



Biodiversity and Sustainable Forestry:
State of the Science Review

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I. Introduction

Biodiversity has become an overarching concept that embraces a host of environmental concerns (Duinker 1996). In the current debate over forest management, it is one of the most complex of terms and needs to be better defined (Kimmins 1999). The utilitarian reason for conserving biodiversity is the role that the mix of micro-organisms, plants and animals play in providing ecological services of value to humanity (Perrings et al. 1994). According to Perrings et al. (1992), there is a threshold of diversity below which most ecosystems cannot function under any given environmental conditions because “all self-organizing living systems require a minimum diversity of species to capture solar energy and to develop the cyclic relation of fundamental compounds between producers, consumers and decomposers on which biological productivity depends”.

This paper focuses on summarizing the research relevant to the current status of science and research efforts related to sustainable forestry practices and biodiversity. The focus is on science relevant to forest management on medium to large tracts of land (100 to 1000 acres or larger) in the United States. The objective is to attempt to include viable populations of a maximum number of species in the sustainable management of forests in managed industrial and non-industrial public and private lands in the United States. Specifically, the paper focuses on the importance of biological diversity in the sustainable management of forests, including elements of diversity of ecosystems, the diversity between species, and genetic diversity in species discussed in Criteria One of the Montreal Process (Table 1).

The overall concept of sustainable forest management has evolved to encompass wider issues and values, including biodiversity conservation, and multi-purpose management of the forest in such a way that its capacity to provide goods and services is not diminished (Christensen 1989; Murphy 1990; Kessler et al. 1992). Although several definitions with broad sustainable forestry mandates have emerged, there still remains the problem of practically implementing the sustainable forest management mandates and applying them on the ground given the multitude of competing resource uses. The disparities between management approaches focussing on maximizing short-term yield for economic reasons over long-term sustainability goals have been exacerbated by inadequate information on biological diversity of environments, lack of knowledge on the function and dynamics of ecosystems, the openness and interconnectedness of ecosystems on scales that transcend management boundaries and “a prevailing public perception that the immediate economic and social value of supposedly renewable resources outweighs the risk of future ecosystem damage or the benefits of alternative management approaches” (Christensen et al. 1996).

The need to formulate internationally acceptable and scientifically testable criteria to characterize sustainable forestry was recognized explicitly by Agenda 21 at the UN Conference on Environment and Development in 1992. Numerous national and international, governmental and non-governmental initiatives have been developed in recent years to meet this need (Newton 1995). Most current initiatives have sought to define sustainability by developing principles, criteria, and indicators for sustainable forest management. However, these terms have been defined in varied and often incompatible ways, which has created a diversity of views of interrelations among these terms. The following definitions have been put forth in Newton (1995):

Principle: A fundamental law or rule as a guide to action; a rule of conduct (e.g., The fundamental role of forests in maintaining global ecological processes must be maintained.).

Criterion: A distinguishing characteristic of a thing by which it can be judged. Criteria provide the basic framework for policy formulation (e.g., protection of biodiversity and maintaining productive capacity of forest ecosystems).

Indicator: Any variable that can be measured in relation to a specific criterion (e.g., percentage area of unique forest types legally protected).

Although several definitions exist, one definition, commonly used in international discussions, has broadly described sustainable forest management as:

“Forest management deals with the overall administrative, economic, legal, social, technical and scientific aspects related to natural and planted forests. It implies various degrees of deliberate human intervention ranging from action aimed at safeguarding and maintaining the forest ecosystem and its functions, to favoring given social or economically valuable species or groups of species for the improved production of goods and environmental services. Sustainable forest management will ensure that the values derived from the forest meet present-day needs while at the same time ensuring their continual availability and contribution to long term development needs.” (FAO 1993)

The FAO further stipulates that forests managed in this way will not only continue to provide timber on a sustainable basis but will also provide fuelwood, food and other services including preservation of biodiversity and genetic resources as well as protecting the environment (FAO 1993). The 1993 Helsinki Declaration of the Ministerial Conference on the Protection of Forests in Europe adopted the following definition of sustainable forest management to stimulate the implementation of the UNCED Forest Principles and Agenda 21 in Europe (Newton 1995):

... “sustainable management” means the stewardship and use of forests and forest lands in a way, and at a rate, that maintains their biodiversity, productivity, regeneration capacity, vitality, and their potential to fulfill, now and in the future, relevant ecological, economic and social functions, at local, national and global levels, and that does not cause damage to other ecosystems.

In the US, one mandate that the American Forest and Paper Association has put forward includes five broad principles that define sustainable forestry (AF&PA 1994):

- I. Sustainable Forestry: To practice sustainable forestry to meet the needs of the present without compromising the ability of future generations to meet their own needs by practicing a land stewardship ethic which integrates the reforestation, managing, growing, nurturing, and harvesting of trees for useful products with the conservation of soil, air and water quality, wildlife and fish habitat, and aesthetics.
- II. Responsible Practices: To use in its own forests, and promote among other forest landowners, sustainable forestry practices that are economically and environmentally responsible.
- III. Forest Health and Productivity: To protect forests from wildfire, pests, diseases, and other damaging agents in order to maintain and improve long-term forest health and productivity.
- IV. Protecting Special Sites: To manage its forests and lands of special significance (e.g. biologically, geologically, or historically significant) in a manner that takes into account their unique qualities.
- V. Continuous Improvement: To continuously improve the practice of forest management and also to monitor, measure and report the performance of our members in achieving our commitment to sustainable forestry.

Because managed forests make an important contribution to the nation by providing economic, consumer, environmental and aesthetic benefits, accomplishing sustainable forestry on private and public lands requires partnerships among landowners and the wood products industry. The American Forest and Paper Association has also put forward specific implementation guidelines for ensuring that these sustainable forest practices are carried out by its members. These are presented in Table 2. Each guideline has associated with it a set of performance measures that would especially encourage biodiversity conservation through sustainable practices.

Although biodiversity is a management goal valued in its own right, the broader sustainability goal in forest management covers many of the aims of protecting biodiversity (Smythe et al. 1996). Both the broader sustainable forestry mandate and the specific definitions discussed above incorporate within them ecosystem sustainability and the associated “bridging concepts” (Drever 2000) of ecosystem integrity and biological diversity. Drever (2000) and others point out that these concepts are human value based in that they connect social values and perceptions about desired states of an ecosystem with scientific concepts about the state or property of an ecosystem (Vogt et al. 1999). However, the bottom line is that if ecological sustainability is compromised, all other aspects of sustainable forest management (administrative, economic, legal, social, political, technical, and scientific) aspects related to natural and planted forests would be impacted. It becomes important to incorporate science based management in managing for biodiversity conservation. In order to conduct a focussed and in depth analysis of the key pillars of sustainable forest management, this paper focuses primarily on ecosystem sustainability and specifically on biological diversity and ecosystem integrity and the role they play in sustainable management of forests.

The Importance of focussing on Temperate and Boreal Forests

Globally, temperate and boreal forests together make up almost 50 percent of the total area of forest in the world and provide over 80 percent of the world's industrial wood supplies (FAO 1993). The total area of temperate and sub-temperate forests, including plantations is about 760 million hectares (Lanly and Allan, 1991; FAO 1993). Overall, the proportion of land area occupied by forests (mainly temperate forests) in industrialized nations of the Northern Hemisphere is surprisingly high (Table 3) (FAO 1993). The United States has about 300 million hectares of forest, covering about a third of its land area, with the forested area about 50 percent greater than that under agriculture. It is estimated that most of the temperate forests are under some form of management although there is no reliable figure for the actual area (FAO 1993).

In contrast, boreal forests encircle the northern parts of the globe covering a vast 920 million hectares of closed forest and 300 million hectares of open woodland in the USSR, Alaska (USA), and northern Canada, Finland, Norway and Sweden (see Table 4). Production from the boreal forests accounts for 50 percent of the global newsprint, 20 percent of paper pulp and 40 percent of sawn wood (FAO 1993).

However, because of harsh climates, difficult and dangerous terrain and remote location, a large proportion of these forests is likely to remain outside the scope of commercial logging at least in the near future compared to temperate forests. On the other hand, large-scale insect (for e.g. spruce bark beetles) and pathogen outbreaks in unmanaged stands as well as in some managed stands, have resulted in massive losses of future timber use and the use of other goods and services in the boreal forests (Patel-Weynand and Gordon 1999). While boreal forests in Nordic countries have been actively managed for sustained timber yield since the 1900s, the political and economic uncertainties in the former USSR, which are reflected in the management of the region's vast boreal forest, remain a major cause for concern.

While the tropics are great reservoirs of biological diversity, the temperate regions in the Northern Hemisphere, are generally not regarded as being as species diverse. However, they are major carbon sinks occupying one third of the land mass (747 million acres) with private ownership of almost two-thirds of that area (424 million acres) in the U.S. (Wayburn et al. 2000; FAO 1993). From a sustainable development perspective, temperate zones are essential to the human future and the preservation of their diversity is important. In addition to the obvious advantages to incorporating biodiversity conservation into management plans in the US, northern systems are well studied and their management receives greater resources than in tropical areas. Thus, biodiversity work conducted here in the US becomes a valuable source of knowledge and methodologies which can be adapted and applied elsewhere (Holdgate 1989).

Definitions of Biodiversity and other Key Terms

There have been numerous publications on biodiversity since the book edited by E. O. Wilson emerged in 1988 (Wilson 1988). Numerous definitions of biodiversity exist. One widely quoted is that of the United Nations included in the Convention on Biological Diversity (UNEP 1992). Biodiversity is defined by the UN as the variability among

living organisms from all sources including terrestrial, marine, and other aquatic systems and the ecological complexes of which they are a part; this includes diversity within species, between species and of ecosystems. The Global Biodiversity Strategy (WRI, IUCN, and UNEP 1992) espouses a shorter definition where biodiversity is the totality of genes, species and ecosystems in a region. Although both definitions refer to the three main components of biodiversity -- genes, species and ecosystems -- little attention is paid to issues of temporal or spatial scale or to hierarchies and to the interactions within, between and among various levels of biodiversity. For example, in a boreal coniferous forest in a temperate region, temporal scales vary widely: needles dropped are replaced annually; the crown or overstory cycles fall within a decadal period; and trees, gaps, and stands are replaced at even longer periods (Holling 1996). The result is an ecosystem hierarchy in which each level has its own distinct spatial and temporal attributes which contribute to ecosystem structure and function and biodiversity conservation. Di Castri and Younes (1990; 1996) suggest that from a practical viewpoint, structural and functional attributes of system stability, productivity and sustainability as well as patterns of ecosystem functioning can only be clarified if hierarchies and scales are considered in terms of their interactions.

Existing Information on Biodiversity Monitoring and Inventories

Often little distinction is made between conserving biodiversity and conserving genetic resources. The difference between the two lies in the fact that the conservation action is focused at different levels. One specifically deals with the changes in the species itself and the other deals with broader system level changes, for example, at the ecosystem or landscape level. It may be possible to conserve an ecosystem or a particular species within it but genetic diversity within a species may be lost. Conversely, it may be possible to preserve genetic diversity within species but there may be a decline in the number of species an ecosystem can support.

II. Biodiversity Monitoring, Measurement, and Consideration of Scales in Biodiversity Management

Types of Biodiversity Measurement for Consideration in Forest Management

Scientists and practitioners have long recognized that biodiversity exists at many levels of biological organization, from genes to landscapes (Angermeier and Karr 1994; Poiani et al. 2000). The diversity of all aspects of life and biological communities, or biodiversity, can be measured in many different ways as shown in Table 5. These measures can be assessed over areas of differing scales (Kimmins 1999; Sharukhan et al. 1996; Whittaker 1972):

<u>Alpha</u> diversity:	Stands (1 to 100 ha);
<u>Beta</u> diversity:	Local landscapes (100 to 10,000 ha);
<u>Gamma</u> diversity:	Regional landscapes (> 10,000 ha).

The variation in the first five measures listed in Table 5 in local stands is alpha diversity. Diversity between local stands having varied soil characteristics and disturbance histories within a single climatic area as evidenced by the same five measures is beta diversity. Variation in both alpha and beta measures I through V over more than one ecological zone is gamma diversity.

At the alpha spatial scale, temporal diversity tends to be high because of disturbance and successional recovery (Kimmins 1999). Temporal disturbance may be moderate at beta scales, and moderate to insignificant at the gamma scale. The severity, frequency, and spatial extent and pattern of disturbance will determine the actual level of temporal disturbance. At the beta scale, temporal disturbance is greatest when there is the widest range of age classes in forest stands.

The three basic scales of diversity mentioned above -- alpha, beta, and gamma -- have been characterized by Noss (1983) in terms somewhat more useful to land managers. Alpha diversity is the number of species within a single habitat, usually assumed to be a small area (a few hectares or less) of uniform vegetation structure. Beta diversity reflects the change in species composition along an environmental gradient or series of habitats. Finally, the total species diversity of a large geographic region (e.g., a landscape or larger) has been called gamma diversity. These three basic types of diversity are affected differently by human land use practices in a given area. Managing for diversity at each scale calls for different goals and methods and each scale offers various advantages and disadvantages (see Table 6).

Land managers have traditionally assumed until recently that achieving maximum local habitat diversity will favor diversity of wildlife. Hence, maximum beta diversity is generally the goal and gamma diversity (except in the case of very large units) is ignored. Alpha diversity is also generally ignored, perhaps because species number within a given vegetation stand is less tractable than the variety of stands in an area. However, as a nature preserve or habitat fragment grows increasingly isolated from other, similar habitat, fewer species may be found than in sample areas of equal size within extensive habitat blocks. In many cases of habitat insularization, species richness does not seem to change, but species composition often shifts towards taxa with low area requirements or high edge affinities (Noss 1983).

However, recent trends in species composition in fragmented landscapes suggest that a more comprehensive view is required for perpetuation of regional diversity. A regional network of preserves, with sensitive habitats insulated from human disturbance, might best perpetuate ecosystem integrity in the long term (Noss 1983). Such an approach would be based on landscape ecology, which studies the interactions and fluxes of energy, mineral nutrients, and species among clustered stands or ecosystems (Forman 1981; Forman and Godron 1981). Landscape ecology deals with an ecological mosaic of patches with continuously varying degrees of connectedness and recognizes the importance of matrix and corridors to terrestrial habitat island dynamics.

Species composition and abundance, not simple number of species, assume primary importance in the context of regional preservation. Native species are preferred over those exotic to the landscape and rare or reduced species over the widespread and superabundant. There are divergent views on using pre-settlement conditions as baselines for evaluating contemporary biodiversity and composition. Although the approach allows for natural dynamism, in most cases pre-settlement diversity can be inferred only generally, through general land office records. This approach may not be appropriate for some purposes such as making land use decisions or for protected area establishment. Others such as the World Wildlife Fund use features such as the diversity baseline, which references the potential of the land to support diversity as a more appropriate baseline for evaluation.

