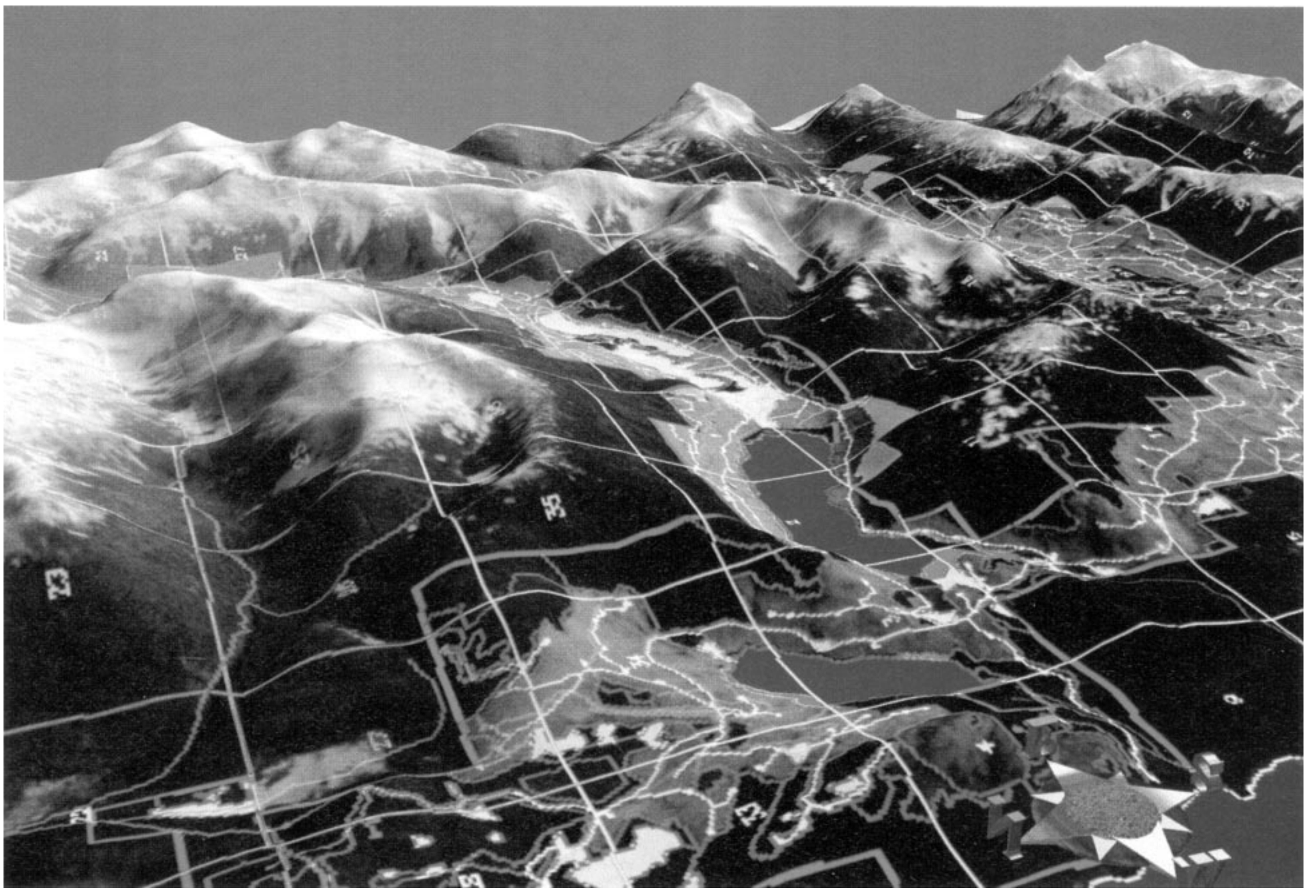
Performance Measures for Ecosystem Management and Ecological Sustainability



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Performance Measures for Ecosystem Management and Ecological Sustainability

The Wildlife Society

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Foreword

Presidents of The Wildlife Society occasionally appoint ad hoc committees to study and report on select conservation issues. The reports ordinarily appear as either a Technical Review or a Position Statement. Review papers present technical information and the views of the appointed committee members, but not necessarily the views of their employers. Position statements are based on the review papers, and the preliminary versions are published in The Wildlifer for comment by Society members. Following the comment period, revision, and Council's approval, the statements are published as official positions of The Wildlife Society.

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Cover: GIS 3-D map of Admiralty Island, Alaska, courtesy of Atterbury Consultants, Beaverton, Oregon.

