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Patterns and Mechanisms of Plant Diversity in Forested Ecosystems: Implications for Forest Management

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PATTERNS AND MECHANISMS OF PLANT DIVERSITY IN FORESTED ECOSYSTEMS: IMPLICATIONS FOR FOREST MANAGEMENT^{1,2}

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Abstract. The objectives of this paper are to (1) review existing diversity models, (2) identify principles that explain patterns of plant species diversity, (3) discuss implications for forest management, and (4) identify research needs. Many current theories cast disturbance as the key player in maintaining species diversity by preventing competitive dominance of one or a few species. Equilibrium and nonequilibrium theories alike agree that maximum diversity should occur at intermediate size, frequency, and intensity of disturbance. These models do not adequately predict patterns at all spatial scales or across community types. A mechanistic theory is needed to explain diversity patterns at the patch, stand, and landscape scales, as well as across site quality and successional gradients. Such a theory should be based upon the interaction between species' life-history characteristics and the nature of disturbance. New research is needed in the following areas: identifying disturbance–life-history interactions, particularly with respect to the short-term and long-term effects of disturbance; quantifying patch diversity and determining its relationship with species diversity; determining relationships between species diversity and structural and functional diversity; and identifying appropriate standards of comparison for managed stands. Comparative studies in different ecosystem types, such as boreal and tropical forests, should be encouraged to help clarify the relative importance of processes that influence diversity.

Key words: *disturbance; diversity theory; equilibrium models; intermediate disturbance hypothesis; life histories; nonequilibrium models; plants; research needs; site quality; spatial scales; species diversity; succession.*

INTRODUCTION

In light of the accelerating loss of species worldwide (Wilson 1988), national and global forestry organizations have recognized the need to manage for biodiversity (Burton et al. 1992). For example, the Society of American Foresters (1991:viii) recommend that "Professional foresters should manage forestlands to conserve, maintain, or enhance the biological diversity of the region in which they work and, collectively, of the nation and the earth." The National Forest Management Act of 1976 (16 U.S.C. § 1600 et. seq. [1988])³ explicitly directs the USDA Forest Service to provide for diversity of plant and animal communities. We interpret these statements to mean that the goal of forest management should be to maintain natural diversity and species composition, as well as to enhance diver-

sity in areas where it has declined due to human activity.

In spite of increasing interest on the part of the public and land management agencies to manage for biodiversity, specific management strategies have, as yet, been poorly defined. Indeed, general theories of biodiversity are lacking (Solbrig 1991). We believe that ecologically sound forest management should be based on an understanding of natural patterns of diversity and the ecological processes that influence these patterns. Thus, it is imperative that we review the state of our knowledge in this area and its applications to management. Before we investigate these processes, however, we must first clarify terms and concepts of biodiversity that are relevant in management and that will be addressed in this review.

In its broadest definition, *biodiversity* is the diversity of life in all its forms and all its levels of organization (Hunter 1990), including the ecological structures, functions, and processes at all of these levels (Society of American Foresters 1991). In an attempt to provide a more operational definition, Crow et al. (1994) have identified three broad types or subgroups of biodiversity: compositional, structural, and functional. "Com-

¹ Manuscript received 2 March 1994; revised 2 October 1994; accepted 9 November 1994.

² For reprints of this 67-page group of papers on plant diversity in managed forests, see footnote 1, page 911.

³ U.S.C. = United States Code, the official compilation of all federal law.

positional diversity” is the variety of items within an area, such as species in a forest stand. “Structural diversity” can be characterized by the vertical or horizontal distribution of plants, plant sizes, or age distributions. “Functional diversity” is characterized by ecological processes, such as nutrient cycling, decomposition, energy flow, and trophic-level relationships. In addition to its different types, biodiversity can also be considered at various hierarchical levels of biological organization. For example, compositional diversity can be viewed at the genetic, species, or ecosystem levels (Probst and Crow 1991).

Each of the types and levels of biodiversity is expressed at a variety of spatial scales, from local to global. Consideration of scale is particularly relevant in management because strategies that favor local diversity may result in a decrease in regional diversity (Crow 1990). For convenience, we consider three spatial scales in this paper: patch, stand, and landscape. A “patch” is a contiguous, uniformly disturbed area in which the subsequent dynamics are similar (Petraitis et al. 1989). A single disturbance event, such as a fire, insect defoliation, or individual tree windthrow, may produce many different types of patches with different characteristics (Petraitis et al. 1989). As such, a patch is generally relatively small in spatial extent. In silvicultural terms, a patch denotes a portion of a stand that may be treated differently because of site, compositional, or structural differences, or to provide for regeneration of desired species, as in patch clear-cutting or patch shelterwood cutting (Smith 1986).

