producers (Schindler 1974; Proulx et al. 1996).

In productive, low-disturbance landscapes, disturbed areas are particularly important because of their relative rarity. Pioneer and early successional plant species, and animals that depend on them, are likely to be rare in these environments. Disturbed areas are particularly important because both the chemical quality of the plants and the overall net productivity of early successional areas are likely to be much higher than those of mature forest (in spite of much lower total biomass). The relative uniformity and high biomass of vegetation that results from high productivity and low disturbance frequencies makes these landscapes subject to rare "catastrophic" disturbances (e.g., stand-replacing fires), which may affect large areas when they occur (Wright and Bailey 1982).

Species diversity on these landscapes reflects two contrasting sets of patterns and processes. First is low diversity among competing species, as a result of competitive exclusion (Fig. 1). High productivity leads to rapid rates of individual and population growth, which accelerates the expression of competitive dominance, leading to competitive exclusion and a reduction in the number of coexisting species. This pattern only occurs among species that are potential competitors, and is most conspicuous among plants, all of which compete for the same basic resources (Grime 1973, 1979; Huston 1979, 1980, 1994; Keddy 1988; Reader and Best 1989; Guo and Berry in press). The second pattern is high diversity among species that do not compete with one another (Fig. 4). High productivity and a low frequency of disturbances allows the survival of populations that would not be able to survive under lower productivity or a high disturbance frequency (or intensity). This increase in diversity results from an increase in the number of functional types of organisms (particularly animals) with different "niches." Such functional types include different feeding guilds, different trophic levels, and many different types of specialization (e.g., McMinn and Crossley 1996).

The effects of environmental or management changes on these landscapes are predictable, and contrast dramatically between plants and animals. Any increase in disturbance...
Figure 4.— Interactive effects of mortality-causing disturbances and productivity (rate of population growth and recovery) on the survival of populations of species that do not compete with one another. The highest probability of population survival, and thus the highest diversity of independent populations, is found under the favorable conditions of high productivity and low disturbance frequencies. Population survival probability, and thus total diversity of non-competing populations, decreases with increasing disturbance frequency and lower productivity (from Huston 1994).

Understanding the patterns of diversity on these landscapes should help resource managers to focus on the most sensitive components of the landscape or ecosystem (Hansen et al. 1991; Oliver and Larsen 1996). In addition, theoretical predictions about the expected direction of change in diversity in response to alteration of disturbance regime or productivity provide guidance that can guide forest management plans, enhance detection of changes measured by monitoring programs, and also distinguish expected from unexpected patterns.

High Productivity - High Disturbance Landscapes—This combination of conditions produces very dynamic landscapes that can be favorable for human activities as well as animal populations that can avoid or minimize the effects of the disturbances (Licht 1997). This type of landscape has also been severely altered by human activities around the world. The primary change humans impose on these landscapes is a reduction in the natural disturbance frequency
and intensity, largely through the control of flooding and fires. Elimination of these disturbances dramatically alters the species diversity and spatial pattern of these landscapes (White 1979).

In the absence of human impacts, these landscapes are typically very heterogeneous with regard to species composition, diversity, and biomass. High productivity allows rapid recovery of plant biomass and animal populations following disturbances and biomass can accumulate to high levels on patches that escape disturbance for long period of time. However, biomass is typically held to moderately low levels by the frequent disturbances. The high spatial heterogeneity of these landscapes (Fig. 3b) can result from two types of processes. First, small "patchy" disturbances can produce a landscape in which there are patches of different ages, with different amounts of biomass accumulation as well as different species composition and diversity reflecting successional dynamics. Second, large disturbances can impose temporary uniformity that rapidly disappears as a result of spatial variation in productivity and the rate of recovery from the disturbances (Huston 1994). Such variation in productivity is found on all landscapes, as a result of topography and associated variation in soil nutrients, water, etc. Classic examples of this type of landscape are fire-maintained prairies and savannas, and riparian zones along streams and rivers.

In addition to high spatial heterogeneity in biomass, these landscapes can vary dramatically in species diversity and composition. The high productivity allows species diversity to be rapidly reduced by competitive exclusion in the absence of disturbances. Consequently, patterns of diversity are very sensitive to variation in disturbance regime and to variation in time since the last disturbance. In addition, the high species diversity of plants, and high landscape heterogeneity also contribute to high diversity of animals specialized on different plants and microhabitats (Huston and Gilbert 1996).