Table of Contents

(*continued*)

Table of Contents (*continued*)

Figures and Tables

SYNOPSIS

Ecosystem management is a landscape planning approach to natural resource management that has the objectives of maintaining the full complement of biodiversity as well as ecosystem integrity while also integrating economic and social objectives. In this report we discuss ecological performance measures of ecosystem management that are also the basis for ecological sustainability. Performance measures are described based on a reference to the historical range of variability at 4 levels: landscape, ecosystem (ecological community), species, and genetic. A hierarchical approach to characterizing performance measures is presented. At the landscape level, measures relate to the mix of ecosystems that occur in the planning landscape relative to the mix that occurred under historical disturbance regimes. At the ecosystem level, each ecosystem can be described in terms of measures of composition, structure, function, and processes, and these measures can be related to the same measures under historical ranges of variability. At the species level, viability and population parameters can be compared to estimates of these same measures under historical ranges of variability. The genetic level addresses genetic content of populations, the occurrence of evolutionary significant units, and the rate of change in the genetic composition within a landscape. Examples are provided of performance measures at each of the 4 hierarchical levels.

INTRODUCTION

Management of natural resources is constantly changing as improvements are made to the understanding of ecological relationships, management methods, and the values of natural resources to diverse stakeholders. Today, managers are expected to plan for more than a single species or vegetation type and to evaluate the ecological and socioeconomic effects of their management activities. Management activities are expected to be conducted so as to assure the maintenance of ecological sustainability. New emphasis has been placed on the maintenance and enhancement of biological diversity and in maintaining or restoring ecosystem integrity, 2 generally accepted components of ecological sustainability. To address these challenges, many natural resource managers have embraced ecosystem management. Ecosystem management, in this report, is simply defined as a process of landscape planning that integrates specific ecological objectives with social and economic objectives.

The definitions, goals, and objectives of ecosystem management have been presented in various ways (Grumbine 1994, Kaufmann et al. 1994, Christensen et al. 1996, Keystone Center 1996, Meffe and Carroll 1997, Cortner et al. 1999). These reports generally agree, however, that ecosystem management involves planning land management activities to integrate and accommodate ecological, social, and economic objectives (Fig.1).

The ecological objectives of ecosystem management are often vaguely stated, but usually emphasize the need to conserve biological diversity and ecosystem integrity (Grumbine 1994, Kaufmann et al. 1994). Biological diversity is the variety of life and its processes (Keystone Center 1996). Maintaining and enhancing biological diversity involves the consideration of landscape, ecosystem, species, and genetic levels of organization. Ecosystem integrity refers to the system being complete, unimpaired, and sound. The concept recognizes the temporal aspects of ecosystem management, and emphasizes the need to consider ecosystem dynamics, processes, and functions. Our definition of ecosystem management is vague, but we distinguish ecosystem management from other efforts such as ecosystem approaches and ecosystem-based management in several ways. Ecosystem approaches and ecosystem-based management are terms that typically describe management activities that address and incorporate ecological processes or multiple species interactions across larger planning landscapes than often addressed in the past. However, they typically do not address the full obtainment of the ecological objectives of maintaining and enhancing biological diversity and ecosystem integrity, nor do they typically allow for the full integration of ecological

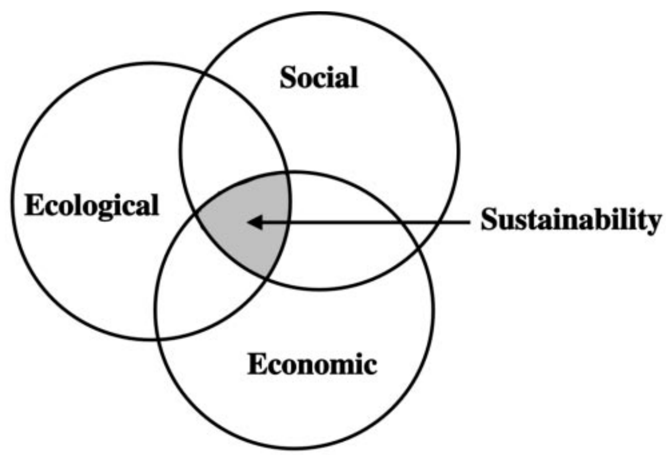

Figure 1. Ecosystem management is concerned with the intersection of ecological, economic, and social factors. The ecological sphere comprises the chemical, physical, and biological processes that maintain ecosystems. The management of populations of animals, plants, and microorganisms is included here. The social sphere encompasses cultural, political, and military considerations and values that influence how resources are used. The economic sphere refers primarily to material transactions among individuals, companies, organizations, and governments. Sustainable use is possible only where the different spheres intersect; consideration of only 1 or 2 spheres will exclude important constraints on the ability to achieve sustainable use.

objectives with social and economic objectives. Ecosystem approaches or ecosystem-based management are appropriate management activities, but ecosystem management incorporates a level of expectation and integration of its objectives that distinguishes it from other planning activities (Haufler 2000).