The “stand” is a group of trees and associated vegetation of similar structure growing under similar site conditions (Oliver and Larson 1990). Although the stand may contain many patches of different kinds, it is sufficiently uniform to be considered a homogeneous ecological unit. The stand is equivalent to an ecological community (Kimmins 1987), although for management purposes several similar stands may be grouped together and treated similarly. The “landscape” is a heterogeneous land area composed of different, interacting ecosystems (Forman and Godron 1986). In a management context, the stand, watershed, or other administrative unit may be considered as the basic ecosystem unit within the forested landscape, depending on management objectives. At the landscape scale, site quality, a notoriously variable characteristic in forested areas, exerts a strong influence on diversity patterns (Auclair and Goff 1971).

Finally, each of the types and levels of biodiversity also occurs within a temporal scale. For example, compositional diversity may show distinctive patterns with successional time according to changes in competitive interactions (Peet and Christensen 1988, Oliver and Larson 1990). The type of diversity, level of biological organization, and spatial and temporal scales must be clearly specified before undertaking any biodiversity assessment.

As in the other papers in this feature on plant diversity in managed forests, we consider primarily compositional (species) diversity of vascular plants, including the herbaceous understorey as well as the woody overstorey, because of the fundamental role that these species play in the structure and function of forest ecosystems. Accordingly, we use the term “species diversity” in preference to “biodiversity” to avoid confusing our relatively narrow focus with the broader concept. Although many different measures and indices of species diversity are available (Peet 1974, Patil and Tailie 1982, Magurran 1988), we refer primarily to species richness (number of species per unit area).

We address diversity primarily at the stand level because the stand is the basic unit of management, and the effects of management disturbances are directly expressed at this level. We agree that managers must focus on ecosystems and landscapes to preserve biodiversity (Franklin 1993). We suggest, however, that this can be done by managing at the stand level provided that management is carried out within the framework of landscape-level objectives. In the words of Crow (1989), managers should manage locally for regional diversity. We also consider species diversity along site quality and temporal gradients because these variables can present serious challenges to forest managers.

The papers in this group reflect a variety of diversity patterns. This diversity of diversities is in large part related to the wide range of ecosystem types that were included in our symposium. Previous studies in forest ecosystems also have found conflicting patterns. For example, many studies have addressed temporal changes in diversity. Monk (1967) found that diversity increased with succession as predicted by Odum (1969). Diversity was highest in the early stages of succession in studies by Habeck (1968) and Peet (1978). Long (1977) reported a similar pattern, but his study included only the first 73 yr of succession. Borrmann and Likens (1979) predicted that diversity should be equally high during both the early post-disturbance and climax stages. Several others have reported an increase followed by a decrease during succession (Loucks 1970, Auclair and Goff 1971, Shafi and Yarranton 1973, Schoonmaker and McKee 1988). Clearly, mechanistic models are needed to explain these conflicting patterns.

Accordingly, the main objectives of our summary paper are to (1) review current diversity models, and (2) based on this review, identify underlying principles that explain diversity patterns across ecosystem types and management schemes. We also consider the implications of these general models for forest management and identify key areas for future research.

REVIEW OF GENERAL MODELS

Connell (1978) divided diversity models into two general types: equilibrium and nonequilibrium models.

According to the *equilibrium* models, species composition recovers to an equilibrium at some point in time following disturbance, and maximum diversity is maintained at this level, either indefinitely or until a subsequent disturbance occurs.

Three hypotheses have been proposed to explain the equilibrium pattern (Connell 1978). In one view, total diversity of a community is a function of the total range of habitat conditions and the degree of specialization of species to those habitats. This is the *niche diversification hypothesis*.

Proponents of the *compensatory-mortality hypothesis* claim that selective mortality of the superior competitor maintains equilibrium. Predation or disease are examples of these mortality agents. This has been called "predator-mediated coexistence" by Petraitis et al. (1989). It is important to note that a form of disturbance is required to maintain diversity by this hypothesis.