III. Role of Biodiversity Conservation in Ecosystem Processes, Structure, and Functions

There is very little information available to date on the role biodiversity plays in ecosystem functioning, functional redundancy, or thresholds for diversity beyond which irreversible changes in a system's structure or even its collapse would occur (di Castri 1996). The function of biodiversity in terms of its role in underpinning the resilience of ecosystems is yet to be conclusively determined by research in this area.

Biodiversity and Broad-scale Ecosystem Functions

We clearly need a better understanding of the relationships between biodiversity and ecosystem functioning (Sala 2001). Understanding the functional significance of biodiversity necessitates considering four key concepts: 1) the levels of biological and ecological organization and their interactions; 2) the numbers of different biological units within each level; 3) the influence and degree of similarity in the roles that biological and ecological units within each level play; and 4) the spatial configuration of the units within any level (Mooney et al. 1995). Because processes at any particular level affect not only the target level, but also levels above and below, ecological systems can be viewed at increasing levels of organization – genetic, population, species, community, ecosystem, and landscape. The term “ecosystem functioning” can be defined as the sum total of processes operating at the ecosystem level, such as the cycling of matter and nutrients, and the flow of energy, as well as those processes operating at lower ecological levels (e.g., interactions among species) which impact patterns or processes at the ecosystem level (NCASI 2000; Mooney et al. 1995; Barnes et al. 1982).

Ecosystems consist of the structure and function of all of the species and interactions among species in a given area and their physical environment. An ecosystem provides human society with a variety of services: clean water, pure air, soil formation and protection, pest control, foods, fuel, fibers, drugs, etc. Within the populations of a species in a given area, the loss of genetic variability may reduce the flexibility of those species to adjust to environmental changes and narrow the options available for the

rehabilitation of specific habitats (Perry 1998; McKeand and Svensson 1997; Mooney et al. 1995). Loss of biological diversity is a major concern primarily because there is mounting evidence showing that indigenous species are important and contribute to ecosystem functioning by influencing rates, seasonality and direction of overall ecosystem processes (Bormann and Likens 1979; Schowalter and Filip 1993; Franklin et al. 1989; NRC 2000). In addition, there are several ecological concepts that come into play in discussions of biological concerns, namely limits to transformability, limits to primary productivity, enhancing biological efficiency, and variation and change in biodiversity as it relates to ecosystem functions.

Impact of Species Additions and Deletions on Ecosystem Functioning

The capacity of an ecosystem to provide ecosystem services can be greatly affected by the addition or deletion of a species especially when there is low functional redundancy between individual species. Since the most abundant species in a community in terms of biomass usually accounts for the greatest proportion of productivity and nutrient cycling, the deletion of community dominants will have a significant impact on some ecosystem processes. The human capacity to predict which species will cause the greatest system impacts, and hence the greatest change in ecosystem services, when added or deleted, is steadily increasing. An important concept that has emerged in conservation biology and ecology over the last several decades is the sources, sinks and metapopulation concept. Sources consist of suitable or optimal habitats and produce excess populations of individuals who migrate to sink areas which consist of unsuitable habitats where population size cannot be maintained without immigration from source areas (Poiani et al. 2000). Pulliam (1988) has reported that as little as 10% of a population may be located in source habitats and still be responsible for maintaining upto 90 % of the population of sink habitats.

The profound effects of adding or deleting species with unique traits such as fixing nitrogen, capturing water, emitting trace gases, etc., are being increasingly understood. However, certain species without readily recognized specialized traits may also have significant effects on the capacity of ecosystems to provide services when added or deleted (Perry 1994, Naiman 1988). The effects of adding or deleting such “keystone” species needs further assessment (Simberloff 1998; Vogt et al. 1996; Noss and Cooperrider 1994).

The essence of the keystone concept is that, like the keystone from an arch, the removal of only one or a few species can have uniquely important effects on the community or ecosystem by virtue of unique traits or attributes. A series of investigations across a wide range of ecosystems has revealed that keystone species have been shown to exist in a broad variety of ecosystems, that they may be more prevalent than originally thought, and that the concept can be applied to individual species or groups of species (Vogt et al. 1996; Mooney et al. 1995; Perry 1994; Thompson et al. 1991; Brown and Heske 1990; Remmert 1980). At the current low level of understanding of the effects of biodiversity on ecosystem processes, it is easiest to recognize these linkages at the level of functional groups, i.e., groups of species that have ecologically similar effects on ecosystem processes. The deliberate or accidental modification of ecosystems by the introduction of

alien species can have either positive or negative effects. However, the effects are often negative because of the reduced biotic controls on the invading species (Mooney et al. 1995). The impact of invasive species can be considerable and include impacts on all ecosystem processes. There is a strong link between invasive alien species, the rate of invasion and the resilience of the system to the disturbance. These invasives can change the whole character of ecosystems, moving them to a new structural state with a very different biodiversity make-up. For example, the future impact of the invasive blue-joint grass on regeneration of Sitka spruce following spruce bark-beetle invasions may considerably change the character of these forest areas (Patel-Weynand and Gordon 1999).

Covington et al. (1994) have reported significant impacts to ecosystems from exotic weedy plant species that alter biodiversity, site productivity, and economic resource values. Colonization by these species usually follow disturbances such as overgrazing, timber harvest, road construction, cropland abandonment, or high intensity fires. Native vegetation is often out-competed by exotics because of the variety of their reproductive systems, high fecundity, efficient dispersal mechanisms, and variation in germination requirements (Covington et al. 1994).

Long-term soil productivity loss can result from the development of extensive exotic plant communities. When shallow fibrous or tap-rooted exotic plants displace deep-spread-rooting native bunchgrass communities, accelerated soil erosion can occur. Forest ecosystem diversity, function, and productivity have been dramatically altered by exotic insects and pathogens. In North America, more than 360 exotic insects and 20 exotic fungal pathogens now attack woody trees and shrubs (Covington et al. 1994).

There are five critical components of diversity needed to predict the functional consequences of species additions or deletions. These are: 1) the number of species in a community; 2) the relative abundance of these species; 3) how strongly an invading or deleted species differs from other species in the community; 4) the traits of the species; and 5) the indirect effects that a species has on other species in the community (Mooney et al. 1995). The greatest impact on ecosystem processes from the gain or loss of a species typically occurs when there are few species in the community, when the species gained or lost is a dominant species, and/or when the species differs strongly from other species in the community (Mooney et al. 1995). The functional importance of species diversity is the provision of insurance against large changes in ecosystem processes. There is very little direct information available as few controlled experiments exist on the extinction of species. However, several trends are apparent. Not all deletions have equal ecosystem impacts. For example, the extinction of keystone species, which have major ecosystem roles at various scales, would have a cascading effect on ecosystem properties and functions. Species with little functional redundancy are most susceptible to dramatic effects of species losses. In the debate on sustainability and how it should be measured, one of the criteria of environmental damage is its reversibility. The most serious and unacceptable damage is least reversible and few things are as irreversible as biological extinction (Tinker 1996).

Biodiversity and Ecosystem Responses to Disturbances and Environmental Changes

The capacity of ecosystems to resist changing environmental conditions, and to rebound from unusual climatic or biotic events, is related positively to species diversity as demonstrated by numerous studies in fields and grasslands (Tilman and Downing 1996; Frank and McNaughton 1991; Leps et al. 1982). Fragmentation and disturbance of ecosystems and of landscapes shift the balance of the kinds of species present – from large, long-lived species to small, short-lived ones. These shifts will have major effects on ecosystem services and reduce the ability of an ecosystem to store nutrients, sequester carbon, and provide pest protection (Vogt et al. 1996; Mooney et al. 1995).

The human disruption of historical disturbance regimes in forests is best exemplified by the suppression of forest fires in the inland West. According to Covington et al. (1994), the basic principles of post-settlement changes in fire regimes is: 1) attempted fire exclusion in forest and woodland types which had infrequent crown fires results in increasingly large crown fires; and 2) attempted fire exclusion in forest and woodland types which had frequent surface fires results in a shift to infrequent crown fires and then to increasingly large crown fires. Fire exclusion and selective harvesting alter the unique association of native insects and pathogens by accelerating forest succession. In the absence of natural disturbance regimes to control succession, accelerated forest succession in all of the major forest ecosystems in the West has created unstable community structures characterized by high stem density and above ground biomass and nutrient reservoirs; increasing dominance of shade-tolerant, pest-intolerant, climax species; and unprecedented build-up of continuous fuels and high-risk host coverage across western landscapes. Because ecosystems under stress commonly exhibit increased tree insect and pathogen activity, the recent extensive tree mortality throughout the US may be symptomatic of declining forest health rather than that caused by insect and pathogen damage (Covington et al. 1994).

The dramatic changes in climate and atmospheric chemistry currently being forecast, coupled with the disruption of natural disturbance regimes by human intervention, present both ecosystems and dependent human social systems with formidable challenges, and possibly exciting opportunities. Ecological systems will most probably be unable to absorb these environmental changes without major disruptions of existing ecosystem structures (species composition and demography, biomass and nutrient storage, and soils) and processes (carbon assimilation, nutrient cycling, trophic dynamics, and successional and landscape dynamics). On an optimistic note, periods of change, within limits, can be beneficial for both biotic and social systems. Evidence is accumulating that indicates that maximum rates of productivity and biodiversity appear to occur during periods of transition over a broad variety of scales in ecological systems (Covington et al. 1994).

Role of Biodiversity in Underpinning the Resilience and Resistance of Ecosystems

It has been argued from a purely theoretical perspective that the loss of one species from a highly interconnected system with randomly assembled food webs necessarily implies

the loss of other species (May 1973; Perrings et al. 1996). This does not necessarily provide evidence for lack of resilience in highly connected systems. We need knowledge not only on when disturbances stress an ecosystem and lead to biodiversity reduction but also on when loss of biodiversity signals the collapse of a system and when the collapse is part of the destruction cycle that in turn leads to regeneration and renewal.

There have been several attempts at defining resilience and resistance of ecosystems to disturbance regimes (see Tables 7 and 8) (Patel-Weynand 2000). Here we define resilience as both the ability of the ecosystem to recover its structural and functional attributes and the rate at which the ecosystem regains these attributes following disturbance to a level where it is able to function at its pre-disturbance state. Resistance, is the ability of an ecosystem to oppose change in functional and structural attributes when faced with a disturbance. By defining the terms thusly, the adaptive nature of species in varied ecosystems is addressed and not just how fast they are able to recover. This becomes important in the development of tools to measure losses in diversity following disturbances because resilience is the period of time that elapses between disturbance at point (a) and recovery at some later point (b).

Some ecosystems may have a higher degree of resistance to disturbance than resilience to disturbance (Patel-Weynand 2000). For example, in California redwood forest ecosystems, thick bark and other adaptations render these forests quite resistant to fire; but if they burn catastrophically, the recovery rate (or resiliency) is very low and they may not recover to pre-disturbance levels. In contrast, California Chaparral vegetation is not very resistant to fire and burns easily, but it recovers very rapidly and is therefore highly resilient (Patel-Weynand 2000 and references therein; Vogt et al. 1997). In general, Odum (1985) considers ecosystems in benign physical environments as characterized by higher resistance and less resilience, and ecosystems in less favorable environments as less resistant and more resilient.

Usually, ecosystems have a built-in capacity to recover from these disturbances (Bormann 1985; Bormann and Likens 1979). Depending on how resilient the system is, when the disturbance is over, in the course of decades sometimes, the system will rebuild itself to pre-disturbance levels of structure and function. Under certain conditions, protecting an area may also result in a reduction of biodiversity and the elimination of plant and animal species with low resilience and lower adaptability to changing conditions. Under the current climate change scenarios, protected areas, by creating an island effect, may affect species that may not be able to adjust their ranges in shorter time frames to compensate for temperature and other environmental changes. Protection of endangered species or maintaining a desired balance may require substantial intervention and interference in the natural working of the ecosystem.

When systems have reached a state where they have used up the flexibility of compensatory functions they move below the normal operating range. In a sense the system is stretched to a point where structural and functional elasticity is very low or negligible. This may cause the system to move to a new threshold and may change the parameters of the normal operating range to a new range which is lower on the structural

and functional scale and further away from the maximum biodiversity achievable (Patel-Weynand 2000). The greater the distance from its pre-disturbance levels, and depending on how far the ecosystem has moved away from its original trajectory, the ecosystem at this point may be so damaged by the loss of species, ecosystem structure, nutrients, and soil that the capacity for self repair is severely diminished. In this case even if the perturbing force is removed, the system may never return to pre-disturbance levels of structure and function or may need centuries or millennia to do so. At this point the basic structure of a forest ecosystem changes (Woodwell 1970) and biotic regulation is affected. Habitat degradation also occurs as an area is depleted of the elements of forest structure that a species may depend on for survival. Both Gordon and Gorham (1963) and Woodwell (1970) describe structure and function loss as peeling off layers of forest structure, starting first with the trees, followed by tall shrubs, and finally under the severest conditions, the short shrubs and herbs are also affected. The capacity of the degraded ecosystem to regulate energy and biogeochemical cycles at this point is severely diminished.

The connection between ecosystem stability and ecosystem resilience and resistance raises questions regarding ecosystem diversity. The relationship between ecosystem stability [as represented by resistance] and diversity are being debated. The controversy arose in the 1960's with the discovery that the least diverse communities were the most resilient because the relatively few organisms in the ecosystem are tolerant to a wide range of environmental conditions (Denslow 1985). However, Kimmins (1987) found that the relationship between resilience and diversity is more complex and that the ability of an ecosystem to recover from a disturbance is "probably more closely related to its ability to process energy than to its diversity".

One view, the diversity-stability hypothesis, holds that species differ in their traits and that more diverse ecosystems are more likely to contain some species that can thrive during a given disturbance and thus compensate for competitors that are reduced by disturbance (McNaughton 1977; Pimm 1984; Schulze and Mooney 1993; Tilman and Downing 1994). This view predicts that biodiversity should promote resistance to disturbance. However, in more diverse communities, the niches are narrower due to greater specialization and if destroyed by large-scale disturbance, these communities may not be as resilient, although they are more stable because of the redundancy of function (Patel-Weynand 2000). In contrast, the species-redundancy hypothesis asserts that many species are so similar that ecosystem functioning is independent of diversity if major functional groups are present (Lawton and Brown 1993; Vitousek and Hopper 1993). The maintenance of long-term productivity correlates strongly to ecosystem resilience and resistance (O'Laughlin 1993). An important way to reduce loss of resilience is to manage for a diversity of successional stages and species across the landscape to reduce homogeneity of vegetation over large areas, which if unchecked could cause considerable damage in the event of a catastrophic disturbance. This will help to retain the functional relationships that lead to resilience and resistance and higher productivity. Conserving biological diversity is a key element in sustaining productivity over the long-term (Norris et al. 1993; Gordon et al. 1992).