The challenge is how to tell whether ecosystem management is achieving ecological objectives while integrating social and economic objectives, or is it truly addressing ecological sustainability? Answering this question is difficult due to the confounding and interacting relationships within and among the objectives of ecosystem management (Box 1-1). If managers can measure how well ecosystem management is "performing," they will be more able to effectively plan future management and interact with, educate, and maintain their credibility among stakeholders concerned with natural resource management. At present, ecosystem management lacks well-defined performance measures (MacCleery and Le Master 1999).

Our primary objective is to review and suggest performance measures for ecosystem management. Because this is a report of The Wildlife Society, the focus is on the ecological objectives of ecosystem management—the maintenance and enhancement of biological diversity and ecosystem integrity. Social and economic objectives are equally important but the focus has been narrowed due to the expertise and primary interest of the sponsoring organization. Thus, the performance measures reviewed in this document are those that relate to the ecological objectives of ecosystem management, and are the foundations of ecological sustainability.

We describe a strategy for establishing wildlife performance measures to meet ecosystem management goals. Specific objectives are to:

- develop a framework for identifying appropriate performance measures for ecosystem management,
- describe selected performance measures at 4 levels of organization, and
- select and present examples of effective performance measures.

Box 1-1. The Role of Ecosystem Management Across Organizations.

Different organizations have different approaches to ecosystem management because of different perspectives, interests, and responsibilities. It is useful to visualize an organization's mission as one or more arrows impinging on the factors affecting the integration of ecological with social and economic objectives (Kaufmann et al. 1994) (Fig. 1). Thus, an organization's mission influences the relative emphasis it will place on the different spheres. Most organizations usually focus on only 2 spheres (Fig. 2). For example, the National Park Service is primarily concerned with the ecological and social spheres, although it is also affected by and must consider economic factors. Even an agency such as the Department of Defense (DoD), which has as its overriding mission support of national security, can contribute to sustainable resource use. Although ecosystem management is not the primary goal of the DoD, it is a necessary approach to managing DoD lands and waters (Goodman 1994) to sustain the training function of DoD. Regardless of an organization's mission, consideration must be given to the ecological sphere. Different organizations vary in the amount of attention paid to ecological factors; however, the social and economic spheres are supported by the ecological sphere. In addition to supporting social and economic outputs, the ecological sphere represents the maximum possible attainment of the objectives of maintaining or enhancing biological diversity and ecosystem integrity.

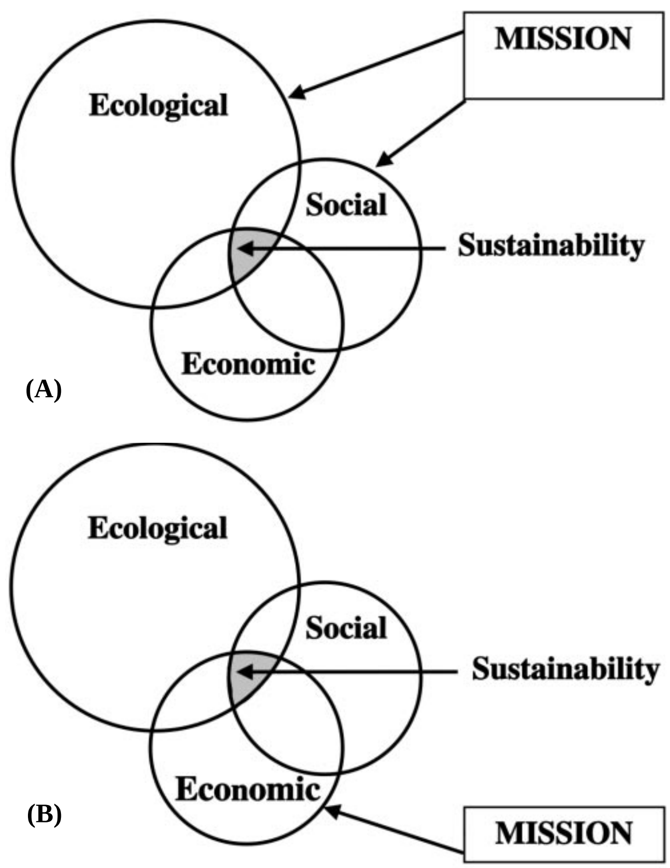

Figure 2. The mission of an organization affects the amount of weight given to ecological, economic, and social factors. Different organizations emphasize different spheres. (A) The mission of the National Park Service emphasizes ecological and social considerations. (B) The mission of private industry emphasizes economic considerations.

Ecosystem management is a valuable approach even for organizations that are not primarily involved with ecological objectives. Thus, we anticipate that this document will be useful for resource managers to whom ecosystem management is an overriding concern, and also for those who seek to manage resources in an ecologically sustainable manner in order to serve other objectives.