Finally, under the *circular-networks hypothesis*, each species uses interference mechanisms that cause it to win over some species but lose to others. This is analogous to a perpetual round-robin tournament in which there is no ultimate winner.

In contrast to equilibrium models, the *nonequilibrium* models state that random (catastrophic) mortality caused by disturbance prevents natural communities from ever reaching equilibrium (Pickett 1980). These disturbances prevent superior competitors from becoming dominant. The patterns in fire-dependent communities, such as the boreal forest (Rowe and Scotter 1973) or longleaf pine (*Pinus palustris* Mill.) ecosystems of the southeastern United States (Campbell 1955), fit the nonequilibrium model.

Connell (1978) identified three nonequilibrium hypotheses. According to the *intermediate-disturbance hypothesis*, disturbance maintains diversity by preventing competitive exclusion. Maximum diversity is maintained at intermediate disturbance size, frequency, and intensity.

The *equal-chance hypothesis* has been proposed to explain situations in which all species appear to be equal in competitive ability. For example, many tree species in the tropical rain forest seem to have similar ecological requirements. Diversity, then, is a function of the number of species available for colonization.

Gradual changes in climate, seasonal and long-term, may cause shifts in species dominance, preventing competitive exclusion. This is the *gradual-change hypothesis*. Similar to the intermediate disturbance hypothesis, disturbance prevents competitive exclusion, but in this case the disturbance is much more gradual. The validity of the gradual-change hypothesis would depend on the rate of competitive exclusion relative to the rate of environmental change.

More recently, several alternative diversity models have been proposed. Huston's (1979) *dynamic-equilibrium model* elaborates on the nonequilibrium theme.

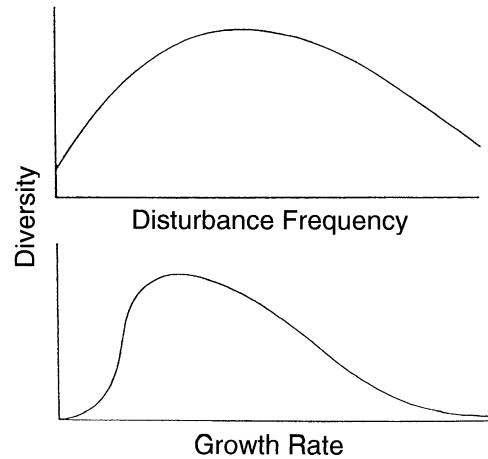


FIG. 1. Response of diversity to disturbance frequency and population growth rate according to the dynamic equilibrium model. (After Huston 1979; printed with permission of the University of Chicago Press from *American Naturalist*.)

The factors that control diversity in this model are the periodicity of disturbance and the rate of competitive exclusion. This model predicts that maximum diversity occurs at low to intermediate growth rates and disturbance frequencies (Fig. 1). Because growth rate is a function of site quality, this model implicitly includes the effects of site quality on diversity patterns.

The *general model of diversity* proposed by Petraitis et al. (1989) includes elements of the equilibrium and nonequilibrium models. By this model, diversity is regulated by species' immigration and extinction rates. The probabilities of immigration and extinction are functions of species number, as predicted by the theory of island biogeography (MacArthur and Wilson 1967). These rates also depend on within- and between-patch characteristics, such as microclimate and resource availability.

Similar to Huston (1979), Petraitis et al. (1989) view disturbance as the key factor that maintains diversity. The general model also predicts that the highest diversity should occur at intermediate disturbance levels. This results from a trade-off in life-history characteristics: no species is adapted to resist both competition and disturbance. Both types of species (i.e., those that resist disturbance and those that resist competition), are present at intermediate scales, intensities, and frequencies of disturbance.

It would be difficult, if not impossible, to conduct critical tests of the above hypotheses. Indeed, elements of several of these models may apply in the same situation. For example, in the Pacific Northwest certain species depend on habitats provided only by forest structure that resembles old growth (Spies 1991), as predicted by the niche diversification hypothesis. At the same time, the intermediate disturbance hypothesis is also applicable here, with diversity peaking during intermediate stages of succession (Schoonmaker and

McKee 1988). In some cases, diversity may show multiple peaks during succession as found by Halpern and Spies (1995), indicating that diversity patterns may not be as predictable as initially presumed. Thus, although these models are useful in organizing our thinking about diversity, they have limited application to management because of their generality.