With an appropriately high disturbance frequency/intensity, plant diversity can be quite high, as it is in frequently burned (or grazed or mowed) prairies (e.g., Huston 1979, 1994; White et al. 1991; Bakker 1989; Collins et al. 1998). However, species that are slowly growing or particularly sensitive to the disturbances are typically eliminated from these landscapes or greatly reduced in abundance. The suppression or elimination of woody vegetation by fire on prairies, as well as the low tree species diversity of fire-maintained savannas in conjunction with the high diversity of herbaceous plants, are good examples of variation in the responses of different "functional types" of plants to the same disturbance regime.

The high productivity of these environments can support a high diversity of animals of various functional types, if they are not severely affected by the disturbances (Fig. 3). The high biomass and diversity of large mammals and various types of birds found on the original North American prairies and on African savannas are good examples of high animal diversity under productive conditions (Norton-Griffiths 1979). These environments are very sensitive to changes in the disturbance regime, which often result from human intervention, but may result from natural climatic variability as well. Any reduction in disturbance frequency or intensity is likely to result in a reduction in the species diversity of some types of plants (e.g., grasses and herbs in prairies or riparian zones) and potentially an increase in the biomass and diversity of other plant types (e.g., more slowly growing woody species). Reduction in disturbance frequency or intensity can also alter the spatial heterogeneity of the landscape, allowing plant succession to proceed toward a stage with higher biomass and lower diversity (e.g., characteristics of a high productivity - low disturbance landscape). Typically, human activities have reduced disturbances in prairies, savannas, and riparian zones, leading to significant reductions in plant diversity, and major changes in the composition of the animal community in response to the changes in the structure and composition of the plants (Licht 1997). The biomass and diversity of some types animals can increase in response to reduced disturbance frequency. However, the major changes in plant diversity and composition, as well as the reduction in landscape heterogeneity, that result from decreased disturbance frequency can greatly alter the species composition of animals, and result in the reduction or elimination of many species that require the conditions produced by frequent disturbances (e.g., the recent decline of grassland bird species, REF).

Any environmental changes that result in a reduction of productivity are likely to reduce animal diversity (Fig. 4), but may actually increase plant diversity (Fig. 5e (right side of curve) or 5f). If the disturbance frequency is not too high (Fig. 5d). Both monitoring programs and resource management activities on high productivity - high disturbance landscapes should focus on the dynamics of spatial patterns that require disturbances for their maintenance. Many plant and animal species become rare very quickly in the absence of disturbance.

**Low Productivity - Low Disturbance Landscapes**

These landscapes are often misinterpreted as having high productivity because the low disturbance frequency allows large amounts of biomass to accumulate over long periods of time, even though the actual rate of accumulation is low. Most of the world's forests probably fall into this category, especially in the tropics, where many of the soils are very poor. These landscapes are not particularly favorable for agricultural activities, and tend to be very sensitive to degradation by human activities that increase disturbance frequency or reduce productivity (Uhl et al. 1997).

Low productivity - low disturbance landscapes have very high spatial heterogeneity at the scale of the dominant disturbance type (e.g., gap disturbance in forests, Fig. 3c). The low productivity results in a slow rate of recovery of biomass following disturbance, as well as a slow rate of plant succession and change in species composition. Plant diversity is typically quite high on these landscapes, as a result of two processes. First, the low productivity results to a low rate of competitive exclusion, which allows high diversity to be maintained over long periods of time in any small area. Second, the low rate of biomass accumulation produces patch-scale heterogeneity composed of patches, all of which are going through the same slow successional sequence. At any particular time, a landscape will have patches of many different ages, with each age of patch differing in biomass, structure, and species composition. These patches of different ages add up to very high diversity at the landscape scale, and this large "species pool" further increases the diversity at the scale of individual patches. Obviously, any additional
spatial heterogeneity that may result from differences in topography or soils will further increase the high plant diversity at large spatial scales on these landscapes.

The high plant diversity of these landscape often includes many rare and endemic species (Flather et al. 1994). The low productivity that reduces the rate of competitive exclusion and allows high species diversity may also contribute to reduced geneflow and higher rates of speciation (Huston 1994). The combination of (hypothesized) high speciation rates and low rates of competitive exclusion leads to high plant diversity across a wide range of spatial scales, from the local patch to large regions.