Environmental Change and Genetic Variation within Species

Although biodiversity conservation efforts to date are focussed on preservation of different species types, conservation of genetic variation within a target species is also important to improve resiliency and resistance to disturbances and overall environmental changes (Christensen et al. 1996). Conservation of forest genetic resources aims at ensuring that the widest possible range of genetic variation for a given target species is identified and conserved (FAO 1993). Research needs on the diversity of chosen species and their eco-geographical structure, sampling strategies (number of individuals on an area basis to avoid genetic drift), and conditions and mechanisms for maintaining genetic variability in natural and semi-natural environments must be addressed for biodiversity management. In situ conservation deals with keeping reproductive organisms in their natural habitat where genetic variability between and within populations is still high (Lefort and Chauvet 1996). Information on which species, where the conservation areas should be located, and how these areas should be managed, is needed.

In situ conservation of genetic resources for maintaining within species variation requires a network of planned and systematically managed conservation and managed resource areas (FAO 1993). The FAO forestry report emphasizes that the primary challenge is to maintain the genetic variability of the target species within a mosaic of economically and socially acceptable land use options rather than to select, set aside and guard protected areas containing the genetic resources (FAO 1993). These options are not mutually exclusive, and in fact forest managers are finding that the most successful biodiversity conservation strategies encompass a full spectrum of ecological assemblages within the landscape (Probst and Crow 1991).

Because forest trees carry high levels of lethal recessive alleles and are particularly susceptible to inbreeding depression, forest geneticists have been greatly concerned about the erosion of genetic diversity through random drift. To maintain diversity within breeding populations, the hierarchical open-ended system (HOPE) and the multiple population breeding system (MPBS) are two systems that have been applied. The HOPE strategy periodically introduces genetic material from populations early in the selection cycle to populations at later stages of selection, while the MPBS approach sets up a number of different breeding populations and exchanges genes in controlled crosses among these. While allozyme studies in loblolly pine show that both strategies maintain relatively high levels of allozyme diversity within the elite breeding populations, neither maintains the diversity found in natural stands (Perry 1998). Any reduction of genetic diversity in forests through the loss of rare alleles highlights the currently unanswerable question of how much diversity is sufficient to maintain resistance to pests and the capacity to adapt to changing environments. Forest geneticists split into two camps – one group arguing that rare alleles contribute little to overall fitness, while the other group argues that such losses could compromise long-term adaptive flexibility. The usefulness of allozyme measurements as predictors of ecological response is limited by the inability to relate allozyme measurements to phenotypic traits with potential adaptive value (Perry 1998). Despite these limitations, it is generally recognized that the reservoir of genetic diversity within individual species and populations is central to their ability to adapt to environmental change (Christensen et al. 1996).

Biodiversity and Functional Redundancy

Inherent in the resistance characteristics of the ecosystem are what some researchers have called “redundancy” of function or a reserve capacity to carry out critical functions of biotic as well as abiotic regulation (e.g., soil structure which resists erosion) through several pathways (Bormann and Likens 1979). This gives the system the ability to use its reserve compensatory options should there be damage to the core system so that there is little long-term change in the ecosystem’s ability to fix carbon and to carry out the basic functions needed to maintain productivity in the normal operating range (for example, more than one species of organism capable of carrying out the same function). However, when disturbances are chronic, with increased severity over time or are cumulative (e.g., air pollution), the redundancy mechanisms may be used up over the long-term (Patel-Weyand 2000).

Thus, redundancy of function may shore up biotic regulation in the short-term, but the changes in species levels may in some cases be permanent and the system may end up operating below the normal operating range as small reductions in the bio-energetic budget of the systems may be linked to subtle declines in the capacity of the ecosystem to regulate energy flow and biogeochemical cycles.

One of the key unanswered questions currently facing ecologists is the degree to which some overall level of biodiversity is required for the delivery of ecosystem services. This question is often re-phrased as: “What is the minimum fraction, of the estimated 13.5 million species now extant, required to keep ecosystems functioning so that they can continue to supply services to mankind?” In other words, how much of the world’s species diversity is redundant? (Mooney et al. 1995).

Biodiversity and Productivity of Forests

Some general observations about ecosystems are particularly relevant to forest ecosystems. Simplifying ecosystems to obtain higher yields of individual products comes at the cost of losses in ecosystem stability and in free services such as controlled nutrient delivery and pest control, which thus need to be subsidized by the use of fertilizers and pesticides (Mooney et al. 1995). Mankind has been more successful in simplifying ecosystems than in restoring complex ecosystems. The lack of success in ecosystem reconstruction suggests that great caution must be exercised in reducing biodiversity through management practices because of the potential loss of goods and services in the long term (Mooney et al. 1995).

A key gap in the biodiversity and sustainable forestry debate deals with how little is known about below ground biodiversity and processes that affect long term productivity. Current knowledge gaps are immense in the case of fungi, bacteria, and viruses (<5% are named), their range, ecological requirements, and their role in ecosystem functioning (Hawksworth 1996). Communities at risk from reduction in microbial diversity are those in extreme environments.

In regulating the productivity of forests, a critical role of an organism is in the decomposition cycle where there is increasing evidence that ecosystems with higher organismal diversity are more efficient at influencing and carrying out biological production (Tilman et al. 1996; Naeem et al. 1994, Ewel et al. 1991) and nutrient retention (Tilman et al. 1996; NRC 2000). Ewel et al. (1991) found that in a tropical system the more diverse plant communities had a higher productivity and were more nutrient conserving. Ecosystem processes are highly sensitive to changes in species that influence the turnover rates of water, nutrients, or space. In terrestrial soils, differences in tissue quality are critical controls over litter decomposition. Thus, the invasion or extinction of a species that changes substantially the litter quality in the community could have a significant impact on ecosystem processes (Mooney et al. 1995).

Increased primary productivity was also associated with higher levels of diversity found in studies of British grassland communities which examined photosynthesis rates with differing plant, herbivore and decomposer diversities. Higher levels of diversity not only resulted in significantly increased primary productivity, but also affected decomposition, nutrient retention, and vegetation structure (NRC 2000). Similar findings were reported by Tilman et al. (1996) in prairie grasslands in the United States where plant diversity was manipulated and found to affect direct total plant productivity, nutrient use and losses due to nutrient leaching. Other studies in fields and grasslands have also found that communities with high plant diversity are able to better maintain higher productivity levels (Loreau and Hector 2001; Reich et al. 2001; Hector 1999) and withstand climate change and stressors such as drought (Tilman and Downing 1996; Frank and McNaughton 1991; Leps et al. 1982). One possible explanation is that diversity increased ecosystem resistance and resilience by including some species that were drought tolerant and showed higher growth rates in response to the decreased abundances of their drought sensitive cohorts. Other non- experimental research on pest outbreaks (Kareiva 1983; Schowalter et al. 1986; Hunter and Aarssen 1988; NRC 2000) shows that highly diverse stands have a higher likelihood of containing disturbance resistant species in them and therefore, on average would be more stable and resistant to disturbance (NRC 2000).

Both Tilman and Downing (1994) and Schowalter and Turchin (1993) have also found that primary productivity was more stable when plant diversity was higher. However, the interpretation of these productivity and diversity experiments has been controversial (Huston 2000; Hector et al. 2000; Kaiser 2000; Huston 1997; Aarssen 1997) because two mechanisms, the “selection effect” and the “complementarity effect”, may be operating together to confound accurate estimations of the effect of biodiversity on productivity. Selection effect is caused by dominance of species with particular traits that affect ecosystem processes and the complementarity effect results in resource partitioning or positive interactions that lead to increased total resource use (Loreau and Hector 2001).

Preserving Ecosystems as a Strategy to Protect Biodiversity

The majority of past and current efforts to preserve biological diversity have focused upon species, subspecies, and populations. This is especially true of actions that have been taken under the Endangered Species Act. However, there may be far too many

species to deal with on a species-by-species basis, and this approach may never be practically applied to the conservation of “smaller” organisms such as invertebrates, fungi, and bacteria. Organisms such as insects and fungi are not necessarily more resistant to human impacts or more effective dispersers than vertebrates or vascular plants. In fact, some insects and fungi are known to be poor dispersers. Such species can be and are lost from disturbed sites and these losses have negative consequences for sustainability (Perry et al. 1989). These physically smaller but overwhelmingly more numerous elements of biodiversity carry out critical ecosystem functions such as decomposition and nitrogen fixation. Based on a very conservative estimate of 5,000,000 species, vertebrates make up <1% and vertebrates and vascular plants make up only ~5% of the total array of species. In contrast, invertebrates will probably compose 90% of the total. Yet the vast majority of these taxa are unknown, and in a practical sense, unknowable. They will be conserved only as ecosystems are conserved (Franklin 1993).

The contention is not to abandon species-based approaches, but to recognize their limitations as society grapples with the immense and pressing task of preserving as much biodiversity as possible. Placing a greater emphasis on larger-scale approaches – at the level of ecosystems and landscapes – is the only way to conserve the overwhelming mass – the millions of species – of existing biodiversity. The ecosystem approach is also the only way to conserve organisms and processes in poorly known or unknown habitats and ecological subsystems. There are many examples from ecological science of the richness of previously unappreciated habitats, such as forest canopies, belowground subsystems, and the hyporheic zones (Franklin 1993). The hyporheic zone is the saturated zone below and adjacent to stream and river channels within the alluvial and materials of the stream channel and floodplains (Naiman 1992), and this eco-subsystem has direct functional links to the associated river or stream. The hyporheic is the site of critical processes – carbon and nutrient transformations – and habitat for a large array of aquatic organisms, many of which are poorly known to science (Franklin 1993).

Belowground eco-subsystems are rich assemblages of spatially complex communities that are highly dependent on the copious, continuing energy supplies from photosynthetically active vascular plants (Harris et al. 1980; Perry et al. 1989). It has become increasingly clear that it is not just the soil that supports the vascular plants, but, at least equally, the plants that function as the life support system for the soil. Maintenance of the belowground elements of diversity requires an ecosystem approach that provides for a healthy and diverse aboveground energy source (Franklin 1993).

To achieve the objective of conserving the vast majority of biological diversity, it is critical to plan and assess at the level of landscapes and regions as well as ecosystems. This is a complex issue that includes the development of an appropriate system of habitat preserves with greatly expanded attention to conditions in the landscape matrix – the complex of semi-natural and domesticated lands within which most reserve systems will be embedded. If a reserve is embedded in a matrix that is highly dissimilar, a much larger reserved area is going to be required to achieve the same level of protection. For example, in the forest landscapes of the Pacific Northwest, a reserved patch of old growth will have to be much larger to provide an unmodified interior environment if it is located

within a clearcut landscape than if it is surrounded by partially cut forest (Franklin 1993) although very small patches of old growth can harbor significant diversity.

IV. Biodiversity and Fragmentation of Landscapes

Fragmentation can result from either anthropogenic or natural disturbances. Loss of biodiversity is often associated with habitat fragmentation. Depending on the policy issues of interest, discussions on the topic of fragmentation have focussed on either the fragmentation of forest vegetation or on the fragmentation or parcelization of land ownership. A major dichotomy in forest fragmentation definitions also exists between the treatment of fragmentation as a process versus as a pattern (Alig et al. 2000). In process terms, forest fragmentation can be defined as the process by which a large block of cover type is divided into smaller, more isolated islands within a mosaic of other land uses, typically agriculture or urbanization (Helms 1998). Alternatively, forest fragmentation has been defined as “the process of reducing size and connectivity of stands composing a forest” (Rochelle et al. 1999). When viewed as a pattern, forest fragmentation can be quantified spatially using various indices of landscape structure (Poiani et al. 2000). There are different metrics for different scales of analysis and measurements of interest. Such statistics can provide a means for comparing the relative degree of fragmentation to other landscapes or to the same one at different periods of time (Alig et al. 2000).

Causes of Fragmentation and National Trends

Forest fragmentation can result from disturbances initiated by humans or by natural elements. Human-caused fragmentation is often more frequent, less random, and more permanent than natural processes. Natural fragmentation processes include fire, wind, and flooding. Human actions that cause fragmentation are land cover conversions, changing ownership patterns, and other disturbances, such as timber harvesting. In the case of urban development, land is converted by persons placing greater emphasis on the property value of the land than on the productive value of the land (Alig et al. 2000).

Increasing urbanization has reduced the supply of economically productive rural lands traditionally used for crops, pasture and forestry, and has had a significant impact on the demographics of forest landowners. Urban and developed areas have expanded by 285 percent from 1945 to 1992, and approximately 15-20 million acres of US forest land may be converted to urban and developed uses over the next 50 years if historical trends continue and the US population grows by another 120 million people (Alig et al. 2000). Continued development of forest and agricultural land, involving forest fragmentation in many cases, is occurring across a national landscape that has a diverse ownership pattern and a mosaic of land uses. The quality, amount, and spatial configuration of habitats on the national landscape are being modified (Alig et al. 2000).

Some two-thirds of all of the forests in the United States are privately owned by almost 10 million owners, and almost 90 percent of the timber harvested in the US in 1997 came from private lands. The analysis of trends shown in 1978 and 1994 Forest Service private land ownership studies indicated that, during that period, there had been a dramatic increase in the number of ownerships in the 10-40 acre size range. These were, apparently coming from the parcelization of 100-1000 acre properties, as shown in

Table 9 (Sampson 2000).

Implications for Biodiversity and Ecosystem Function and Structure

Forest fragmentation reduces the total area of contiguous forest and isolates to varying degrees the remaining forest patches. The potential threat to biodiversity is perceived as a consequence of direct loss of habitat for wildlife, increased predation and nest parasitism, interference with dispersal and introduction of non-native species (Lancia et al. 2000). Two of the recognized phenomena associated with fragmentation of habitats are the “island” effect and “edge” effects.

A number of studies (DeGroot 2000; Smith 1990; Rey 1981; Simberloff and Wilson 1969; Preston 1962) have documented that isolated islands around the world often have less species diversity than similar sized areas on the nearby mainland, but the reasons for this were not understood until fairly recently. In Venezuela, land areas were turned into isolated islands by hydroelectric impoundment, which led to the demise of the top predators and to the release of small to mid-sized predators. This resulted in widespread reduction in the numbers of ground-nesting birds and other terrestrial vertebrates. The destruction of top carnivores also allowed populations of herbivores to erupt in certain areas. Over-browsing by the now abundant animals has resulted in the loss of certain species of plants and trees and prevented the regeneration of these species. According to DeGroot the same thing appears to be happening all over North America as wildlife and plants are being marooned on “islands” of protected land, fragmented and isolated by land filled with people. DeGroot (2000) notes that nature tends to stay in balance as long as the animal kingdom remains intact. It falls out of balance when too many consumers of vegetative material or too many small predators exist.

The borders or perimeters between different land uses or land covers are known as “edges”. The core or interior area is the area not influenced by neighboring land uses or covers (i.e., the area of the patch minus the area that is influenced by the edges). In general, the process of fragmentation increases the number of landscape pieces, the extent of forest-opening edges, and the isolation of residual forest patches, while decreasing interior habitat area (Alig et al. 2000). Edge length and height can be measured precisely, but the width or “depth-of-edge” influence, the transition zone between the different land uses or covers, is always arbitrary depending on the variable of interest, timing of measurement, and the approach used for calculation (Chen 1991). Differing ecological phenomena associated with the transition zone are called “edge effects”.