FRAMEWORK FOR SELECTING AND USING PERFORMANCE MEASURES

Prior to the adoption of ecosystem management, natural resource managers generally focused on species and products of particular interest or value for recreation or commodity production. Ecosystem management, however, attempts to conserve all biological diversity as well as ecosystem integrity. To accomplish this goal, ecosystem management needs to incorporate all levels of biodiversity organization. We suggest that a hierarchical approach is an effective way to approach and monitor this objective (Fig. 3). In this approach, we identify measures at 4 levels: landscape, ecosystem or ecological community, species, and genetic. Gaines et al. (1999) proposed a similar hierarchical organization. One advantage of this approach is that it may conserve poorly known species that would otherwise be overlooked (Franklin 1993a). This approach assumes that managing at higher levels of the hierarchy will conserve components at the lower levels. This has seldom been tested directly, however, and ecosystem managers have been criticized for operating on this assumption in the of absence supportive data (Simberloff 1998). For this reason, it is

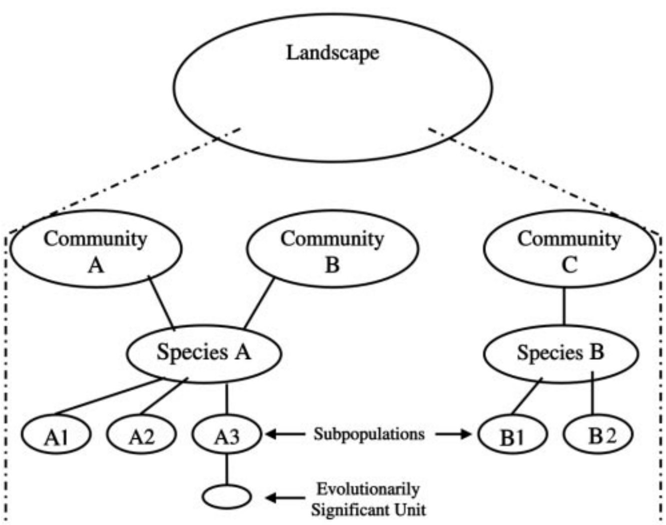

Figure 3. Levels of organization considered by ecosystem managers. Ecosystem management is concerned with conserving ecosystem diversity, species diversity, and genetic diversity at the level of the ecosystem, species, and subpopulation or evolutionarily significant unit respectively.

critical that monitoring be conducted at both the higher and lower levels of biological organization. We provide guidelines for identifying performance measures for ecosystem management at each level of biological organization. We describe specific attributes that can be monitored to assess the state of biological diversity or ecosystem integrity at each level of organization, and how these performance measures can be organized in a coherent framework. The method we outline involves using historical range of variability as a guide in the selection of standards against which current conditions are evaluated.

The term ecosystem has no specific scale associated with it. A puddle or the biosphere can be an ecosystem. Because of this range of scale of ecosystems, the term ecosystem management can be confusing, and defining performance measures can be equally confusing. However, attainment of the full integration of the objectives of ecosystem management does require the management of a relatively large landscape (e.g., 100,000's–1,000,000's ha). Within this landscape, contributions to the overall objectives can be made from many scales. Therefore, performance measures for ecosystem management should recognize these multiple spatial scales. A hierarchical framework allows such recognition.

We recommend approaching performance measures as quantifiable comparisons between desirable threshold or target levels determined from reference conditions and existing conditions (Kaufmann et al. 1994, Moore et al. 1999). Our view on threshold levels is that they represent reference points below which there is a likely unacceptable risk to ecosystem integrity or biological diversity. Performance measures may best be viewed as comparisons to appropriate standards that apply to a range of scales. This statement implies several components of performance measures. First, measures related to various scales need to be identified and quantified. Second, for each measure, an appropriate reference condition should be described for comparison purposes. Third, acceptable threshold or target levels developed from the reference conditions should be identified that will meet the specific ecological objectives of the ecosystem management initiative. Finally, current or planned future conditions can be compared to this threshold or target level and evaluated for their level of risk. The appropriate level of risk is ultimately a societal decision, but through an organized framework of performance measures, risks can be much more effectively articulated, quantified, and evaluated.