Although low productivity contributes to high plant diversity in infrequently disturbed landscapes, it can have a strong negative effect on the abundance and diversity of animals. Animal population densities tend to be low, and populations recover more slowly from disturbances than they would in a more productive environment. The size of the area (range) required to support individual animals or family groups is larger than in more productive environments. This effect is most pronounced at the highest trophic levels, and the abundance of predators is often low.

Even though the spatial density and population sizes of most animal species are low in unproductive environments, the overall diversity of animals can be quite high. This high animal diversity results primarily from species that are specialized on different plant species and on different successional stages and structural patterns of vegetation. Most of the high animal diversity of tropical forests results from this type of specialization.

The plant and animal populations on these landscapes are very sensitive to changes in either productivity or disturbance regimes. Any increase in mortality-causing disturbances is likely to result in the elimination of those populations that cannot recover between disturbances, with a consequent reduction in species diversity (Fig. 5a). Animal species are likely to be more susceptible to local extinction from increased disturbances than plants because of the loss of available energy (for growth and reproduction) with each trophic transfer. Plant diversity can be also reduced by either an increase in productivity (e.g., resulting from fertilization or atmospheric deposition) that increases the rate of competitive exclusion (Fig. 5f), or from a decrease in productivity, which increases the probability that some populations will not recover between disturbances (Fig. 5e, left side of curve).

Critical issues on these landscapes include preventing any increase in the disturbance (mortality) rates of plants and animals beyond the low natural rates. Major changes in productivity are likely to affect both plants and animals. Any decrease in productivity is likely to decrease plant diversity and have an even greater negative effect on animal populations, and human populations as well. However, increases in productivity may actually increase animal population sizes and diversity, assuming the reduction in plant diversity is not too great. The precarious situation for most animal species in low productivity environments means that isolated "hot spots" of high productivity can be critical for the survival of many species. Monitoring and resource management should pay close attention to the rare, highly productive areas on these landscape (e.g., riparian zones, alluvial deltas, wetlands) whose importance is much greater that their area would suggest. Unfortunately, these rare productive areas are precisely where human activities are likely to be concentrated on these landscapes.

Low Productivity - High Disturbance Landscapes—These landscapes are unfavorable for plants, animals, and most human activities, except perhaps for off-road vehicle recreation. Nonetheless, the various ecosystems found under these conditions are often strikingly beautiful, and fascinating because of the remarkable adaptations evolved by plants and animals in order to survive under these conditions.

Low productivity makes recovery from disturbance slow for both plants and animals. Disturbances are often associated with climatic extremes, with mortality caused by extreme droughts, or fires following periods of favorable growth conditions and fuel accumulation (Minnich 1983; Romme and Despain 1989). Slow growth rates leads to the persistence of patterns caused by disturbances, and maximum standing biomass levels are typically very low (Fig. 5a). The spatial and temporal variation in productivity, associated with variation in water or nutrients, have dramatic effects on the ecosystems of these landscapes. Interannual variation in rainfall often produces "boom and bust" cycles in animal and plant populations. Slight variation in soil water or nutrients associated with topography or geology can produce conspicuous spatial pattern in the structure and species composition of vegetation.

The most common diversity pattern on these landscapes is a positive relationship between productivity and small scale species diversity for both plants and animals (Fig. 5d). Productivity is rarely high enough that competitive interactions reduce plant diversity, although increases in either nutrients or water can lead to major shifts in plants species composition, with the potential loss of some species at the landscape scale (e.g., Berendse and Bobbink 1993). Much of the diversity at the landscape scale results from spatial heterogeneity associated with variation in productivity (e.g., Kerr and Packer 1997).

Areas with high resource concentrations, such as valley bottoms and riparian zones, are critical for the survival of many animal species in these environments (Pulliam 1988; Hansen and Rotella, in press). One of the greatest threats to the diversity of these landscapes is loss of these small areas of resource concentration, which should be a primary focus of both ecosystem monitoring and resource management.

Differences Between Animal and Plant Diversity Patterns

Across the range of landscape types described above, plant and animal diversity patterns are not always well correlated. Understanding plant and animal diversity patterns in ecosystems requires subdividing "biodiversity" into groups of organisms that have similar responses to the environment, as described above. The key distinction is that between groups of organisms that potentially compete with one another (among which competitive exclusion is a possibility), and groups of organisms in which the species are sufficiently different (i.e., different "niches") that competition is unlikely.
A fundamental fact of ecosystem energetics is the reduction in available energy each time one organism consumes another. Typically, 90% of the energy of the food organism is lost or respired with each transfer of energy by herbivory or predation. Consequently, the first trophic level (plants) inevitably have more energy (and usually higher biomass) than the next trophic level (herbivores), which has more than the predators, etc. One consequence of this reduction in energy available to higher trophic levels is that the productivity and growth rates of organisms at higher trophic levels it inevitably lower than energy available at lower trophic levels (Odum 1953; Oksanen et al. 1981; Abrams 1993).