For years, wildlife biologists have promoted forest edges as beneficial to wildlife and other components of biological diversity (Thomas et al. 1979; Lovejoy et al. 1986). Forest managers were urged to create as much edge as possible because some wildlife species are a product of the places where two habitats meet. However, with increasing concern about biological conservation of species and about many associated processes and suitable habitat that require interior environment, resource managers must now assess the balance between edge and interior environment (Yahner 1988; Hunter 1990).

Edge effects (such as altered light conditions, animal activities, or species composition) can extend more than 100m into a forest stand (Chen et al. 1992), which means a 3 ha stand can be impacted by edge effects throughout. Other edge effects may extend several hundred meters into the forest from the edge. Types of edges and fragments differ in structure and function. For example, an old growth fragment surrounded by clear cuts would be very different in composition from one surrounded by mature forests. The vulnerability and biological values of small patches depend heavily on the character of the landscape in which they are embedded and no absolute statement regarding minimum size of old growth forests can be made (NRC 2000; Old Growth Definition Task Group 1986).

There are a number of factors to consider when looking at sizes of fragments. Small fragments are more vulnerable to drought and related fire and wind damage than larger stands and smaller fragments may not be conducive to providing habitats for some species. Various levels of natural patchiness may also occur in many forest ecosystem types and community types. Also, patch ecosystems occurring naturally at various geographic scales need to be factored in when considering natural and human induced fragmentation processes (Poiani et al. 2000; Anderson et al. 1998). Ralph et al. (1995) have reported that the presence of a particular species in a fragment does not necessarily reflect or indicate the quality of the habitat (for example, marbled murrelets nesting in very small old growth patches are more vulnerable to predators in such restricted habitats).

Biological investigations of edge effects have focused on changes in residual forest structure, function, and species composition associated with forest boundaries. Near the edge, the forest floor receives more light but also experiences stronger winds and greater variation in temperature and moisture. Edge effects on tree seedlings and saplings have been found to vary by species. Biological responses at forest edges are influenced not only by distance from the edge, but also by forest type, edge age, orientation, and formation (i.e., clearcut vs. natural bog), patch shape and size, and topographic features. Biotic factors, as well as abiotic factors such as microclimate, need to be explored to completely characterize ecosystem behavior at forest edges. Furthermore, knowledge of edge phenomena must be extended to the landscape level, incorporating landscape features such as residual forest-patch size and shape, and their spatial configuration, to meet the needs of current and future forest management (Chen et al. 1992).

Human-caused changes in land use and land cover are a primary force driving changes in ecosystem attributes. Affected ecosystem attributes include: ecosystem diversity, species diversity, and genetic diversity; productive capacity of forest ecosystems; forest ecosystem health and vitality; conservation and maintenance of soil and water resources; forests' contribution to global carbon cycles, and maintenance and enhancement of long-term multiple socioeconomic benefits (Alig et al. 2000).

Implications for Forest Management Regimes

Forests are a critical natural resource of the United States, and the distribution of forest types is an indicator of the health and sustainability of the nation's forests. Projections of

land use and land cover changes are critical inputs when evaluating indicators of conservation and sustainable management of forest, agricultural, and urban-based ecosystems (Alig et al. 2000).

The trends and impacts of forest fragmentation discussed above have at least four implications for the management of forest resources to conserve biodiversity. First, the parcelization of private lands into smaller and smaller units affects land management quality, as small parcels are less likely to be managed with professional resource assistance, and many management tools, such as prescribed fire, may become difficult or impossible to use. Maintaining forest lands in sustainable production may be increasingly unattractive to large forest products companies, who seem to be selling land and either seeking long-term supply contracts or looking abroad to meet their needs for industrial wood. Neither of these trends seem positive for the future of managing small to medium-sized sustainable forests, and support the need for public policies that improve program assistance to forest owners holding 10 to 500 acre parcels (Sampson 2000). Such assistance should encourage landowners to coordinate their forest management goals and implement management practices that cross property boundaries and respond to the larger temporal- and spatial-scale issues of ecosystem management (Hull et al. 2000).

Second, state and federal forest managers are increasingly seeking ways to re-connect together “islands” of habitats caused by fragmentation to allow seeds and genes to be disseminated more freely for all species. One of these ambitious projects will provide wildlife connecting corridors from the Yellowstone Park in Wyoming all the way through Canada to Alaska. In an example at the state level, Maryland’s Department of Natural Resources has created a program called the “Green Infrastructure” to link together isolated parks and forests under its management. Its purpose is to identify what areas have the greatest concentration of biological diversity, and decide how best to connect them with corridors to ensure permanently protected conduits for the movement of plants and animals (DeGroot 2000). As mentioned above, any linkages between habitats should establish strip corridors as opposed to line corridors wherever possible.

Third, forest products companies are recognizing that the consolidated ownership of large tracts of forestland presents an opportunity to evaluate and manage the effects of forest fragmentation. These industry-owned landscapes typically result in a diverse mixture of habitat types and spatial arrangements that could be managed more effectively for both protecting ecosystem functions and biodiversity and for producing timber supplies. For example, the Westvaco Corporation uses an Ecosystem-Based Multiple Use Forest Management System to provide fiber for its mills while maintaining, protecting, and enhancing ecosystem elements and functions on the approximately 500,000 acres it owns in the Coastal Plain of South Carolina. One aspect of this system is a network of corridors kept in pine or hardwood habitat that are two to four times the typical rotation length. These corridors are designed to protect and maintain water quality, wildlife habitat, visual quality, and biodiversity (Lancia et al. 2000).

Fourth, given that the width of the zone where “edge effects” from habitat fragmentation vary widely, the traditional notion of creating as much edge as possible should be re-

evaluated, especially for the management of biological species that require old-growth interior environments (Chen et al. 1992).

In the US, fragmentation of forests resulting from changing land use patterns is becoming an increasingly important topic with regards to biodiversity conservation specifically with concerns raised about such issues as habitat protection and timber supply. Although some wildlife species need edge areas caused by the fragmentation of forest cover, forest fragmentation can lead to consequences such as loss of biodiversity, increased populations of invasive and non-native species, changes in biotic and abiotic environments, “edge effects”, and decreased or more costly natural resource availability in the case of timber management. While recognizing substantial variation in fragmentation processes and patterns across the country, research on fragmentation issues is needed on a number of fronts and must go hand in hand with an augmentation of policy analyses to mitigate and/or modify fragmentation trends (Alig 2000).

V. State of the Current Knowledge on the Impact of Management Practices on Biodiversity

Direct impacts of forest management on levels of biological diversity are not clear. What is apparent is that habitat alteration is key in contributing to changes in biodiversity. Research findings in different forest types suggest that the effects of forest management on biodiversity are highly variable, depending on the species examined as well on the spatial and temporal context (Halpern and Spies 1995; Meier et al. 1995; Hix and Barnes 1984; Oliver and Larson 1996; Bormann and Likens 1979; NCASI 2000).

Biodiversity and Stand Character

Ecosystems are dynamic and continue to change temporally and spatially at varied rates even when left untouched and especially when new species evolve or are introduced while others decline (Botkin 1990). As levels of biodiversity can be extremely variable depending on the developmental stage of the forest stand, sustainable management of forests must factor in the differences in the structure and composition of the stand in order to incorporate biodiversity conservation into management plans. Several general models exist that describe the progression of development stages following disturbances, as shown in Table 10. In actively managing forests to take on the objective of protecting biodiversity, it is important to specify whether the intent is to maintain the current mix of species (e.g. by perpetuating the existing successional stage) or to maintain a high degree of species diversity that may or may not include the current species composition.

In examining the developmental stages and the levels of biodiversity associated with them, the few studies that have been completed found striking differences between old growth and younger forests in structure and function of ecosystems and guilds of species associated with them. A large-scale conversion of old growth forests into second growth plantations leads to a simplification of forest structures at multiple scales. As stands age

structural complexity increases and with it habitat complexity increases as well. With the increase in complexity of stands associated with the various developmental stages of forests, Oliver and Larson (1996) and Bormann and Likens (1979) have found that species diversity increases over time as forest composition becomes more complex.

In terms of productivity, Vitt, Marsh and Bovey (1988) have hypothesized that bryophytes and lichens would account for a significant portion of the biomass in old growth forests. They have suggested that as much as half of the biomass produced in some forests can be attributed to these species. In addition to species of liverworts and mosses found on the forest floor, abundant epiphytic bryophytes are defining characteristics of the large areas of older coniferous forests of the Cascade and Coast Ranges of the Pacific Northwest and the *Picea sitchensis*-*Tsuga heterophylla* forests of the Prince William Sound and coastal forests of South Central Alaska (Patel-Weynand 2000; Peck et al. 1995a; Pike et al 1977; Hoffman and Kazmierski 1969; Hoffman 1971). In old growth forests, Pike et al. (1975) reported that epiphytic bryophytes and lichens can amount to as much as 10-20 percent of the biomass of a whole tree. While for the same forest type, McCune (1993) estimated epiphytic biomass for old stands at 2.6 tons/ha and for younger stands at 1 ton/ha.

Arthropods and other small organisms account for the bulk of diversity in terms of species diversity, numbers and functional importance, but have been largely overlooked until recently (Parsons et al. 1991). Arthropods commonly account for at least 70-90% of all species present (Schowalter 2000) with the diversity being greater in old growth stands compared to young plantations. Schowalter (1995) found that diversity was 5 to 6 times greater in old growth stands with the structure of arthropod communities differing significantly between the two types. In the younger stands phytophage biomass (largely aphids) was 800% greater than that of predators (for example, gnats, wasps and spiders) whereas in the older communities defoliator biomass was on average 20% greater than that of the predators. This pattern reported by Schowalter (1995) suggests that there are more effective internal controls over plant eaters in older stands than in younger stands.

NRC (2000) has reported that although different environments result in different patterns of forest development, the dominance of hardwoods and shrubs in younger stands in the northwest in part reflects the suppression of conifers by insects and pathogens at this stage. Insects and pathogens play an important role in channeling successional processes by their choice of particular host species. They affect seed production, dispersal, tree growth and survival, tree characteristics, nutrient cycling and soil fertility and thereby influence the rates and direction of successional changes. Examples include spruce bark beetle infestations in Alaska that result in accelerated transition to open hemlock or mixed hardwood communities (Patel-Weynand and Gordon 1999) and attacks by several insects and root pathogens that accelerate changes from Douglas fir to Hemlock or cedar forests in the Pacific Northwest (Goheen and Hansen 1993).

Effects of Intensive Management on Biodiversity

Management objectives vary substantially among and within ownership categories. Whether public, private or communally owned, extreme objectives are usually

incompatible (for example, obtaining the highest possible sustainable timber yield will probably be incompatible with preserving the maximum biodiversity in the same location) (FAO 1993). A clear set of achievable and prioritized objectives which have been analyzed for compatibility in particular systems need to be in place before firm decisions can be made on the management methods to be adopted (FAO 1993).

Intensive forestry is responsible for altering the spatial and temporal structure of forests and of forested landscapes in a significant way (Perry 1998). From the perspectives of stand development and biodiversity habitat conservation, natural disturbances, through the structural legacies they leave behind, tend to result in a more variable patch mosaic of habitats than forests that are intensively managed. Evidence from the Pacific Northwest shows that many species associated with old growth also occur in younger stands that originate from natural disturbances (Perry 1998). These presumably are the result of post disturbance structural legacies such as remnant green trees, large dead wood, snags, and sprouting shrubs (Hansen et al. 1991; Perry 1998).

Uncertainty exists about the long-term viability of sustaining populations of species that require large contiguous areas of forest in forests managed under short rotations. There are also large knowledge gaps on the viability of organisms associated with shrub-herb layers in early successional forests or in late successional forests. Most industrial forest management rotation periods for forest crops are shorter than the period between natural disturbance in unmanaged forests. Because of the legacies and spatial patchiness, natural disturbances tend to initiate different early successional patterns than intensive forestry which focuses on rapid site capture by single cohort stands (Perry 1998). Harvesting practices that focus on a particular stand component significantly alter stand structure (Fajvan 2000) and impact ecological as well as biodiversity conservation efforts. Most stands which are single cohort stands, when high-graded, are reduced to less diverse stands of low vigor (and therefore low resilience). Fajvan (2000) notes that the sustainability of hardwood forests depends on ensuring a diversity of species in the next generation. Recent assessment of harvesting practices in mature hardwood forests in West Virginia, New York and Pennsylvania revealed that in the West Virginia Harvest Assessment, most sites displayed a reduction in tree species diversity compared to the previous stand (Fajvan 1998). Only 10 percent of the areas sampled were adequately stocked with commercial species of sufficient size to consider regeneration successful (Fajvan 2000).

Examination of the shortcomings of existing practices with regards to conserving some elements of biodiversity has led to a “new forestry” approach that seeks to more closely emulate natural cycles. Also referred to as “variable retention harvest” the basic idea of this approach is to leave a certain number of large, green trees at harvest, either dispersed or aggregated, with the objective of providing three functions not found in current intensively managed forests: habitat continuity for species requiring large, green trees; a diversity of age classes with concomitant vertical and/or horizontal heterogeneity; and future sources of large dead wood. Results to date show that young stands with remnant old trees support a significantly greater abundance of some old-growth associates than do

young stands without old remnants (Perry 1998). The “large sloppy cuts” are designed to create a heterogenous mosaic of intermingled successional stages across the landscape.

The variable retention harvest system is appropriate where management objectives include rapid restoration or maintenance of environmental values associated with structurally complex forests (Franklin et al. 1997). The retention of the structure of forests allows for “life-boating” of species such as rare or endangered species, which are of esoteric or peripheral interest in managed stands. Life-boating of species is achieved by providing structural elements that fulfill habitat requirements for various organisms, by ameliorating microclimatic conditions versus those encountered by other intensive management practices such as clear-cutting, and by providing energetic substances to maintain non autotrophic organisms (Franklin et al 1997). In addition to providing suitable habitat, variable retention harvesting techniques allow for enrichment of the structural complexity of managed forests for an entire rotation while ensuring suitable conditions for species re-establishment at an earlier time than would otherwise be possible. Through structural retention movement and dispersion of organisms is also facilitated although it can be disadvantageous to some organisms when favorable conditions are created for predation of specific species (Franklin et al. 1997).

Generally, the Variable Retention Harvest scheme can create landscape patterns that approximate those imposed by historic wildfires in western forests. A combination of large sloppy cuts and long rotations, coupled with the retention of both very early and very late successional habitats, would seem to move intensive forestry in the direction of more closely imitating natural ecosystem processes (Franklin, Perry, and Schowalter 1988).

Overall, findings on the effects of forest management on biodiversity tend to be variable depending on the species in question and the spatial or temporal scale examined (NCASI 2000). For example, Hix and Barnes (1984) found that clear-cutting and species diversity were positively related in the hemlock dominated forests of the Northern Lake States while others have found that diversity is fairly high immediately following clear-cutting (5-15 years) and in the climax or old growth stage (Oliver and Larson 1996; Bormann and Likens 1979). Studies in the southern Appalachians and in the Pacific Northwest have suggested that longer rotations, rather than shorter rotation plantation forests, are necessary to conserve and manage for biodiversity (Halpern and Spies 1995; Meier et al. 1995).