Establishing Reference Conditions: Historical Range of Variability

There are a number of possible strategies for addressing the conservation of biological diversity (Haufler 1999a,b). Each strategy (Table 1) has its own philosophical basis and resulting method of application. We suggest a strategy for meeting ecological objectives of ecosystem management that uses the historical range of variability as a reference point, and identifies both coarse and fine filter measures. By coarse filter (The Nature Conservancy 1982, Noss 1987), we mean an approach to landscape planning that focuses on ecosystems or ecological communities. Fine filter, in contrast, is an approach to landscape planning that focuses on species or groupings of species. We believe that this strategy has the advantages of being scientifically defensible and feasible to implement, and allows for the integration of social and economic objectives. Ecosystem management, based on this hierarchical framework of performance measures, will require substantial costs to fully implement. However, the costs of not using a comprehensive approach in terms of unorganized and often conflicting management directions, law suits and similar challenges to planning decisions, and the risk of not meeting the ecological objectives provide an economic and ethical imperative. Ecological objectives of ecosystem management can range from rates of biogeochemical cycling to the percentage of a landscape remaining in a particular plant association. Establishing reference conditions for ecological objectives is important for comparison purposes. A key concept for establishing reference conditions for ecosystem management is that of historical range of variability (Swanson et al. 1993, Morgan et al. 1994, Holling and Meffe 1996, Stanford et al. 1996, Landres et al. 1999, White et al. 1999), the variance of ecological parameters over a past time period. This strategy assumes that the range of conditions produced by past disturbance regimes has provided the diverse conditions that have supported the complex of ecosystems and species that comprise biological diversity. If the historical range of variability were maintained, then biological diversity would also be maintained (Poff and Ward 1989, Swanson et al. 1993, Morgan et al. 1994, Richter et al. 1996, and Poff et al. 1997). In effect, the historical range of variability in our approach defines the ecological sphere (Fig. 1) of ecosystem management. However, to meet the goal of ecosystem management, that of integrating ecological, social, and

Table 2-1. Approaches to conservation of biological diversity (after Haufler 1999a).

Approach	Philosophy	Method of application
Bioreserve	Human effects have led to loss of biodiversity. Conservation of biodiveristy is best achieved by minimizing human activities across a system of core reserve areas with surrounding buffers and corridor connections.	Delineate a series of core bioreserve areas across the landscape that are restricted from human activity and connect these with a similar set of corridors.
Coarse filter—habitat diversity	If a diversity of habitat conditions can be maintained across a planning landscape, then biodiversity will be maintained.	Identify different successional conditions, or other indicators of temporal dynamics, and assure that all successional conditions are provided across the landscape.
Coarse filter—historical range of variability	Biological diversity evolved with and adapted to the conditions produced as a result of the complex of historical disturbances. Maintaining a landscape within this historical range of variability for disturbances will maintain biodiversity.	Determine historical disturbance regimes and manage landscape to stay within the historical range of variability of those disturbances.
Coarse filter—historical range of variability-based	Biological diversity depends upon the complex of conditions produced as a result of the complex of historical disturbance regimes, but can be maintain with a representation of those conditions.	Determine complex of conditions produced by historical disturbance regimes, and manage to maintain representation of this full complex of conditions.
Fine filter	Species are the basic units of biodiversity, so if all species can be maintained, biodiversity will be maintained.	Develop approaches that will account for the viability of all species. May use guilds, life forms, umbrella species, indicator species, or other such approaches.

economic objectives, historical ranges of variability can rarely be the desired condition for a planning landscape. Rather, an appropriate representation of the historical range of variability, at all levels of biological organization, is needed so that ecological objectives can be met as well as providing for society. This philosophy forms the basis for our approach to performance measures for the ecological objectives of ecosystem management.

The use of historical range of variability involves identifying the types of disturbances that influenced ecosystems over time, and the magnitude, periodicity, and extent of their influences. These disturbances operated at all spatial and temporal scales; nevertheless the historical range of variability can be described and quantified in a consistent manner and can serve as a tool of establishing reference conditions for ecosystem management performance measures. Historical range of variability is often used to characterize the magnitude, frequency, and intensity of disturbances, and the resulting ecosystem types at the landscape level. However, the concept also applies to variables at all levels of organization, such as tree density, population size, water temperature, colonization rate, or gene flow (Dahms and Geils 1997). We regard the historical range of variability as the unifying principle that is essential for defining ecologically meaningful performance measures.

Morgan et al. (1994) recommended that "historical range of variability should be assessed over a time period characterized by relatively consistent climatic, edaphic, topographic, and biogeographic conditions." Steele (1994) recommended 100–400 years as an appropriate time span in North America. The ranges of historical variability in ecosystem structure, composition, and function thus serve as a reference for the period immediately prior to major European influence. Miller and Woolfenden (1999) discussed how the Little Ice Age spanned much of the later part of the last millennium, thus complicating the use of the time period recommended by Steele (1994). However, Miller and Woolfenden (1999) also pointed out that this does not negate the merits of the historical range of variability. The historical time span should describe conditions prior to major European settlement and allow for understanding of the substantial change in landscapes that occurred subsequently. We are not setting up a dichotomy between people and nature, nor are we suggesting that the period before the arrival of Europeans was devoid of human influence in North America, as clearly Native Americans induced changes in North America for the last 12,000 years (Bonnicksen et al. 1999, Engstrom et al. 1999). On the contrary, we recognize that people have exerted important effects on past conditions. However, due to the substantial ecological changes that occurred after the arrival of Europeans, we suggest that the period prior to European impact can serve as an important reference, even though this period was clearly not "natural" in the sense of lacking people, nor static in terms ecosystem and species dynamics.