Many of the above models agree that intermediate disturbance levels maintain diversity. Indeed, we view disturbance theory as central to management because management activities are simply different forms and intensities of disturbance. Accordingly, we return to the intermediate-disturbance hypothesis (IDH) to assess its applicability to forest management scenarios.

EVALUATION OF THE INTERMEDIATE-DISTURBANCE HYPOTHESIS

The intermediate-disturbance hypothesis (IDH) postulates that diversity is highest during intermediate stages of succession because enough time has elapsed for a variety of species to invade but not enough time for any species to dominate. For example, in disturbance-prone temperate forests there is a strong tendency for one or a few shade-tolerant species to become dominant with increasing time since disturbance (Loucks 1970). There is a dynamic equilibrium between disturbance rates and the rates of competitive exclusion among species (Huston 1979).

The rationale for the IDH is that few species (ruderals *sensu* Grime 1979) can persist under frequent, severe disturbances and few species (stress-tolerators *sensu* Grime [1979], or superior competitors) can persist in the absence of disturbance, whereas many species can persist in patches in various stages of recovery. A variety of ruderals, superior competitors, and intermediate species occur in the different-aged patches.

In addition to the time since disturbance and the rates of competitive displacement, whether or not the present disturbance regime approximates the historically characteristic regime for that community is an additional factor contributing to diversity (Denslow 1980). The important implications of the IDH are as follows (Denslow 1980, 1985):

1) Maximum diversity occurs at intermediate disturbance size, frequency, and intensity.

2) The natural community is richest in species adapted to establish in the type of patch most commonly created by disturbance. For example, in communities in which large-scale disturbance is common, such as the boreal forest, we find a relatively large number of species adapted to establishment in large gaps. In contrast, shade-tolerant species, which depend on small gaps for establishment, predominate in the tropical rain forest where small-scale disturbance is common.

3) The diversity of native species at the landscape level is greatest when disturbance occurs at its historic frequency and pattern. In other words, the average historic disturbance regime (defined in terms of size, fre-

quency, and intensity) is equivalent to the intermediate-disturbance regime. In management terms, this suggests that changing the natural frequency and pattern of disturbance by harvesting, fire prevention, or other treatments would cause a reduction in diversity.

In assessing the applicability of the IDH to management, we must again consider the issue of scale. It is not clear whether the IDH applies to the patch, stand, or landscape levels or to all scales. At the landscape scale it is easy to envision how a variety of stand types and development stages would maximize diversity. If only the intermediate disturbance were to occur, however, with no variability in size, frequency, or intensity, then landscape-level diversity would likely be reduced because species dependent on the extremes of disturbance would be eliminated. At the patch level the highest diversity may very well occur at intermediate-disturbance size, frequency, and intensity as predicted by the IDH. At the stand level, however, diversity may be higher if there is a variety of disturbance sizes, frequencies, and intensities. For example, species diversity may be low within a small patch but high within the stand if patch diversity is high. Thus, one problem with the IDH is that it considers only the intermediate-disturbance regime without reference to the range of disturbance frequencies, intensities, and sizes that are encompassed within the historic regime.

Another problem with the IDH model is that it does not attempt to predict differences in diversity between communities, such as those resulting from variations in site quality (Denslow 1980). This is a critical shortcoming for managers because they must deal with a wide range of site quality. Clearly a more mechanistic, predictive model is needed to explain diversity patterns at patch, stand, and landscape scales.

ELEMENTS OF A MECHANISTIC MODEL OF SPECIES DIVERSITY

Many workers have argued that a reductionist approach emphasizing species' life histories is required to deepen our understanding of succession (Drury and Nisbet 1973, Pickett 1976, Peet and Christensen 1980). This approach would also help explain changes in diversity over time, because temporal changes in diversity are influenced by successional processes, including competitive interactions and plant-mediated changes in resource availability. Several authors have classified plants into categories based on growth forms (Monk 1983) or reproductive characteristics (Bormann and Likens 1979, Canham and Marks 1985) to explain changes in species composition with time. Halpern (1989) related the timing of establishment and peak abundance of forest understory species to the origin of propagules, phenological traits, and potential for vegetative expansion. In general, we would expect a shift from weedy invaders to residual species to occur with time. The timing of the peak in diversity could very

well depend on the relative abundance of ruderal species and superior competitors in the local flora.