For a given level of plant productivity, the productivity of herbivores and carnivores will be significantly lower. Since plant diversity is highest at relatively low levels of productivity, the population density and overall diversity of many types of herbivores and predators is unlikely to reach its maximum under the conditions where plant diversity is highest. In fact, the diversity of increasingly higher trophic levels is most likely to be maximum at increasingly higher levels of plant productivity (Fig. 6).

Thus, it is very unlikely that high diversity of all types of organisms will occur in a single type of environment, either as a result of management efforts or natural processes. As described above, different types of organisms will reach their highest diversity under different conditions. Understanding the conditions under which various functional types of organisms reach their highest (or lowest) diversity is critical for designing and planning monitoring programs, for assessing observed responses, and for resource management planning.

### Predicting Invasions of Exotic Species

Although invasions of problem-causing exotic species can occur naturally, they more commonly occur as a result of human activity. Humans increase invasions in two primary ways: 1) by transporting species long distances and across barriers that they could not naturally cross; 2) by disturbing or otherwise altering natural communities in ways that make them more easily invaded and dominated by new species.

Just as some combinations of environmental conditions tend to have higher species diversity than others, some combinations of productivity and disturbance dynamics are more easily invaded than are other combinations. Ecologists have long theorized that high diversity communities are more resistant to invasion than low diversity communities (Elton 1958; MacArthur 1972). This belief was based on the concept of ecological niches and competition for resources. It was assumed that the many species in a high diversity community would more completely utilize the environmental resources than the fewer species of a low diversity community, and make it more difficult for new species to invade. However, most patterns of invasion do not support these theoretical predictions. For example, extensive vegetation surveys in Great Plains grasslands and meadows in the Rocky Mountains (Stohlgren et al., in press) demonstrate that the highest rates of invasion of exotic species is found in the areas with the highest diversity of native species. These observations are consistent with the predictions of the Dynamic Equilibrium Model are that high diversity environments should be more invasible than low diversity environments (Fig. 7).

These invasion patterns can be understood in terms of the effect of productivity and disturbance on plant biomass or cover. When plant cover is high, as in forests or productive grasslands, rates of invasion by additional plant species are low because of intense competition, regardless of species diversity. Likewise, when plant cover is low, as a result of disturbances or low productivity, invading species can easily become established, regardless of the species diversity of the native community. The same processes that regulate species diversity, affect the survival and growth of species that are entering, or “invading,” a particular habitat, regardless of whether the invading species are native or exotic.

Observations around the world indicate that low productivity habitats, such as infertile or rocky soils, are readily invaded. However, invaders of unproductive areas rarely become dominant unless they are free of natural pests or are able to escape some of the limitations on growth and survival.
Dynamic Landscape Models

The critical effect that environmental conditions have on the growth and survival of particular species, as well as on patterns of species diversity, makes environmental modeling an essential component of environmental assessment and resource management. This fact is the basis rationale for "Habitat Suitability Indices (or models)" that have been developed and used for assessment and management (Short and Williamson 1987, Short 1992). These models typically combine a number of biological and physical properties of the environment into a statistical model that is correlated with the population size of a particular species. Such models are being widely used in a variety of different applications, ranging from conservation planning to evaluation of wetland mitigations (Scott et al. 1993).

A fundamental problem with habitat suitability indices is that they are typically based on a one-time assessment of habitat conditions, even though environmental conditions in any particular habitat are constantly changing. Habitat that can support high populations densities of a particular species during certain climatic conditions, may be totally unsuitable under different climatic conditions. Likewise, the habitat with optimal conditions may shift from one part of the landscape to another as climate varies, or other environmental conditions change. Depending on the length of favorable conditions in relation to unfavorable conditions, a given species may or may not be able to maintain a viable population in an area of habitat that is, on average, suitable. Static habitat suitability indices simply cannot predict the year-to-year variability in population sizes and reproductive rates, although such information on spatial and temporal variability is essential for planning resource management activities, and for evaluating the results of monitoring programs. One approach to overcoming this limitation is through the use of "dynamic habitat models," which are computer-based simulation models of landscapes that use climatic data together with information on topography, soils, and vegetation, to predict how habitat conditions change from year to year, or from season to season.