We also do not suggest that the best management is that which maintains conditions as close to the historical range of variability as possible. To do this would over-emphasize the importance of the ecological sphere of the 3 objectives of ecosystem management. We do think that appropriate representation of conditions supported historically is the best way to assure the attainment of the ecological objectives and ecological sustainability. We acknowledge that not all managers or scientists are ready to accept the representation of historical range of variability approach as the most effective way of addressing ecosystem management. However, we find no other approach that is as effective. Fine-filter or species-based approaches cannot feasibly account for the thousands of species that ecosystem management efforts need to address. Course-filter approaches that are not based on the historical range of variability provide little assurance that they can meet the needs of all species as well as meeting ecosystem integrity objectives, as there is no consistent basis for reference conditions. "Natural" conditions are advocated by some, but what is natural if not defined by what has been present in terms of ecosystems, species, and genetics over a defined time-period prior to recent major human modifications? For these reasons, we strongly suggest that the representation of historical range of variability approach is the most effective way of integrating the complex set of objectives addressed by ecosystem management.

Historical range of variability requires understanding and quantifying past disturbances and ecological processes. Evidence of these is often lacking, and the use of historical ranges of variability is often criticized because this information can be either difficult or impossible to collect. However, this does not reduce the relevance and appropriateness of the scientific basis of this approach, nor preclude its use. In many instances, where historical information is not available, comparisons will need to be made with existing reference sites, selected based on their similarity to the desired historical conditions. Alternatively, historical conditions can be modeled. Sources of information on historical conditions are discussed in Box 2-1.

Establishing Threshold or Target Levels

Once information about historical conditions has been obtained, management thresholds or targets related to historical range of variability will need to be selected so that success in achieving these can be measured. The thresholds or targets selected are scale related. For example, at the landscape level, a representation goal expressed as a threshold might be a percentage of the maximum area of each ecosystem or community type that occurred under historical range of variability (Haufler et al. 1999). For each ecosystem, the management target for representation of conditions of the ecosystem might be expressed in terms of its composition or structure, and might be the mean of the historical range of species composition for stands of that type of ecosystem. For aquatic ecosystems, the acceptable risk for the range for variation in flow rates of a river might be set to a certain percentile of historical flow rates.

Threshold levels or targets should be identified for each performance measure at each level of the performance measure hierarchy. These should identify an acceptable level of risk to various ecosystem elements, functions, or processes. Failure to maintain these threshold levels entails a high probability that the elements of biological diversity or ecosystem processes in question will fail to fulfill their roles in maintaining viable populations of species, nutrient cycling, or other functions. Likely outcomes may be additional listings of species, making coordinated management much more difficult, and failing to meet

Box 2-1. Sources of Information on Historical Conditions.

Information on historical ecology can be obtained from several sources, including paleoecology, archives and documents, long-term ecological research, and time-series data of environmental measurements (Kaufmann et al. 1994; Swetnam et al. 1999, Periman et al. 1999, Engstrom et al. 1999). Archival records can be divided into natural archives—those that have been recorded by natural processes such as sedimentation, animal activity, or growth—and documentary records. Deposits of pollen, charcoal, and phytoliths are examples of records preserved in sediments; packrat middens result from animal activities; and tree rings, coral layers, and annual growth rings in the bones of seasonally inactive animals are records of growth patterns (Swetnam et al. 1999). Documentary archives include written descriptions by surveyors (Galatowitsch 1990), settlers, explorers, naturalists, and ethnographers; tabular data; photographs (Hastings and Turner 1965; Skovlin and Thomas 1995); and maps. Modern genetic techniques have made it possible to retrieve the DNA in museum specimens. Where museums have enough specimens from one or more populations (>15 of each) and when the species is considered potentially informative because of ecological considerations, historical genetic baselines can be established.

At the ecosystem level, paleoecological data are useful for defining reference conditions for ecosystem composition and for determining rates of species expansions and contractions. Historical tree density and other tree measurements can be determined from early surveys such as general Land Office Public Land Survey (Almendinger 1996), early cruise information (Haufler et al. 1996), or photographs. In addition, historical stand structural conditions may be measured through fire scar analyses (Agee 1993, Covington et al. 1997) or they may be modeled (Harrod et al. 1998). Features of historical disturbance regimes (i.e., type, frequency, extent, intensity) have been estimated from a variety of sources including fire histories (Heinselman 1973, Crane and Fisher 1986, Sloan 1998), wind event records (Canham and Loucks 1984, Foster 1988) lake deposits (Clark 1988) insect outbreaks (Schowalter 1985, Knight 1987, Swetnam and Lynch 1993), landslides and debris flows (Swanson and Dryness 1975, Lamberti et al. 1991), and beaver activity (Ives 1942). Networks of fire histories can be aggregated across spatial scales to characterize regional fire regimes (Swetnam et al. 1999). Richter et al. (1996, 1997) described methods for characterizing historical variation in hydrological data using existing records or reconstructing or estimating data where such records are unavailable. A variety of innovative techniques have been developed to obtain data on historical values for ecological parameters. For example, studies with stable isotopes can to used characterize past diets of museum specimens (Hilderbrand et al. 1996, Jacoby et al. 1999).