In addition to life-history characteristics, knowledge of the effects of different types and intensities of disturbance is needed to construct a predictive model of diversity. Ultimately it is the interaction between the nature and intensity of disturbance and the life-history characteristics of the component species that drives successional and diversity patterns (Pickett 1976, Halpern 1989). It is important, then, to determine the role that disturbances of various types play in controlling diversity and to identify successional changes in diversity. Several reviews of disturbance have been presented (e.g., White 1979, Oliver 1981). Oliver and Larson (1990) provided a classification of disturbances based on the following four factors: (1) frequency; (2) spatial extent; (3) amount of existing forest removed above the forest floor; and (4) amount of forest floor vegetation, forest floor, and soil removed. Taken in conjunction with species' reproductive and survival strategies, the characteristics of particular disturbances are useful in predicting vegetation response. For example, McMinn (1992) found that a combination of timing of seedfall and increased soil disturbance resulted in higher abundance of pines (*Pinus* spp.) on sites harvested in the dormant season relative to sites harvested during the growing season. After dormant-season harvests, evenness and diversity of woody species (Shannon's index) were lower because of the dominance of pines.

Halpern and Spies (1995) have suggested that we separate disturbance effects into two classes: initial and long-term effects. This division seems reasonable because different mechanisms are involved in each case.

The *initial effects* influence plant community response through destruction of vegetative stems and propagules, effects on propagule availability and species invasion, and modification of habitats, including seedbed conditions, light, temperature, and moisture. Management treatments such as harvesting and site preparation could have a wide variety of initial effects depending on how they are implemented. The type of disturbance in terms of its effects on the vegetation and environment is the important consideration here. As an example of these effects, the establishment of raspberry (*Rubus idaeus* L.) and yellow birch (*Betula alleghaniensis* Britton) seedlings was greater on patches with the forest floor removed than on the undisturbed patches after harvesting (Roberts and Dong 1993). Mortality of seedlings was lower on the mineral soil because of more stable temperature and moisture conditions.

The *long-term effects* are manifested as changes in species composition, rate of stand development, and competitive interactions. Control of competing vegetation with herbicides is a typical example of a treatment that has all of these long-term effects, (e.g., Horsley 1994). Other long-term effects include composition and density of planting, timing and intensity of

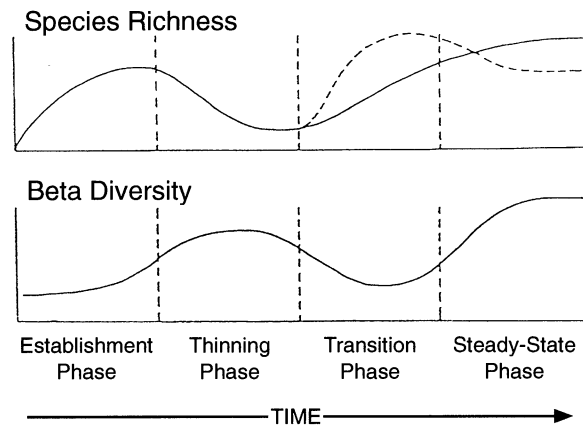


FIG. 2. Hypothesized changes in species richness and beta diversity with stand development. Species richness may decline (dashed line) or reach a new peak (solid line) during the steady-state phase. (After Peet and Christensen 1988; printed with permission of SPB Academic Publishing.)

thinning, and length of harvest rotation (Halpern and Spies 1995).

To be useful in management, models must explain diversity patterns across successional and site quality gradients. Peet and Christensen (1988) hypothesized that diversity would wax and wane during stand development according to the level of competition. For example, species richness is at a minimum during the thinning phase when competition among the overstory trees is at a maximum (Fig. 2). Beta (between-habitat) diversity should increase during the periods of most intense competition because of a decrease in niche breadth induced by competition. Gilliam et al. (1995) suggested that the link between forest strata becomes tighter as competition increases following the establishment phase. These patterns are related to the intensity of the disturbance as determined by the management regime.