Other intensive management practices such as fire prevention policies designed to maintain the balance of tree species and associated flora and fauna may result in forests that are more vulnerable to fires as the understory and low vigor trees increases. By reducing the competitive advantage of fire resistant and pioneer tree species long-term sustainability of the system may also be compromised (FAO 1993). By altering the natural fire regimes of forests, those forests with a history of frequent low intensity fires, such as ponderosa pines in the West and long leaf pine forests in the South, have seen increases in insect and pathogen outbreaks and greater risks associated with catastrophic fires (Covington et al. 1994; Perry 1998)

Other structural differences between mature and younger stands especially those that have been traditionally intensively managed, include a marked absence of woody debris and decomposing logs. Woody debris in older forests create optimal conditions for a number of species as boles of old trees contain terpenoid and phenolic compounds that inhibit decay and provide structure and resources for soil and aquatic systems for long periods of time following treefall or death. Decomposing logs also provide nutrients and organic matter to mycorrhizae and roots of surrounding plants that penetrate the wood (Schowalter et al. 1992; Harmon et al. 1986).

Forest soils, in addition to being large reservoirs of biodiversity, also contribute significantly to global carbon pools. Intensive forest management techniques such as windrowing, hot fires and tilling have been recognized as causing immediate impacts on soil carbon whereas longer-term impacts on soil carbon pools (for example, removal of coarse woody debris) have yet to be determined (Perry 1988).

Sites throughout North America are routinely prepared for forest planting through either windrowing or burning residues in place (broadcast burns). Windrowing compacts soils and removes large amounts of soil organic matter (SOM) and nutrients; hot broadcast burns volatilize large amounts of carbon and nitrogen (Perry 1998). Reductions in SOM and soil pore space due to compaction are a significant forest management concern. SOM stores nutrients (especially N), provides cation exchange and water-holding capacity, and serves as substrate for numerous soil functions. Immediate impacts of forest management on soil carbon (C) are mainly associated with extreme site preparation techniques (hot fires, windrowing, and tilling), whereas practices that remove sources of future soil C (trees and litter layers) have undetermined long-term effects (Perry 1998). Following clear-cutting, soil bacteria serve as important nutrient sinks, a phenomenon tied to the availability of labile soil C and likely to be impacted by intensive site preparation. Nutrient inputs from weathering, the major source of all essential elements except N, C, and oxygen (O), are difficult to measure and poorly understood. Recent research shows that conifers have some capacity to renew soil fertility, with their symbiont fungi and bacteria accelerating rock weathering and speeding the recovery of soil fertility. Better understanding of this capacity of trees and their symbionts to renew soil fertility, and how that varies with site, species, and environmental conditions, promises to provide new perspectives on the subject of ecosystem nutrient budgets. For example the type of vegetation may control the N availability and the type of carbon compounds produced which affect organic matter accumulation in soils (Vogt et al. 1999).

One area that has received little attention to date is whether site impacts can disrupt these biologically mediated renewal processes (Perry 1998). The possibility of influencing these renewal processes through management has been supported by a few studies. Some examples include N-fixation in Douglas-fir stands, which have been shown to be stimulated by proximity to certain hardwood species, suggesting excessive vegetation control will reduce associative N fixation where this relationship exists (Perry 1998). SOM accumulation has been shown to be higher in deciduous dominated forests and

forests composed of a mixture of evergreen and deciduous species than in evergreen dominated forests where N availability is lower (Vogt et al. 1995; 1999). In cold temperate wetlands, the presence of *Equisetum*, with its deep-rooting habit, has been shown to act as a nutrient pump, helping to bring up phosphorus and other minerals to the soil surface, making them available to other species and contributing to high levels of net primary productivity (Marsh et al. 2000).

VI. Implications for Management

The effect on forest biodiversity from the tide of lumbering that swept from east to west across the U.S. in the 18th and early 19th centuries was substantial with the significant reduction in forest habitat. However, it was not until the alarm bells over the northern spotted owl and the Pacific salmon species that caused a sudden and dramatic reduction in timber harvesting in the Pacific Northwest, one of the most productive timber growing areas in the world. It was largely in response to this dramatic effort to salvage the remaining biodiversity in forest ecosystems that scientists and forest managers began experimenting with a variety of different approaches to biodiversity conservation in the context of active forest management (Johnson et al. 1991, Johnson 1997).

These approaches included new regulatory approaches and innovative market based approaches like forest certification on the basis of management standards that are aimed in part at providing greater protection for biological diversity. These various approaches have been experimented with widely on public and private forest lands and have profoundly influenced the management of forest industry lands in the U.S.

The mixed success of these approaches makes clear the need to continue exploring and experimenting with new and creative means and mechanisms for sustainable wood production and biodiversity conservation. This includes increased recognition for the role that more specialized forest management can play. Lower-intensity forest management or “new forestry”, if applied everywhere, would likely still result in the loss of forest species and reduction in biological diversity in many forest ecosystems. It would also further increase the U.S. net import of wood products, and exacerbate the impacts of U.S. wood demands on forests in other countries. Most recently, there is renewed interest in the establishment of new protected areas in high conservation value forests and “hotspots” of high biological diversity, offset by an expanded area of intensively managed forests in areas of relatively low biodiversity value, in addition to more biologically sensitive moderate intensity management on a majority of U.S. forest lands (Howard and Stead 2001; Sedjo and Botkin 1997)

Adaptive Management Strategies

Land is often managed at the local level to maximize “species richness”, an approach that favors “generalist” organisms found in a variety of ecosystems at the expense of “habitat specialists” that are limited to few ecosystems such as old growth forests and native

grasslands (Probst and Crow 1991). To prevent loss of species from large areas or whole regions, special attention must be paid to plant and animal species that are “habitat specialists”, those species with low population densities that require large home ranges, with poor dispersal and colonizing abilities, or those that are prone to local extinction. In contrast, species capable of prospering under a variety of land use patterns include common species, habitat “generalists”, or species able to colonize disturbed habitats. Thus, maintaining regional diversity requires maintaining ecosystems that are rare and endangered (Probst and Crow 1991).

Because preserving biodiversity is a complex problem that encompasses a variety of scientific, social, and economic considerations, Probst and Crow (1991) developed the following list of general recommendations to assist foresters in managing forest resources to maintain and enhance biological diversity:

1. Use a regional perspective when considering biological diversity.
2. Think beyond the boundaries of specific ownerships when planning and managing.
3. Plan and manage over large areas rather than using a stand-by-stand approach. Consider the cumulative impact of individual projects on regional populations and resources.
4. Emphasize multi-species and ecosystem management instead of single-species and tree management. Simply stated: become an ecosystem manager.
5. Provide habitat sufficient to maintain species of concern (e.g., large wide-ranging mammals), not just sufficient habitat to attract immigrants from more productive sources.
6. Maintain or create spatial patterns (large patches, landscape linkages, low contrast between adjacent patches) that enhance conditions for problem species.
7. Include the full spectrum of ecological assemblages within the landscape, from early successional to old-growth communities. Provide a variety of sites for each forest type and age as a coarse filter for genetic and ecosystem diversity.
8. Conduct ecological surveys and inventories. Know what is on the land, where it is, and how much is there.
9. Monitor problem species and problem ecosystems. Wherever possible, supplement monitoring of indicator species with guild (groups of species occupying similar niches) monitoring and direct ecosystem monitoring. Relate changes to local treatments. Interpret local changes relative to broader regional changes.
10. Become better informed. Action follows awareness.

Forest managers must often balance multiple management objectives that sometimes create conflict between and among different scales. Failing to integrate planning across different scales may result in unintended consequences. Traditional forestry practices relying on single species stands and uniform management (tillage, fertilizers and tree work) have affected biodiversity and adaptability of forests to disturbances. The Global Biodiversity Strategy (WRI, UNEP, & IUCN 1992) discusses some broad principles to incorporate into adaptive biodiversity conservation management. These include managing timber production forests taking into consideration preservation strategies for key habitats and keystone species, avoidance of fragmentation, regeneration with native species, and gaining a better understanding of natural disturbances on forest dynamics.

Managing Timber Lands for Biodiversity Conservation

In looking at implementing biodiversity conservation into the management of industrial, public and private forests that are actively managed for timber production, more intensive

management and monitoring of target species is necessary (Brown et al. 2001). FAO (1993) states that places outside protected areas that are used for wood production “are not inherently less compatible with genetic conservation of the species being harvested in a sustainable manner, or of the associated species, than are strictly protected areas.” It is possible to conserve genetic resources with sustainable use of much of the land area of a country by including tenets for genetic conservation of a target species as a major component in land use planning in management strategies (FAO 1991). Methods to ensure this may include employing a variety of tools used in different combinations depending on the management objective. These tools may include surveys, demarcation, management and monitoring of conservation areas and collection and storage of seed or tissues. Management interventions may include silvicultural manipulations such as eliminating or controlling competing species or creating gaps in forest canopies to make growing space available, promote increases, and enhance regeneration of target species.

However, recent findings indicate that for many tropical forest areas, even low-intensity “environmentally sensitive” timber removal results in disruptions that lead to the loss of key species. A recent report from Conservation International posits this as the basis for their recommendation that highly sensitive areas simply be protected, while wood needs are satisfied through more intensive management of other less sensitive forest areas (Conservation International 2001).

Monitoring Biodiversity for Informed Management

In response to the Endangered Species Act, many fine-filtered approaches have been developed to monitor biodiversity. While these approaches have been useful in implementing recovery actions for species that are in immediate danger of extinction or threatened with the possibility of extinction, there is no comparable system available for the vast majority of species and ecosystems not yet endangered but at risk from habitat fragmentation, loss of habitat, and disruption of ecological processes. Two major programs in the US working in concert to address this problem are the Gap Analysis Program and the Natural Heritage Program (NCASI 2000). The goal of Gap Analysis is to provide a quick overview of the distribution and conservation status of several components of biodiversity to identify gaps, i.e., vegetation types and species not represented in the network of biodiversity management areas but that may be filled through the establishment of new reserves or changes in land management. Gap Analysis uses satellite data and Geographic Information Systems (GIS) to map the distribution of actual vegetation types and vertebrate and butterfly species as indicators of, or surrogates for, biodiversity. Gap Analysis is not a substitute for a detailed biological inventory, and care must be taken remote sensing data sets do not become confounded when applied to determining ground-level vegetation types (NCASI 2000). The Natural Heritage Program has been established in all 50 states by The Nature Conservancy, in cooperation with state agencies who now operate the program. Unlike Gap Analysis, the TNC applies a fine-filtered approach to rare species inventory and protection and a coarse-filtered one to community inventory and protection. Like Gap Analysis, the TNC utilizes vegetative composition as a surrogate for biodiversity. TNC estimates that 85-90% of species can be protected through the coarse-filtered approach, without having to inventory or plan reserves for species individually. Through a systematic process, TNC is identifying

biodiversity conservation objectives for all Ecoregions in the US and other parts of the world (NCASI 2000).

VII. Findings and Recommendations

Summary of Knowns and Unknowns in the Biodiversity and Sustainability Discussion

Theories derived from well-known ecological relationships predict that biodiversity can be one of several significant factors governing the stability, productivity, nutrient dynamics, and invasibility of ecosystems. These theories predict that greater biodiversity in general should: 1) increase community temporal stability; 2) decrease population temporal stability; 3) increase community standing crop and/or productivity; 4) decrease amounts of unconsumed limiting resources; 5) increase ecosystem stores of limiting nutrients by decreasing loss; and 6) decrease invasions by exotic species (Tilman 1999). However, the role of biodiversity must be kept in perspective. In none of the above cases is diversity the only, or even the strongest force. Species composition, productivity, disturbance regimes, climate, and edaphic factors can be as important or more important than biodiversity.

Diversity is both a measure of the chance of having certain species present in a system and of the variation in species traits in an ecosystem (Tilman 1999). Both the chance of having certain species present and the range of traits present influence species interactions and abundances, which, in turn, influence population, community, and ecosystem processes. In total, experiments and theoretical concepts demonstrate that diversity impacts the structure and functioning of ecosystems, and must be added to composition, disturbance, nutrient supply, and climate as a determinant of ecosystem structure and dynamics (Tilman 1999).

Research over the last twenty years has delineated the critical role that species composition plays in the dynamics and functioning of ecosystems. Composition plays such a vital role because organisms drive ecological processes, and species exhibit different traits. Large differences in traits can have large impacts on ecosystem processes. Examples include the absence or presence of nitrogen fixation, or of deep roots, or of flammable tissues. Although species composition is regarded as one of the one of the major determinants of stability, primary productivity, nutrient dynamics, invisibility (Tilman 1999), and other ecosystem traits by many, there is a major ongoing debate on issues of complementarity and selection effects and how they influence productivity in systems with high diversity (Huston 2000; Hector et al. 2000; Kaiser 2000; Huston 1997; Aarssen 1997)

Composition and diversity are often correlated in both natural and managed ecosystems, indicating that diversity may also impact ecosystem processes. Because of the correlation between the two attributes, it is difficult to unambiguously attribute effects to

one or the other based on observational studies (Tilman 1999). The strong correlation between these two factors also means that care must be taken in applying the above observations about diversity to management issues. Shifts in composition, disturbance, and nutrient loading are just as likely as shifts in biodiversity to impact ecosystem processes. Attributing effects to one of these variables without controlling for the others could lead to poorly targeted interventions. A management strategy with a myopic focus on diversity would be a poor one, because diversity is only one of many factors that influence ecosystem processes (Tilman 1999).

Awareness is growing among resource professionals and managers that diverse flora and fauna are critical to the maintenance of healthy and productive ecosystems, and that genetic diversity has an important relationship to site productivity. Decomposition, nutrient cycling, and other ecological processes are facilitated by biotic diversity. Biodiversity provides alternative food chains, biological pest controls, and broader silvicultural options. “Invisible diversity” that is out of sight and out of mind represents much of the diversity responsible for ecosystem health and sustainability. Community composition can be a sensitive environmental monitor for climate change or pollution, since diverse life forms vary in their responses to environmental stress. Many valuable site indicators for forestry and agriculture can be found among non-commercial species (Probst and Crow 1991).

Recommendations

Examination of the above information reveals a number of gaps in the knowledge base that need to be addressed so that better informed decisions can be made with regards to sustainable forest management and biodiversity conservation. One cross-cutting need is for information to be communicated in forms that allow for quick action. Forest managers need access to current information to apply measures to improve and shape management decisions. Communicating information on land management decisions being made by other owners elsewhere within the landscape matrix in an efficient manner helps managers make informed decisions.

With the change in land use and ownership patterns, and the extensive volume of forests on private property in the US any successful biodiversity conservation strategy must align with the variety of management objectives and policies on both public and private lands. Documentation of management approaches that successfully build on partnerships between government, private landowners, the wood products industry, and environmental groups is needed. The Westvaco example described previously in Section IV is one example. Another example is Environmental Defense’s Safe Harbors Program, which helps landowners restore critical habitat voluntarily without adding new federal restrictions on their property (Environmental Defense 2001).