The record of the past is often incomplete and fragmentary. This does not lessen the value of information on historical conditions, but it does suggest that information on historical ecology should be interpreted with caution and with an awareness of its limitations (Swetnam et al. 1999). Even if past conditions can be reconstructed with a fair degree of certainty, there is still the problem of determining whether changes over time are due to human impacts or other causes. In addition to land-use history, factors such as climate change, environmental gradients, and unique site characteristics can influence observed patterns. Long-term reconstructions from multiple sites can help to disentangle these effects (Swetnam and Baisan 1996, Millar and Woolfenden 1999).

When historical sources of information are lacking, comparisons can be made to existing reference areas. These are areas with minimal anthropogenic effects that can span the entire range of historical disturbance. Such areas may not exist for some ecosystems.

society's expectations of ecological sustainability. The level of risk that is acceptable is largely a political decision, influenced by social and economic considerations, as well as a scientific evaluation of the ecological objectives at various temporal and spatial scales.

A Hierarchical Organization of Ecosystem Performance Measures

To assess how well ecosystem management is succeeding at conserving biodiversity and ecosystem integrity, it is necessary to monitor at multiple levels. Several hierarchical frameworks for monitoring have been proposed (e.g., Noss 1990, Hunsaker and Carpenter 1990). We provide guidelines for relating hierarchical monitoring to the concept of historical range of variability.

<u>The Landscape Level</u>

At the landscape level, we suggest that the relevant performance measures for ecosystem management are the amounts, sizes, and configurations of ecosystems or ecological communities and the frequency, magnitude, and duration of disturbances influencing these ecosystems. Ecological communities are repeatable assemblages of species and their interactions, and are defined by any of a large number of classification systems. When these communities are further related to the abiotic environment that supports them, they are ecosystems, as defined by classification systems that include such physical relationships. A landscape perspective is critical for understanding the distributions, disturbances, and functions of ecosystems, as well as restoration needs (Kenna et al. 1999). Planning based on providing a mix of ecosystems has been termed a coarse filter for conservation (The Nature Conservancy 1982, Noss 1987). The coarse filter can be used for setting thresholds for adequate ecological representation or, in other words, the amounts of each ecosystem needed in the landscape to address the ecological objectives (Kaufmann et al. 1994, Haufler 1994). Using this approach, a coarse filter identifies the ecosystems to be represented and then performance measures at genetic, species, and ecosystem levels are used to assess whether or not the components, structures, and functions of these ecosystems that occurred under historical range of variability are sufficiently represented. These additional levels function as a check on the sufficiency of adequate ecological representation at the landscape level. Thus, landscape level performance measures define reference and threshold levels for the areas of the ecosystems identified by the coarse filter.

The coarse filter should identify discrete, mappable ecosystems that can describe both existing and potential ecosystem conditions (Carpenter et al. 1999). This can be done through a series of coarse filters covering forested ecosystems, shrub and grassland ecosystems, riparian and wetland ecosystems, and aquatic ecosystems (Haufler et al. 1996, 1999).

This coarse filter approach to meeting ecological objectives assumes that a set of ecosystems can be described and delineated across planning landscapes. The debate over the use of the community concept has been ongoing for many decades (Mueller-Dombois and Ellenberg 1974). This debate continues today, and now extends beyond plant communities to animal distributions (Hansen and Rotella 1999). While the role and complexities of gradients, as expressed by Whittaker (1970) and others, is recognized and is critical to understanding niche relationships of species, land management planning requires the ability to delineate discrete areas with similar responses to management activities. The coarse filter approach accommodates this need, but the classification needs to be carefully applied to produce meaningful and effective ecosystem descriptions.

The coarse filter approach for landscape level performance measures should estimate the area of each ecosystem needed for adequate ecological representation based on various identified risks. Ecosystem area is a critical measure for evaluating the success of ecosystem management because measures at other levels of the organizational hierarchy link to this measure. Landscape level performance measures should identify the minimum acceptable amount of each ecosystem that was identified in the coarse filter as having occurred under historical disturbance regimes. The minimum amount must be provided at all times for the representation of ecosystems to sufficiently address an acceptable level of risk.