Based on a review of other studies, Tilman and Pacala (1993) concluded that diversity peaks in habitats with low to intermediate nutrient supply, although these studies did not include extreme environments. We might expect relatively low diversity in extreme environments, such as tundra or desert, because few species are adapted to these conditions (Grime 1979). Auclair and Goff (1971) hypothesized that total diversity and the timing of the peak in diversity would vary with site quality. Diversity should peak relatively early in succession on mesic sites, whereas it should increase to an asymptote in the mature stages on xeric and hydric sites (Fig. 3). MacMahon (1980) predicted that there would be little change in diversity with successional time in harsh environments because the effects of the biota on the environment are minor under these conditions. In favorable and constant environments such as are found in a tropical rain forest, the environmental gradient between a clearing and closed canopy is much

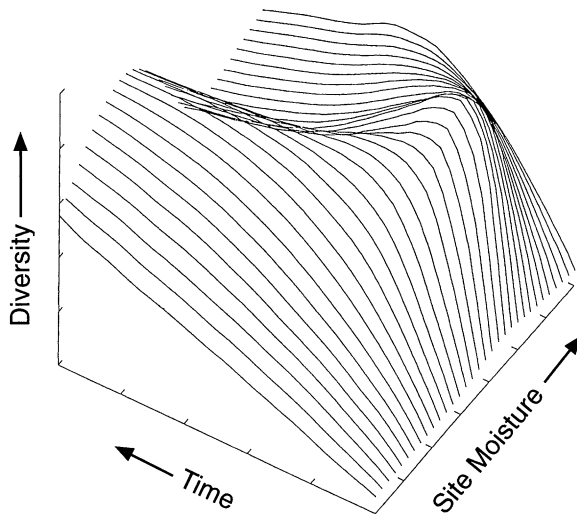


FIG. 3. Changes in species diversity with site conditions and successional time in temperate forest communities as hypothesized by Auclair and Goff (1971). (Modified from Burton et al. 1992; printed with permission of the Canadian Institute of Forestry.)

greater. Therefore, species turnover is great and rapid during succession (MacMahon 1980).

In conclusion, the IDH provides a useful theoretical model for diversity studies. To predict the response of forest ecosystems to management, however, we also must account for the effects of different disturbance regimes in terms of initial effects with respect to the life-history characteristics of the species and long-term effects with respect to competitive interactions. These effects must also be assessed at all scales from the patch to landscape and across site quality gradients.

PREDICTIONS BASED ON CURRENT THEORIES

Based upon this review of models and concepts related to diversity, we would predict that maximum diversity at the landscape level would occur under the historic (natural) disturbance regime. Although the intermediate-disturbance regime is based on the historic disturbance regime, it is defined in terms of averages and does not include the range of sizes, frequencies, and intensities that occur within the historic regime. Thus, if we wish to avoid reducing diversity at the landscape level, we should design management strategies that mimic the historic disturbance regime rather than the intermediate-disturbance regime. There are problems, however, with this approach. Given the extent of habitat modification and disturbance by humans, determining the historic disturbance regime may not be possible in many locations. Even if the historic regime could be determined, there may not be areas of sufficient size to support the historic regime in all ecosystem types. Finally, we do not know if it is necessary to mimic the historic disturbance regime in its entirety to provide habitats for all species, or if this could be

accomplished within a smaller range of disturbance sizes, frequencies, and intensities.

We would expect species diversity to be maximum under the intermediate-disturbance regime at the patch level. Diversity should peak during the stand establishment and steady-state phases of stand development when competition is reduced (Peet and Christensen 1988), although this pattern would be expected to vary with local site conditions. A more nearly linear increase in diversity with increasing stand age might occur on xeric, hydric, or infertile sites as compared to mesic, fertile sites (Auclair and Goff 1971). In terms of management, we should not be concerned if diversity is low at the patch level (in patches undergoing self-thinning) provided that stand-level diversity is maintained.

At the stand level, patch diversity should exert a strong effect on species diversity (Petraitis et al. 1989). Thus, disturbances or management treatments that result in a greater variety of patch types, such as different gap sizes or varying degrees of forest floor disturbance, should result in greater stand-level diversity.

There is currently considerable controversy over the contention that diversity peaks in the old-growth stage of stand development (Meier et al. 1995, and see summary review of temporal diversity patterns in *Introduction*, above). Nonetheless, diversity patterns in old-growth forests are commonly used as a standard of comparison for managed forests (Schoonmaker and McKee 1988, Swindel and Grosenbaugh 1988, Hansen et al. 1991). It would be more realistic, however, to use the entire successional sequence following natural disturbance as a standard. Each stage in the managed-stand succession could then be compared to the equivalent stage from the natural successional sequence. This approach recognizes the natural role that disturbance plays in temperate forest ecosystems.