One application of landscape models is predicting how the pattern and properties of the habitats on a landscape will change over time as a result of natural succession, or of management activities and natural disturbances (such as with deep roots to water, or nitrogen fixation, see however, Mack 1986; Billings 1990). In contrast, productive environments, which are difficult to invade (UNLESS they have been disturbed), can be dominated by successful invaders or by successful native species (Fig. 7). This pattern of susceptibility to invasion and dominance is strongest for plants and sufficiently predictable that it can provide some guidance to managers.

Although the patterns of plant invasion are fairly predictable, invasions by organisms at higher trophic levels, such as diseases, pests, and predators, are much less predictable and can have severe and rapid impacts. Epidemics such as chestnut blight, Dutch elm disease, and tracheal mites of bees, as well as the recent invasion of predators in tropical environments, can be extremely difficult or impossible to control once they are started.

Figure 7.— Predicted community susceptibility to invasions and degree of dominance of invading species in environments classified according to disturbance and productivity (Huston 1979). A. Predicted susceptibility of communities to invasion. Darker shading indicates higher susceptibility. Note that communities with low diversity are least likely to be invaded successfully. B. Predicted life histories of successful invaders under various combinations of productivity and disturbance. Shading indicates expected dominance of a community by a successful invader. Note that if invaders alter the disturbance regime by increasing frequency or intensity, the community will shift to lower diversity and higher dominance by the invader (from Huston 1984).
of plant and animal populations. One type of mechanistic model that produces predictions ranging from population dynamics to ecosystem processes is "individual-based models" (Huston et al., 1988). In these models each individual is represented separately, with parameters that indicate its size, health, age, and reproductive condition, and change through time as each individual ages, grows, moves across the landscape (if an animal), reproduces, and dies. Models of this type generally treat resource acquisition by organisms in great detail, such as the feeding and growth of animals as they experience prey abundance that may vary through time or from place to place, or the light, water, and nutrient use by plants. These models have been particularly useful in dealing with organisms that vary greatly in size over their lifetime, such as fish and plants. Similar model structures have been used to look at changes in size distributions over time in both plants and fish (Huston and DeAngelis, 1987), and models of this type are being increasingly used to investigate stock management issues in fisheries (VanWinkle et al., 1993).

Forest dynamics models were among the first individual-based community models developed (Botkin et al., 1972; Shugart and West 1977, Shugart 1984). These models were originally designed to examine the effects of environmental conditions on forest structure and successional dynamics, but were quickly modified to address harvesting and other sources of mortality such as fire (Shugart and Noble 1981; Shugart et al. 1981). The great advantage of using individual-based models for forests (or any plant community) is that plants vary greatly in size as they grow from seedling to adult, and the amount of light available to any particular plant depends on how tall and how dense its neighbors are. A tall plant intercepts light and shades a small plant whether they are the same species or not. Consequently, the same type of model can be used for both single-species populations and multi-species communities (Huston et al. 1988).

Individual-based plant models can be used to predict successional dynamics under different environmental conditions or harvesting regimes (Huston and Smith 1987; Smith and Huston 1989; Shugart et al. 1981), and have been developed for a wide range of forest types, and for issues ranging from theoretical ecology to applied (Shugart 1984). Several investigators have developed spatially explicit versions of these models, in which either groups of plants (Urban 1990) or each individual plant (Busing 1991; Pacala et al. 1993) can be assigned a specific spatial location. These models can be used to look at spatial patterns that develop as a result of variation in environmental conditions (e.g., gradients or patches of soil nutrient availability, Huston and Smith 1987; Huston 1994) or processes such as tree mortality or dispersal (Smith and Urban 1988; Pacala and Deutschman 1995).