The documentation and evaluation of forest management approaches at the ecosystem and landscape level are also needed. The effectiveness and general organizing principles of approaches that encompass multiple ecosystems and both protected and un-protected areas would be especially valuable. Approaches that incorporate the results of Gap Analysis and the Nature Reserves program, as well as those that have attempted to

connect isolated habitats with corridors, need documentation, evaluation, and continued experimentation. More issue-focused research is needed to further biodiversity prediction and management (Smythe et al. 1996).

More information is needed on the relationship between biodiversity and ecosystem functioning, especially the importance of species additions and deletions. More information on the delineating keystone species is a critical need. The influence of biodiversity on ecosystem resistance and resilience to disturbances is another important gap in the knowledge base that needs to be addressed as it impacts ecosystems at multiple geographical scales. Other issues which are currently under consideration and need further investigation include biodiversity issues related to streams, wetlands and riparian areas and management driven issues such as the role of management techniques for example, the Variable Retention Harvest System in conservation of biodiversity.

In the area of the impact of fragmentation on biodiversity and ecosystem functioning, a number of needs have been specifically identified (Alig 2000):

- Develop more rigorous definition(s), recognizing that changes in land use, land cover, and ownership can result in a variety of “fragmentation” outcomes.
- Better document forest fragmentation and parcelization, and develop a long-term database.
- Investigate causes of any forest fragmentation, considering both natural and human-related factors.
- Consider possible suite of consequences of forest fragmentation, including ecological and economic impacts of forest fragmentation.
- Augment policy analyses to mitigate and/or modify fragmentation trends.

In addition, to move the discussion on fragmentation forward and as a practical measure, focusing on what the landscape patterns should look like to satisfy biodiversity objectives, becomes important. Developing a proactive policy agenda to reflect these concerns would be a valuable contribution to the fragmentation discussion.

More research is also needed on the impact of forest management practices on below-ground ecosystem processes, especially soil structure and nutrient cycling. This is especially true for those forests being managed for timber, but is also important for the long-term health of forests managed as wilderness reserves.

The long-term impacts on biodiversity associated with changes in atmospheric chemistry and associated climate change effects need investigation. The expected changes in climate variability and in the number of extreme weather events will have potentially devastating impacts on forest ecosystems, as well as the gradual shift in climatic zones. In addition, the potential effect of global warming on shifts in the natural ranges of plant and animal communities, the difficulties this will pose for species that do not migrate quickly and the subsequent stresses placed on these species survival also merit investigation. The largest and earliest impacts induced by climate change are projected to occur in boreal forests where weather-related disturbance regimes and nutrient cycling

are primary controls on productivity (IPCC 2000) where additional research on biodiversity is important.

While much of the past discussion of biodiversity and forest management has focused on the creation of reserves that could be left undisturbed to serve as protective reservoirs, today's discussion now focuses on the need for continued human involvement in the management of ecosystems to preserve both biodiversity and ecosystem services. However, managing actively in the current context may encompass leaving areas as conservation areas. Active management does not necessarily imply active and resource intensive management in all areas, but incorporating more of a big-picture holistic perspective keeping in mind the landscape scale. Probst and Crow (1991) summed it up as follows:

“It is ironic that as humans alter the ecosystems on which they depend, conserving diversity will increasingly depend on active human involvement. Active management, not just passive protection, is needed to coordinate different land ownership objectives.”

Even in the face of incomplete knowledge and the recognition that chance exists in the natural world, managers must accept that it is possible to narrow the choice of purposes, to contract the range of ambiguity surrounding objectives, and to shrink the domain of ignorance (Christensen et al. 1989). Assisting managers is the emergence of new synthesis disciplines such as conservation biology, restoration ecology, and ecological economics. Traditional, basic and applied disciplines appear to be coming together to seek solutions to complex problems of ecosystem sustainability and human welfare (Kessler et al. 1992). While additional research is needed to address the knowledge gaps identified above, greater use should be made of information on spatial dynamics and temporal variability of populations from long-term research sites to include biodiversity conservation in management efforts.

VII. Tables

Table 1: The Montreal Process Criteria One and Indicators for the Conservation and Sustainable Management of Temperate and Boreal Forests.

Criterion 1: Conservation of biological diversity

Biological diversity includes the elements of the diversity of ecosystems, the diversity between species, and genetic diversity in species.

Indicators:

Ecosystem diversity

- a. Extent of area by forest type relative to total forest area-(a);¹
- b. Extent of area by forest type and by age class or successional stage-(b);
- c. Extent of area by forest type in protected area categories as defined by IUCN² or other classification systems-(a);
- d. Extent of areas by forest type in protected areas defined by age class or successional state-(b);
- e. Fragmentation of forest types-(b);

Species diversity

- a. The number of forest dependent species-(b);
- b. The status (threatened, rare, vulnerable, endangered, or extinct) of forest dependent species at risk of not maintaining viable breeding populations, as determined by legislation or scientific assessment-(a).

Genetic diversity

- a. Number of forest dependent species that occupy a small portion of their former range-(b);
- b. Population levels of representative species from diverse habitats monitored across their range-(b)

¹ Indicators followed by an “a” are those for which most data are available. Indicators followed by a “b” are those which may require the gathering of new or additional data and/or a new program of systematic sampling or basic research.

² IUCN categories include: I. Strict protection, II. Ecosystem conservation and tourism, III. Conservation of natural features, IV. Conservation through active management, V. Landscape/Seascape conservation and recreation, VI. Sustainable use of natural ecosystems.

Table 2: Sustainable Forestry Implementation Guidelines (AF&PA 1994).

Objective 1. Broaden the practice of sustainable forestry by employing an array of scientifically, environmentally, and economically sound practices in the growth, harvest, and use of forests.
Objective 2. Promptly reforest harvested areas to ensure long-term forest productivity and conservation of forest resources.
Objective 3. Protect the water quality in streams, lakes, and other waterbodies by establishing riparian protection measures based on soil type, terrain, vegetation, and other applicable factors, and by using EPA-approved Best Management Practices in all forest management operations.
Objective 4. Enhance the quality of wildlife habitat by developing and implementing measures that promote habitat diversity and the conservation of plant and animal populations found in forest communities.
Objective 5. Minimize the visual impact by designing harvests to blend into the terrain, by restricting clearcut size and/or by using harvest methods, age classes, and judicious placement of harvest units to promote diversity in forest cover.
Objective 6. Manage company lands of ecologic, geologic, or historic significance in a manner that accounts for their special qualities.
Objective 7. Contribute to biodiversity by enhancing landscape diversity and providing an array of habitats.
Objective 8. Continue to improve forest utilization to help ensure the most efficient use of forest resources.
Objective 9. Continue the prudent use of forest chemicals to improve forest health and growth while protecting employees, neighbors, the public, and sensitive areas, including streamcourses and adjacent lands.
Objective 10. Broaden the practice of sustainable forestry by further involving nonindustrial landowners, loggers, consulting foresters and company employees who are active in wood procurement and landowner assistance programs.
Objective 11. Publicly report AF&PA members' progress in fulfilling their commitment to sustainable forestry.
Objective 12. Provide opportunities for the public and the forestry community to participate in the AF&PA membership's commitment to sustainable forestry.

Table 3: Temperate Forests (760 million hectares including plantations) (FAO 1993)

Country	Land Area Occupied by Forests
USSR	40%
France	25-30%
Germany	25-30%
Italy	25-30%
Poland	25-30%
Greece	45%
Austria	45%
United States	33%

Table 4: Boreal Forests (Total closed forest- 920 million hectares, Total open woodland 300 million hectares) (FAO 1993)

Country	Percent of Total Boreal Forest
USSR	75%
Canada & Alaska	20%
Nordic countries	5%

Table 5: Biodiversity Measures (adapted from Kimmins 1999).

Measure	Definition
I. Genetic:	The diversity of genotypes within a species in the area of interest.
II. Species:	The number of species in the area of interest and the relative abundance of the different species in the area.
III. Taxonomic:	The number of genera, families, and higher taxa.
IV. Structural:	The diversity in the vertical structure and understory layers of the plant community, and the horizontal diversity in structure; the diversity of plants and animals of different life forms.
V. Functional:	The diversity of different functional groups in the area.
VI. Temporal:	The degree of change over time in all the other measures.

Table 6: Managing for Different Scales of Diversity (Noss 1983). [NOTE – The three strategies are not necessarily mutually exclusive.]

Scale	Methods	Advantages	Disadvantages
Alpha (within-habitat)	Achieve optimum levels of limiting resources (e.g., food supply) to ameliorate interspecific competition; increase structural complexity (e.g., vertical strata, substrate) to provide more physical niche space; control unwanted species.	Increased number of species within habitat, and/or increased population levels of particular species; desired community structure maintained.	May be arduous and costly to implement; considerable uncertainty about effects of management actions on particular species (undesirable species could reach pest proportions, and critical species could decline).
Beta (between-habitat including “edge effect”)	Maintain variety of successional stages; intersperse different habitat types; construct roads, trails, and other swaths.	Increased local species richness; increased population levels of edge-adapted species (e.g., many game animals); increased human recreational potential.	Decreased population levels or extirpation of interior specialists; proliferation of “weedy”, opportunistic species; community destabilization; possibly decreased regional diversity (may limit options for regional diversity).
Gamma (regional)	Preserve sufficiently large areas of of unaltered indigenous ecosystems on a regional scale; inter-connect habitat patches; limit human intrusion in sensitive areas.	Adequate population levels and genetic variation of indigenous species maintained; critical ecosystem processes perpetuated; long-term human welfare promoted.	Some loss of local species richness with declines in edge species; more land taken out of “productive” human use; short-term economic losses.

Table 7: Definitions of Resilience (Patel-Weynand 2000 and references therein).

Term	Definition	Synonymies
Resilience	Degree, manner, and pace of restoration of initial structure and function in an ecosystem after disturbance	Stability
		Elasticity
	The ability of ecosystems to return to original state following disturbance	Recurrence
		Stability
		Elasticity
Asymptotic Stability		
	Rate at which an ecosystem's composition returns to the point at which community processes and interactions function as they did before disturbance	Elastic Stability
Resiliency	Number of times a system can recover after displacement	Amplitude
Ultrastability	In systems theory, ultrastable systems return to the same structural and functional state	Resilience
Components Of Resilience		
Elasticity	Rapidity of restoration of a stable state following disturbance	Resilience
Amplitude	Zone of deformation from which the system will still return to its initial state	Resiliency
Hysteresis	The extent to which the path of degradation under chronic disturbance, and of recovery when disturbance ceases, are mirror images of each other	
Malleability	Degree to which the new steady state established after disturbance differs from the original steady state	

Table 8: Definitions of Resistance (Patel-Weynand 2000 and references therein).

Term	Definition	Synonymies
Resistance	Opposition to change in ecosystem processes due to disturbance	Amplitude Stability
Stability	Ability to weather a stress period or perturbation and return to normal	Fitness
	Frequency and magnitude of fluctuations in population size are small	Low Variability Constancy
Persistence	The ability of a system to maintain its population levels within acceptable ranges in spite of disturbances	Resistance/Stability
Inertia	Ecosystem resistance to change under stress	Resilience
		Resistance
Components of Resistance		
Response flexibility	Refers to the ability of genotype to function in a variety of environments. It results from the plasticity of some traits and the stability of others.	
Phenotypic plasticity	Refers to the ability of traits in a given genotype to express different phenotypes in different environments. Plasticity is adaptive when that expression confers an advantage to the genotype that expresses it in a particular environment	Component of Response Flexibility
Acclimation	The ability of a genotype to change the biochemical, physiological and morphological characteristics of its already established modules in response to a change in environment.	

Table 9: Private forest land acres and ownership in the US, 1978 and 1994, by the size of ownership (acreage category) (Sampson 2000).

Acreage Category	1978 Owners	1994 Owners	1978 to 1994 Change	1978 Acres	1994 Acres	1978 to 1994 Change
1-9	5,528,000	5,795,000	267,000	11,000,000	16,600,000	5,600,000
10-49	1,164,000	2,762,000	1,598,000	28,100,000	60,400,000	32,300,000
50-99	464,000	717,000	253,000	32,900,000	47,200,000	14,300,000
100-499	538,000	559,000	21,000	102,600,000	91,600,000	(11,000,000)
500-999	40,000	41,000	1,000	26,900,000	24,500,000	(2,400,000)
1000+	23,000	27,000	4,000	131,600,000	153,000,000	21,400,000
Total=	7,757,000	9,901,000	2,144,000	333,100,000	393,300,000	60,200,000

Table 10: Progression of Developmental Stages Following Disturbance (Oliver and Larson 1996; Bormann and Likens 1979).

Phase	Description
Stand initiation or reorganization	Occupation of growing space vacated by previous vegetation.
Stem exclusion or aggradation	Few or no individuals are established as resources and growing space become limited with canopy closure.
Understudy re-initiation or transition	Where new cohorts are established due to density-dependent mortality.
Old growth or steady state	The stand is in equilibrium barring another major disturbance in the phase,

IX. References

- Aarssen, L.W. 1997. High Productivity in grassland ecosystems: effected by species diversity or productive species? *Oikos*80:183-184
- AF&PA [American Forest & Paper Association]. 1994. Sustainable Forestry Principles and Implementation Guidelines. AF&PA Board of Directors. Washington, DC.
- Alig, R., B. Butler, and J. Swenson. 2000. Fragmentation and National Trends in Private Forest Lands: Preliminary Findings from the 2000 Renewable Resource Planning Act Assessment. In: Proceedings of the Forest Fragmentation 2000 Conference: Sustaining Private Forests in the 21st Century (L.A DeCoster, ed.). The Sampson Group, Alexandria, VA.
- Alig, R. 2000. Where do we go from here? Preliminary scoping of research needs. In: Proceedings of the Forest Fragmentation 2000 Conference: Sustaining Private Forests in the 21st Century (L.A DeCoster, ed.). The Sampson Group, Alexandria, VA.
- Anderson, M.A., F.B. Biasi, S.C. Buttrick. 1998. Conservation site selection:Ecoregional planning for biodiversity. Paper presented at the ESRI International User Conference. San Diego, CA
- Angermeier, P.L., J.R. Carr. 1994. Biological integrity versus biological diversity as policy directives. *BioScience* 44:690-697.
- Barnes, R. 1989.Diversity of organisms: How much do we know? *American* 29: 1075-84.
- Barnes, B.V., K.S. Pregitzer, T.A. Spies, V.H. Spooner. 1982. Ecological Forest Site Classification. *Journal of Forestry* 80:493-498.
- Benton, M. 1995. Diversification and extinction in the history of life. *Science* 268: 52-58.
- Bormann, B. 1985. Air pollution and forests: an ecosystem perspective. *BioSci.* 35: 434-441.
- Bormann, B. and G. Likens. 1979. Pattern and Process in a Forested Ecosystem. Disturbance, Development, and the Steady State Based on the Hubbard Brook Ecosystem Study. Springer-Verlag. New York, NY.
- Brown, J.H. and E.J. Heske. 1990. Control of a Desert Grassland Transition by a Keystone Rodent Guild. *Science* 250:1705-1707.
- Chen, J., J. Franklin, and T. Spies. 1992. Vegetation response to edge environments in old growth Douglas-fir forests. *Ecological Applications*. 2(4): 387-396.
- Chen, J. 1991. Edge effects: microclimatic pattern and biological responses in old-growth Douglas-fir forests. Dissertation. University of Washington, Seattle, WA.