Certain species occur only in old-growth forests (Peet and Christensen 1988, Spies 1991). Thus, one of the values of old-growth forests may be in providing unique habitats for these species. It is important to consider individual species and their habitat requirements in addition to the total number of species. In some cases, it may be the expressed goal of management to provide habitats for certain species, such as those that are designated as rare or endangered.

FUTURE RESEARCH

Additional research will be needed to identify diversity patterns and mechanisms with respect to site quality, successional age, and management treatments. It is unrealistic to expect to predict exact changes in species composition and diversity. Rather, our goal should be to discover the limits of our predictive capabilities (MacMahon 1980). Because of current gaps in our knowledge, we do not yet know where these limits lie.

Forest managers need to know the potential effects of different types of treatments on diversity patterns

over time in order to design environmentally sound management practices. A range of management intensities currently exists, from clear-cutting with intensive site preparation, artificial regeneration, and herbiciding, to selection systems. Comparing these treatments to natural forest succession in terms of diversity patterns will allow us to identify those human-made disturbance scenarios that most closely approximate natural disturbances.

Comparisons could be made using the framework of disturbance effects (initial and long-term) suggested by Halpern and Spies (1995). In terms of initial effects, the response of individual species to different management schemes should be tracked. Since species composition and species diversity responses are not always related (i.e., rapid species turnover can result in large compositional changes without a change in diversity), it is essential to consider species composition as well as diversity per se in these studies.

Specifically, these studies should focus on the interactions between species' life-history characteristics and disturbance characteristics (Canham and Marks 1985). Species can be classified into synusia or growth forms as suggested by Peet and Christensen (1988) to facilitate this work. Permanent plots should be established before disturbance so that the response of individual species can be followed in relation to their life-history characteristics.

Few studies have compared patch diversity following different disturbances. The disturbed area could be classified by patch type, and environmental conditions in each patch type quantified (light, nutrients, moisture, degree of forest floor and soil disturbance, etc.). This work could be used to test the intermediate-disturbance hypothesis at the patch and stand scales.

To address long-term effects, studies that track the response of species in relation to stand development stages and site quality are needed. Stand density indices based on density-size relationships such as the $-3/2$ law of self-thinning (Yoda et al. 1963) are useful indicators of stand development (Drew and Flewelling 1977, Peet and Christensen 1980, Roberts and Richardson 1985). Denslow's (1995) hypothesis of the relationship between tropical tree density and diversity could be tested with these studies. Site quality can be assessed within the context of regional site-classification systems. Special habitat requirements of sensitive species and how these habitats develop over time should be considered as part of these studies. For example, late-successional species such as some lichens and Pacific yew (*Taxus brevifolia* Nutt.) may require habitats found only in old-growth forests (Spies 1991). Again, we emphasize the importance of tracking individual species as opposed to following only diversity. This approach will help explain the patterns observed by Meier et al. (1995) and others.

Although this paper has addressed species diversity primarily, we emphasize the importance of considering

the relationships between species diversity and structural and functional diversity (Franklin 1988, Crow et al. 1994). Structural diversity could be measured as variation in vertical structure (e.g., plant heights and crown sizes) or horizontal structure (spatial pattern). Rates of nitrogen fixation and cycling or decomposition could be assessed as elements of functional diversity.

We also need to develop the appropriate standards of comparison for managed or disturbed stands. Managed stands are typically compared to the old-growth condition, even though this ignores the role of natural disturbance in communities. Alternatively, naturally disturbed stands at the same stage of development as the managed stands would provide a more realistic standard. We do not question the importance of maintaining old-growth forests but we wish to point out that these may not be appropriate standards of comparison in all cases. Managed stands also could be compared to degraded ecosystems as suggested by Lugo et al. (1993) and Lugo (1995). Finally, some measure of relative floristic richness within a given region could provide a reasonable average diversity standard (Wade and Thompson 1991).

Comparative studies in different ecosystem types would provide insights into the relative importance of processes that influence diversity (Tilman and Pacala 1993). These studies would help clarify the patterns and mechanisms that different ecosystems have in common as well as those that are unique. For example, comparisons of the tropical rain forest and boreal forest would help clarify the roles of different types and scales of disturbance (Denslow 1980, 1995).

In response to societal demands, national and global forestry organizations have recognized the necessity to manage for biodiversity. Research on diversity patterns in natural stands and response to treatments would provide the scientific basis for these management decisions. This work is requisite for sustainable and responsible management of natural resources.

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