These models require information on the properties of each species that is modeled (e.g., maximum growth rate, nutrient and water responses, shade tolerance) as well as of the environmental conditions that affect tree growth (temperature, nutrients, water). Many different versions of individual-based forest succession models have been developed, and there is ongoing improvement both in model formulation and the quality of the species-specific parameters used in the models (Urban et al., 1991; Deutschman et al., in press).
Plant models can also be used to predict the dynamics of animal populations through the effect of habitat structure and food resource on animals. The effects of forest succession on the number and types of birds found in an area are well known (Ralph et al. 1991; Mills et al. 1996), and forest succession models can be used to make predictions about how the bird community will change through time in response to changing forest structure (Smith and Urban 1988; Urban and Smith 1989). Similarly, the influence of the amount and quality of food available to herbivores on the growth and population dynamics of the herbivores can be evaluated using this type of model (Pulliam and Dunning 1995; Comisky et al. 1997; Pastor and Cohen 1997). The effects of animals on plants, as a result of herbivory or other forms of damage, can be incorporated in models that predict how forest dynamics differ in response to the presence or absence of herbivores such as deer (Pastor and Naiman 1992; Pastor et al. 1993; Mladenoff and Stearns 1993; Pastor and Cohen 1997).

Once the basic parameters for a species have been obtained from field and/or laboratory measurements of individual plants or animals, these models can be applied to many different localities, as long as each locality can be characterized in terms of the spatiotemporal variation in environmental properties and food resources important to the species. For example, models of this type typically require "GIS" information such as topography, soil properties, vegetation type, forage or prey availability, etc., as well as information or estimates of how these environmental conditions vary across the landscape and change through time (Coughenour 1991; Franklin 1995). Spatially-explicit individual-based models can be linked to dynamic biophysical models of landscape processes (see above) to develop the capability to predict how populations might respond to different combinations or patterns of environmental conditions that could occur in the future. Thus, a particular population management plan could be evaluated in terms of how the population might do under various extremes of conditions, such as prolonged droughts or cold winters.

In the models developed for the Everglades Restoration Project, spatiotemporal variation in environmental conditions related to water flow was used to compare the ecological performance of alternative water management plans (USACE, 1998). As part of this effort, a spatially-explicit individual-based model of the Florida panther was developed using physiological, growth, and behavioral information from wildlife research (Comisky et al., 1997). Each individual panther is represented by the same basic set of equations about the energy requirements of different activities (e.g., moving, resting, nursing), but differs from other individuals because of its local environment, age, health, and interactions with neighboring panthers. Because the availability of quality food (specifically white-tailed deer) is essential for successful reproduction and growth, the Florida panther model is linked with a white-tailed deer model which uses the same type of energetic and behavioral model structure to predict the distribution and abundance of white-tailed deer in response to seasonal and interannual variation in their food availability. The deer model is linked to a vegetation model that predicts the distribution of forage of several quality classes across the South Florida landscape in response to seasonal and interannual variation in water.

Such dynamic landscape models are likely to become increasingly important for environmental assessment, planning, and resource management applications. The ability to predict how landscapes and their biotic communities change through time is invaluable for planning ecosystem monitoring and inventory programs and for interpreting data collected by these programs. Predictions of expected changes in plant and animal populations greatly increases the capability to identify such changes (e.g. allowing using of one-tailed rather than two-tailed statistical tests) and greatly facilitates interpretation of the causes of observed changes.

Conclusion

Ecological theory has helped identify complex, but consistent, patterns in the distribution and diversity of organisms. These patterns are found across all landscapes and aquatic systems, and can be classified in terms of fundamental (and quantifiable) properties of landscapes: specifically disturbance dynamics and potential productivity. A variety of sources of information, from direct field measurements to the use of satellite images, can be used to quantify the spatial and temporal patterns in disturbance and productivity at a range of spatial scales ranging from small watershed to the entire globe. Dynamic landscape models can greatly increase the temporal and spatial resolution of information on these landscape properties by interpolation based on mechanistic models of ecosystem processes.

Dynamic landscape models include hydrological and biogeochemical processes, as well as ecological processes, and can be used to translate the general predictions of ecological theory into predictions tailored to specific landscapes and time periods. The predictions of these models can contribute to planning ecosystem inventory and monitoring programs by identifying the types of species and the locations on the landscape that are most sensitive to disturbance or other environmental changes. Such models are currently under development for several different types of landscapes in North America.

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Literature Cited

Abstract


The general objective of this Symposium was to build on the best science and technology available to assure that the data and information produced in future inventory and monitoring programs are comparable, quality assured, available, and adequate for their intended purposes, thereby providing a reliable framework for characterization, assessment, and management of forest ecosystems in North America. Central to the syntheses delivered in this Symposium was the conclusion that a fundamental improvement in the approaches used for inventorying and monitoring ecosystem resources is required to meet current and future environmental uncertainties. Specific actions were proposed to address these challenges. These strategic actions are described in the last chapter of these proceedings.

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