- Christensen, N., A. Bartuska, J. Brown, S. Carpenter, C. D'Antonio, R. Francis, J. Franklin, J. MacMahon, R. Noss, D. Parsons, C. Peterson, M. Turner, and R. Woodmansee. 1996. The Report of the Ecological Society of America Committee on the Scientific Basis for Ecosystem Management. *Ecological Applications* 6 (3): 665-691.
- Christensen, N., J. Agee, P. Brussard, J. Hughes, D. Knight, G. Minshall, J. Peek, S. Pyne, F. Swanson, J. Thomas, S. Wells, S. Williams, and Henry Wright. 1989. Interpreting the Yellowstone Fires of 1988: Ecosystem responses and management implications. *Bioscience* 39 (10): 678-685.
- Covington, W., R. Everett, R. Steele, L. Irwin, T. Daer, and A. Auclair. 1994. Historical and anticipated changes in forest ecosystems of the inland west of the United States. *Journal of Sustainable Forestry*. 2(1/2): 13-63.
- Covington, W. and M. Moore. 1994. Postsettlement changes in natural fire regimes and forest structure: ecological restoration old-growth ponderosa pine forests. *Journal of Sustainable Forestry*. 2(1/2): 153-181.
- Daily, G. and P. Ehrlich. 1994. Population extinction and the biodiversity crisis. In: *Biodiversity Conservation*. (Perrings, C.A., K.G. Maler, C. Folke, C.S. Holling and B.O. Jansson, eds.). Kluwer Academic Publishers. London.
- DeGroot, B. 2000. Reconnecting the Environment. In: *Proceedings of the Forest Fragmentation 2000 Conference: Sustaining Private Forests in the 21st Century* (L.A DeCoster, ed.). The Sampson Group, Alexandria, VA.
- Denslow, J. 1985. Disturbance mediated co-existence of species. In: *The Ecology of Natural Disturbance and Patch Dynamics* (P.S. White and S.T.A. Pickett, eds.) Academic Press, NY. pp. 307-323.
- di Castri, F. 1996. Opening Address of International Union of Biological Sciences (IUBS). In: *Biodiversity, Science and Development: Towards a New Partnership* (F. di Castri and T. Younes, eds). Wallingford, UK.
- di Castri, F. and T. Younes (eds). 1990. Ecosystem function of biological diversity. *Biology International (Special Issue)* 22: 1-20.
- di Castri, F. and T. Younes. 1996. Introduction: Biodiversity, the Emergence of a New Scientific Field – Its Perspectives and Constraints. In: *Biodiversity, Science and Development: Towards a New Partnership* (F. di Castri and T. Younes, eds). CAB International. Wallingford, UK.
- Drever R. 2000. *A Cut Above: Ecological Principles for Sustainable Forestry on BC's Coast*. The David Suzuki Foundation. Vancouver, BC, Canada.

- Duinker, P.N. 1996. Managing Biodiversity in Canada's Public Forests. In: Biodiversity, Science and Development: Towards a New Partnership (F. di Castri and T. Younes, eds). Wallingford, UK.
- Ewel, J., M. Mazzarino and C. Berish. 1991. Tropical soil fertility changes under monocultures and successional communities of different structure. *Ecological Applications* 1(3): 289-302.
- Fajvan, M.A. 2000. Effects of harvesting practices on the sustainability of non-industrial private forests. In: Proceedings of the Forest Fragmentation 2000 Conference: Sustaining Private Forests in the 21st Century (L.A DeCoster, ed.). The Sampson Group, Alexandria, VA.
- Fajvan, M.A., S.T. Grushecky, and C.C. Hassler. 1998. The effects of harvesting practices on West Virginia's wood supply. *J. of Forestry*. 96(5): 33-39.
- FAO [Food and Agriculture Organization of the United Nations]. 1993. The challenge of sustainable forest management: What future for the world's forests? FAO. Rome, Italy.
- FEMAT [Forest Ecosystem Management Assessment Team]. 1993. Forest Ecosystem Management: an ecological, economic and social assessment. U.S. Government Printing Office 1993-793-071. Washington, DC.
- Forman, R. 1981. Interactions among landscape elements: a core of landscape ecology. In: Perspectives in Landscape Ecology, Proceedings of the International Congress of Landscape Ecology. Pudoc Publ., Wageningen, The Netherlands.
- Forman, R. and M. Godron. 1981. Patches and structural components for a landscape ecology. *Bioscience* 31: 733-740.
- Frank, D. and S. McNaughton. 1991. Stability increases with diversity in plant communities: empirical evidence from the 1998 Yellowstone draught. *OIKOS*. 62(3): 360-362.
- Franklin, J.F., D.R. Berg, D.A. Thornburgh, J.C. Tappeiner. 1997. Alternative silvicultural approaches to timber harvesting: Variable Retention Harvest Systems. In: Creating a Forestry for the 21st Century (Komb, K and J.A. Franklin, eds.). Island Press, Washington, DC).
- Franklin, J. 1993. Preserving Biodiversity: Species, Ecosystems, or Landscapes? *Ecological Applications* 3(2): 202-205.
- Franklin, J.F., D.A. Perry, T.D. Schowalter, M.E. Harmon, A. McKee and T. Spies. 1989. Importance of ecological diversity in maintaining long-term site productivity. In: Maintaining the Long-Term Productivity of Pacific Northwest Forest Ecosystems (D.A. Perry, R. Meurisse, B. Thomas, R. Miller, J. Boyle, J. Means, C.R. Perry, and R. F. Powers, eds.) Timber Press. Portland, OR.

- Goheen, D. and E. Hansen. 1993. Effects of pathogens and bark beetles on forests. In: Beetle-Pathogen Interaction in Conifer Forests (T.D. Schowalter and G.M. Filip, eds.) Academic Press. London, U.K.
- Gordon, A. and E. Gorham. 1963. Ecological aspects of air pollution from an iron-sintering plant at Wawa, Ontario. *Can. J. Bot.* 41: 1063-1078.
- Gordon, J., B. Bormann, and A. Keister. 1992. The physiology and genetics of ecosystems: A new target or "Forestry contemplates an entangled bank". In: Proc. 12th. N. Am. For. Bio. Wksp., Sault Ste. Marie, Ontario. Ontario Ministry of Natural Resources, Ontario Forest Research Institute and Forestry Canada, Ontario Region. pp 1-14.
- Grier, C. 1975. Wildfire effects on nutrient distribution and leaching in a coniferous ecosystem. *Can. J. For. Res.* 5(4): 599-607.
- Hagle, S. K. and D. J. Goheen. 1988. Root disease response to stand culture. In: Proceedings: Future Forests of the Mountain West: A stand culture symposium. General Technical Report (GTR INT-243), USDA, Forest Service, Intermountain Research Station. Ogden, UT.
- Hammond, P.M. 1992. Species Inventory. In *Global Diversity: status of the earth's living resources* (B. Groom-bridge, ed). Chapman and Hall, London.
- Hansen, A.J., S.L. Garman, F.J. Swanson, J.L. Ohmann. 1991. Conserving Biodiversity in Managed Forests. *BioScience* 4:6:382-392
- Harmon, M.E., J.F. Franklin, F.J. Swanson, P. Sollins, S.V. Gregory, J.D. Lattin, N.H. Anderson, S.P. Cline, N.G. Aumen, J.R. Sedell, G.W. Lienkaemper, K. Cromack and K.W. Cummins. 1986. Ecology of coarse woody debris in temperate ecosystems. *Adv. Ecol. Res.* 15: 133-302.
- Harris, W., D. Santantonio, and D. McGinty. 1980. The dynamic belowground ecosystem. In: *Forests: fresh perspectives from ecosystem analysis* (R.H. Waring, ed.). Oregon State University Press, Corvallis, OR.
- Hawksworth, D. 1996. Microorganisms: The Neglected Rivets in Ecosystem Maintenance. In: *Biodiversity, Science and Development: Towards a New Partnership* (F. di Castri and T. Younes, eds). Wallingford, UK.
- Hector, A. et al. No consistent effect of plant diversity on productivity. *Response. Science* 289:1255
- Hector, A., B. Schmidt, C. Beierkuhnlein, M.C. Caldeira, M. Deimer, P. Dimitrakopoulos, J.A. Finn, H.Freitas, P. Giller, J. Good, R.Harris, P. Hogberg, K. Huss-Danell, J. Joshi, A. Jumpponen, C. Korner, P.W. Leadley, M. Loreau, A. Minns, CP Mulder, G.Donovan, S.J. Otway, J.S. Pereira, A. Prinz, D.J. Read, M. Scherer-Lorenzen, E.D. Schulze, A.S. Siamantziouras, EM. Spehn, A.C. terry,

- A.Y. Troumbis, F.I. Woodward, S. Yachi, J.H. Lawton. 1999. Plant diversity and Productivity experiments in European Grasslands. *Science* 286:1123-1127.
- Helms, J. (ed.). 1998. The dictionary of forestry. Society of American Foresters. Bethesda, MD.
- Hoffman, G.R. 1971. An ecologic study of epiphytic bryophytes and lichens on *Psuedotsuga menziesii* on the Olympic Peninsula, Washington II. Diversity of the vegetation. *The Bryologist* 74: 413-427.
- Hoffman, G.R. and R.G. Kazmierski. 1969. An ecologic study of epiphytic bryophytes and lichens on *Psuedotsuga menziesii* on the Olympic Peninsula, Washington I. Diversity of the vegetation. *The Bryologist* 72: 1-19.
- Holdgate, M.W. 1989. Conservation in a world context. In: The scientific management of temperate communities for conservation. The 31st syposium of the British Ecological Society, South Hampton. (I.F. Spellerberg, F.B. Goldsmith and M.G. Morris, eds.). Blackwell Scientific Publications, Oxford.
- Holling, C. 1996. Biological Foundations for Sustainability and Change. In: Biodiversity, Science and Development, Towards a New Partnership (F. di Castri and T. Younes, eds.) CAB International, Wallingford, UK.
- Howard, S. and J. Stead. 2001. The forest industry in the 21st century. World Wildlife Fund for Nature, London, UK
- Hull, R., J. Johnson, and M. Nespeca. 2000. Forest Landowner Attitudes Toward Cross-Boundary Management. In: Proceedings of the Forest Fragmentation 2000 Conference: Sustaining Private Forests in the 21st Century (L.A DeCoster, ed.). The Sampson Group, Alexandria, VA.
- Hunter, M. 1990. Wildlife, forests, and forestry – principles of managing forests for biological diversity. Prentice-Hall, Englewood Cliffs, NJ.
- Hunter, A.F. and L.W. Aarssen. 1988. Plants helping plants. *Bioscience*. 38(1): 34-40.
- Huston, M.A. 1997. Hidden treatments in ecological experiments:reevaluating the ecosystem function of biodiversity. *Oecologia*. 110:449-460.
- Huston, M.A. et al. 2000. No consistent effect of plant diversity on productivity. *Science* 289:1255
- Johnson, K.N., J.F. Franklin, J.W. Thomas and John Gordon. 1991. Alternatives for management of late successional forests of the Pacific Northwest. A report to the Agricultural Committee and the Merchant Marine Committee of the U.S. House of Representatives. Corvallis, OR: College of Forestry, Oregon State University.
- Kaiser, J. 2000. Rift over biodiversity divides ecologists. *Science* 289:1255

- Kareiva, P. 1983. Influence of vegetation texture on herbivore populations: resource concentration and herbivore movement. In: *Variable Plants and Herbivores in Natural and Managed Ecosystems* (R.F. Denno and M.S. McClure, eds.) New York: Academic Press.
- Kimmins, J.P. 1999. Biodiversity, Beauty and the “Beast”: Are beautiful forests sustainable, are sustainable forests beautiful, and is “small” always ecologically desirable? *The Forestry Chronicle* 75 (No. 6): 955-960.
- Kimmins, J.P. 1987. *Forest Ecology*. MacMillan Publishing Company. New York, NY.
- Lancia, R, J. Gerwin, M. Mitchell, W. Baughman, and T. Wigley. 2000. Avian diversity and productivity on an intensively managed, industrial forest in South Carolina: The Westvaco example. In: *Proceedings of the Forest Fragmentation 2000 Conference: Sustaining Private Forests in the 21st Century* (L.A DeCoster, ed.). The Sampson Group, Alexandria, VA.
- Landres, P.B., J. Verner, and J.W. Thomas. 1988. Ecological uses of vertebrate indicator species: A critique. *Conservation Biology* 2: 316-328.
- Lanly, J.P. and T. Allan. 1991. Overview of status and trends of world forest. In *Proceedings of the Technical Workshop to Explore Options for Global Forestry Management, Bangkok 1991*. Office of the National Environment Board, UK, International Institute for Environment and Development, Japan, ITTO.
- Lawton, J. and V. Brown. 1993. Redundancy in ecosystems. In: *Biodiversity and Ecosystem Function* (E.D. Schulze and H.A. Mooney, eds.). Springer-Verlag New York.
- Leps, J., J. Osbomova-Kosinova and M. Rejmanek. 1982. Community stability, complexity and species life history strategies. *Vegetatio*. 50(1): 53-63.
- Levort, M. and M. Chauvet. 1996. Biodiversity and Agriculture, Grasslands and Forests. In: *Biodiversity, Science and Development: Towards a New Partnership* (di Castri, F and T. Younes, eds). Wallingford, UK.
- Loreau, M and A. Hector. 2001. Partitioning Selection and Complementarity in biodiversity experiments. *Nature* 412:72:76
- Lovejoy, T., R. Bierregaard, A. Rylands, J. Malcolm, C. Quintela, L. Harper, K. Brown, A. Powell, G. Powell, H. Schubart, and M. Hays. 1986. Edge and other effects of isolation on Amazon forest fragments. In: *Conservation Biology* (M. Soule, ed.). Sinauer, Sunderland, MA.
- May, R.M. 1973. *Stability and Complexity in Model Ecosystems*. Princeton University Press. Princeton, NJ.

- McCune, B. 1993. Gradients in Epiphyte biomass in three *Psuedotsuga-Tsuga* forests of different ages in Western Oregon and Washington. *The Bryologist* 96(3): 405-411.
- McKeand, S.E. and J. Svensson. 1997. Loblolly Pine: Sustainable Management of Genetic Resources. *Journal of Forestry*, March 1997, pp 4-9
- McNaughton, S. 1977. Diversity and stability of ecological communities: a comment on the role of empiricism in ecology. *American Naturalist* 111: 515.
- Mooney, H., J. Lubchenco, R. Dirzo, and O. Sala (Co-ordinators). 1995. Biodiversity and Ecosystem Functioning: Basic Principles. In: *Global Biodiversity Assessment* (V. Heywood, exec. ed.). United Nations Environment Programme. Cambridge University Press. Cambridge, UK.
- Naeem, S., L. Thompson, S. Lawler, J. Lawton, and R. Woodfin. 1994. Declining biodiversity can alter the performance of ecosystems. *Nature* 368: 734-737.
- Naiman, R. (ed.) 1992. *New perspectives in watershed management*. Springer-Verlag, New York, NY.
- Naiman, R. J. 1988. Animal influences on ecosystem dynamics. *BioScience* 38:750-752.
- NCASI [National Council for Air and Stream Improvement]. 2000. *Land Management Tools for the Maintenance of Biological Diversity: An Evaluation of Existing Forestland Classification Schemes*. Technical Bulletin No. 800. NCASI. Research Triangle Park, NC.
- NCSSF [National Commission on Science for Sustainable Forestry]. 2001. *Science Program Plan, Draft 1.0*. NCSSF. Washington, DC.
- Newton, A. 1995. *Conservation and Sustainable Management of Trees*. WCMC/IUCN SSC Project. University of Edinburgh. Edinburgh, UK.]
- Norris, L., H. Cortner, M. Cutler, S. Haines, J. Hubbard, M. Kerrick, W. Kessler, J. Nelson, R. Stone, and J. Sweeney. 1993. *Sustaining long-term forest health and productivity*. Task force report, Society of American Foresters, Bethesda, MD.
- Noss, R. 1983. A Regional Landscape Approach to Maintain Biodiversity. *Bioscience* 33(11): 700-706.
- Noss R.F> and A.Y. Cooperrider. 1994. *Saving natures legacy: Protecting and restoring biodiversity*. Island Press, Washington DC.
- NRC [National Research Council]. 2000. *Environmental Issues in Pacific Northwest Forest Management*. National Academy Press. Washington, DC.

- O'Dowd, D.J., and P.S. Lake. 1991. Red Crabs in Rain forest, Christmas Island: removal and fate of fruits and seeds. *Journal of Tropical Ecology* 7: 113-121.
- O'Laughlin, J. 1993. Exploring the definition of forest health. In "Proceedings, Forest Health in the Inland West". USDA Forest Service, Boise National Forest; Dept. of Forest Resources, Univ. of Idaho, Moscow. Pp. 9-14.
- Old-Growth Definition Task Group. 1986. Interim Definition for Old-Growth Douglas-Fir and Mixed-Conifer forests in the Pacific Northwest and California. Research Note PNW-447. USDA, Forest Service, Pacific Northwest Research Station. Portland, OR.
- Oliver, C.D. and B.C. Larson. 1996. *Forest and Stand Dynamics*. John Wiley & Sons, Inc. New York, NY.
- Parsons, G.L., G. Cassis, A.R. Moldenke, J.D. Lattin, N.H. Anderson, J.C. Miller, P. Hammond, and T.D. Schowalter. 1991. Invertebrates of the H.J. Andrews Experimental forest, Western Cascade Range, Oregon: V. An annotated list of insects and other arthropods. Gen. Tech. Rep. PNW-GTR-290. USDA, Forest Service, Pacific Northwest Forest and Range Experiment Station. Portland, OR.
- Patel-Weynand, T. 2000. Evaluating Ecosystem Adaptation, Productivity, Resilience and Resistance to Disturbance in the Copper River Delta. Ph.D. Dissertation, Yale University, New Haven, CT.
- Patel-Weynand, T. 1996. *Forests and Poverty: A View towards Sustainable Development*. United Nations Development Programme Report, UNDP/SEED, New York.
- Patel-Weynand, T. and J. Gordon. 1999. Modeling Succession Patterns, Forest Health and Adaptation in Spruce Beetle (*Dendroctonus rufipennis* Kirby) Infested Ecosystems on the Kenai Peninsula, Alaska. In: *Stocking Standards and Reforestation Methods for Alaska: Proceedings of the Alaska Reforestation Council April 29, 1999 Workshop*. Agricultural & Forestry Experiment Station Misc. Publication 99-98. University of Alaska. Fairbanks, AK.
- Peck, J. and B. McCune. 1997. Remnant trees and canopy lichen communities in western Oregon: a retrospective approach. *Ecological Applications* 7(4): 1181-1187.
- Peck, J.E., W.S. Hong, and B. McCune. 1995a. Diversity of epiphytic bryophytes on three host tree species, Thermal Meadows, Hotsprings Island, Queen Charlotte Islands, Canada. *The Bryologist* 98(1): 123-128.
- Peck, J.E., W.S. Hong, and B. McCune. 1995b. Autoecology of mosses in coniferous forests in Central Western Cascades of Oregon. *Northwest Science* 69(3): 184-190.

- Perrings, C., C. Folke, K.G. Maler. 1992. The ecology and economics of biodiversity loss: the research agenda. *Ambio* 21: 201-211.
- Perrings, C.A., K.G. Maler, C. Folke, C.S. Holling, and B.O. Jansson. 1994. Biodiversity conservation and economic development: the policy problem. In: *Biodiversity Conservation* (C.A. Perrings, K.G. Maler, C. Folke, C.S. Holling, and B.O. Jansson, eds). Kluwer Academic Publishers. Dordrecht, The Netherlands.
- Perry, D.A. 1994. *Forest Ecosystems*. Johns Hopkins University Press, Baltimore, MD
- Perry, D. 1998. The Scientific Basis of Forestry. *Annu. Rev. Ecol. Syst.* 29: 435-466.
- Perry, D., M. Amaranthus, J. Borchers, S. Borchers, and R. Brainerd. 1989. Bootstrapping in Ecosystems: Internal interactions largely determine productivity and stability in biological systems with strong positive feedback. *Bioscience* 39 (4): 230-237.
- Perry, D. 1988. Landscape pattern and forest pests. *The Northwest Environmental Journal* 4(2): 213-228.
- Pike, L.H., R.H. Rydell, and W.C. Dennison. 1977. A 400-year old Douglas-fir tree and its epiphytes: biomass, surface area, and their distributions. *Can. J. For. Res.* 7: 680-699.
- Pike, L.H., W.C. Dennison, D.M. Tracy, M.A. Sherwood, and F.M. Rhoades. 1975. Floristic survey of epiphytic lichens and bryophytes growing on old-growth conifers in Western Oregon. *The Bryologist* 78: 389-402.
- Pimm, S. 1984. The Complexity and Stability of Ecosystems. *Nature* 307: 321-326.
- Poiani, K.A., B.D. Richter, M.G. Anderson, H.E. Richter. 2000. Biodiversity conservation at multiple scales: Functional sites, landscapes and networks. *BioScience* 50:2: 133
- Preston, F.W. 1962. The Canonical Distribution of Commonness and Rarity: Parts I and II. *Ecology* 43:185-215, 410-432.
- Probst, J.R. and T.R. Crow. 1991. Integrating Biological Diversity and Resource Management. *Journal of Forestry* 89:2:12-17
- Pulliam, H.R. 1988. Sources, sinks and population regulation. *American Naturalist* 132:652-661.
- Ralph, C., G. Hunt, M. Raphael and J. Piat (eds.) 1995. *Ecology and Conservation of the Marbled Murrelet*. Gen. Tech. Rep. PSWGTR-152. USDA, Forest Service, Pacific Southwest Research Station. Albany, California.

- Reich, P.B., J. Knops, D. Tilman, J. Craine, D. Ellsworth, M. Tjoelker, T. Lee, D. Wedin, S. Naeem, D. Bahaeddin, G. Hendrey, S. Jose, K. Wrage, J. Goth and W. Bengston. 2001. *Nature* 410: 809-812.
- Remmert, H. 1980. *Arctic Animal Ecology*. Springer-Verlag, Berlin, Germany.
- Rey, J.R. 1981. *Ecological Biogeography of Arthropods on Spartina Islands in Northwest Florida*. *Ecol. Monographs* 51:237-265
- Rochelle, J., L. Lehmann, and J. Wisniewski (eds.). 1999. *Forest Fragmentation: Wildlife and management implications*. Koninklijke Brill NV, Leiden, The Netherlands.
- Sala, O.E. 2001. Price put on biodiversity. *Nature* 412:34-36
- Sampson, N. 2000. *People, Forests and Forestry: New Dimensions in the 21st Century*. In: *Proceedings of the Forest Fragmentation 2000 Conference: Sustaining Private Forests in the 21st Century* (L.A DeCoster, ed.). The Sampson Group, Alexandria, VA.
- Salwasser, H. 1994. Ecosystem management: can it sustain diversity and productivity? *Journal of Forestry* 92(8): 6-10.
- Schowalter, T.D. 1995. Canopy arthropod communities in relation to forest age and alternative harvest practices in western Oregon. *Forest Ecology and Management* 78 (1/3): 115-126.
- Schowalter, T.D., B.A. Caldwell, S.E. Carpenter, R.P. Griffiths, M.E. Harmon, E.R. Ingham, R.G. Kelsey, J.D. Lattin and A.R. Moldenke. 1992. Decomposition of fallen trees: effects of initial condition and heterotroph colonization rates. In: *Tropical Ecosystems: Ecology and Management* (K.P. Singh and J.S. Singh, eds.) Wiley Eastern. New Delhi, India.
- Schowalter, T.D. and G.M. Filip (eds.) 1993. *Beetle-Pathogen Interactions in Conifer Forests*. Academic Press. London, UK.
- Schowalter, T.D. and P. Turchin. 1993. Southern pine beetle infestation development: interaction between pine and hardwood basal areas. *For. Sci.* 39(2): 201-210.
- Schowalter, T.D., W.W. Hargrove, and D.A. Crossley, Jr. 1986. Herbivory in forested ecosystems. *Ann. Rev. Entomol.* 31: 177-196.
- Schulze, E. and H. Mooney. 1993. Ecosystem function of biodiversity: a summary. In: *Biodiversity and Ecosystem Function* (E.D. Schulze and H.A. Mooney, eds.). Springer-Verlag. New York.
- Sedjo, R. and D. Botkin. 1997. Using forest plantations to spare natural forests. *Environment*:39:10:15-20

- Simberloff, D. 1999. The role of science in the preservation of forest biodiversity. *Forest Ecol. and Management* 115: 101-111.
- Simberloff, D. 1998. Flagships, umbrellas and keystones: Is single species management passe in the landscape era? *Biological Conservation* 83:247-257.
- Simberloff, D. and E.O. Wilson. 1969. Experimental Zoogeography of Islands. The Colonization of empty Islands. *Ecology* 50:278-296.
- Smith, R.L. 1990. *Ecology and Field Biology*. 4th ed. Harper and Row, New York. 922pp
- Smythe, K., C. Bernabo, T. Carter, and P. Jutro. 1996. Focusing Biodiversity Research on the Needs of Decision Makers. *Environmental Management* 20 (6): 865-872.
- Spies, T. Forest stand structure, composition, and function. In: *Creating a Forestry for the 21st Century* (Komb, K and J.A. Franklin, eds.). Island Press, Washington, DC).
- Spies, T and J.F. Franklin. 1995. The diversity of maintenance of old growth forests. In: *Biodiversity in managed landscapes* (Szaro, R.C. and D.W. Johnson eds.) Oxford University Press, New York.
- Stork. N.E. 1988. Insect Diversity: Fact, fiction and speculation. *Biological Journal of the Linnean Society* 35: 321-37.
- Thomas, C. 1990. What do real population dynamics tell us about minimum viable population sizes? *Conservation Biology* 4(3): 324-327.
- Thomas, J., W. Maser, and J. Rodiek. 1979. Edges. In: *Wildlife habitats in managed forest: the Blue Mountains of Oregon and Washington* (J. Thomas, ed.). USDA Forest Service Agricultural Handbook Number 553.
- Thompson, D.B., J.H. Brown, W.D. Spencer. 1991. Indirect Facilitation of Granivorous Birds by Desert Rodents: Experimental Evidence from Foraging Patterns. *Ecology* 72:852-863
- Tilman, D. 1999. The Ecological Consequences of Changes in Biodiversity: A Search for General Principles. *Ecology* 80(5): 1455-1474.
- Tilman, D., D. Wedlin, and J. Knops. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* 379: 718-720.
- Tilman, D. and J. Downing. 1994. Biodiversity and stability in grasslands. *Nature* 367: 363-365.
- Tinker, P. 1996. Inventorying and Monitoring Biodiversity. In: *Biodiversity, Science and Development: Towards a New Partnership* (F. di Castri and T. Younes, eds). Wallingford, UK.

- Turner, J. and J.N. Long. 1975. Accumulation of organic matter in a series of Douglas-fir stands. *Can. J. For. Res.* 5: 681-690.
- UNEP [United Nations Environmental Programme]. 1992. Convention on Biological Diversity, June 1992. United Nations Environmental Programme. Nairobi, Kenya.
- Vitousek, P. and D. Hooper. 1993. Biological diversity and terrestrial ecosystem biogeochemistry. In: *Biodiversity and Ecosystem Function* (E.D. Schulze and H.A. Mooney, eds.). Springer-Verlag. New York.
- Vitt, D.H., J.E. Marsh, and R.B. Bovey. 1988. Mosses, Lichens and Ferns of Northwest North America. Lone Pine Publishing, Alberta Canada.
- Vogt, K., J. Gordon, J. Wargo, D. Vogt, H. Asbjornsen, P. Palmiotto, H. Clark, J. O'Hara, W. Keaton, T. Patel-Weynand, and E. Witten. 1997. *Ecosystems: Balancing Science with Management*. Springer-Verlag, New York.
- Vogt, K., E. Moore, D. Vogt, M. Redlin, and R. Edmonds. 1983. Conifer fine root and mycorrhizal root biomass within the forest floors of Douglas-fir stands of different ages and site productivities. *Can. J. For. Res.* 13(3): 429-437.
- Wayburn, L.A., J.F. Franklin, J.C. Gordon, C.S. Binkley, D.J. Mladenoff, and N.L. Christensen, Jr. 2000. *Forest Carbon in the United States: Opportunities and Options for Private Lands*. Pacific Forest Trust, Inc. Santa Rosa, CA.
- Whittaker, R. 1972. Evolution and measurement of species diversity. *Taxon*. 21: 213-251.
- Wilson, E.O. (ed). 1988. *Biodiversity*. National Academy Press. Washington, DC.
- Woodwell, G. 1970. Effects of pollution on the structure and physiology of ecosystems. *Science*. 168: 429-433.
- WRI, IUCN, and UNEP. 1992. *Global Biodiversity Strategy: Guidelines for Action to Save, Study, and Use Earth's Biotic Wealth Sustainably and Equitably*. World Resources Institute Publications. Baltimore, MD.
- Yahner, R. 1988. Changes in wildlife communities near edges. *Conservation Biology* 2: 333-339.