<u>The Ecosystem Level</u>

In this report, we use the term ecosystem to refer to a discrete area (e.g. type of forest stand, sward, stream reach) that can be characterized by its plant and animal communities as well as the associated abiotic conditions. Ecosystem is a more inclusive term than community. Communities are described as any group of interacting populations. This definition limits the use of the term "community" to associations of biotic organisms: the plants and animals interacting in an area. However, animal communities cannot exist without plant communities, and plant communities cannot exist without energy and nutrients assimilated from a site. The interaction between biotic communities and abiotic factors such as energy and nutrients defines an ecosystem. Odum (1971) defined ecosystem as "any unit that includes all of the organisms in a given area interacting with the physical environment so that a flow of energy leads to a clearly defined trophic structure, biotic diversity, and material cycles."

The representation of historical range of variability approach is based on the assumption that risks to ecosystem integrity and biological diversity can be minimized by identifying adequate amounts of inherent ecosystems in a landscape to provide the building blocks of biological diversity. Thus, the ecosystems described by the coarse filter are the elements around which planning decisions for ecosystem integrity and biological diversity are made. The ecosystems identified for representation at the landscape level must meet certain requirements defined by the historical range of variability. The coarse filter assumes that these designated ecosystems have conditions within them sufficiently similar to the historical range of variability for that particular ecosystem to provide for the occurrence of the proper array of species, processes, and functions.

The landscape level defines the amounts of each ecosystem that need to be represented to address threshold requirements for ecological sustainability. The ecosystem level defines features such as composition, structure, and function of an ecosystem that must be present if a particular site can be considered to be contributing to a representation threshold. For a forest stand or stream reach to qualify for this criterion, it needs to be substantially within the historical range of variability for all conditions of that type of ecosystem. For example, at the ecosystem level, performance measures may include species richness and appropriately identified threshold levels relative to historical species richness. Threshold levels for each measure can be set to indicate when a stand or reach, representing a particular ecosystem, has departed from the historical range of variability so that the ecosystem no longer serves its purpose in providing representation. For example, if a stand in northern Michigan is designated to represent a specific late-successional beech-maple forest ecosystem, it should have rates of nutrient cycling that are within threshold values for the historical range of variability for this cycling. It also should have a certain species composition of trees and understory vegetation, defined by the historical range of variability for this measure. If it does not have these characteristics, then this stand cannot be considered to adequately represent the late successional beech-maple forest ecosystem, and its area would not count toward representation at the landscape level. Every stand or reach does not need to be sampled to confirm its appropriate composition, structure, or function, but rather selected stands or reaches should be sampled to check on the effectiveness of the planning and implementation process.

Many, or even most ecosystems within a landscape will be outside of the historical range of variability. These ecosystems can still contribute to ecological goals by providing habitat conditions, soil or water holding functions, or other benefits in contributing to the environmental matrix in which representative communities occur.

The reference to historical range of variability can be used as a measure of deviation away from reference conditions, and may also help identify points beyond which an ecosystem may not be able to return to historical functions or composition without major restoration efforts. Some sites in the landscape may be so altered by human activities that there is a low probability of them ever returning to conditions similar to the historical range of variability. Dramatic losses of soils, changes in water tables, alteration of stream channel conditions or flow regimes, or any number of additional possibilities could cause such changes in stand conditions.

<u>The Species Level</u>

Species are critical components of biological diversity, and may be the best understood level for some management purposes. However, the sheer number of species and the failure of a fine-filter approach to directly measure ecosystem integrity make species a poor level as a primary focus for performance measures of ecosystem management. The assumption of the representation of historical range of variability approach is that a properly represented coarse filter will provide the habitat conditions to support all species that historically occurred within an appropriate landscape. Performance measures at the species level provide a check on the proper functioning of the represented coarse filter (Haufler et al. 1996, 1999). At the species level, various measures of historical range of variability are of interest. For example, the historical range of population size and fitness of species present within the planning landscape could be important measures. The distribution of the species under historical range of variability may also be important in order to understand the extent of range contractions or expansions. Of particular interest is the distinction between populations within a landscape that were consistently viable under historical disturbance regimes and those that historically had inconsistent viability and may have been supported by immigrations from neighboring landscapes. Populations that were not consistently viable in the past should not be expected to be viable at the present or in the future for that particular landscape. For those species that had consistently viable populations under the historical conditions, a performance measure might be the range of the size of a viable population. Further, population structure and linkage capability might be identified as important measures at the species level as a check on the representation of the coarse filter.

In the representation of historical range of variability approach, species that did not occur within the landscape are not considered as contributing to performance measures for the ecological objectives of ecosystem management or ecological sustainability. Such species may have management goals and objectives at the present or in the future, but management of these species falls within economic or social objectives of the landscape, not the ecological objectives of maintenance and enhancement of biological diversity and ecosystem integrity.

Additionally, it should be noted that not all species requirements may be met by the representation of historical range of variability approach. This approach should provide for adequate habitat conditions to support all native species. However, species limited by factors other than habitat, such as pollutants, high direct human-induced mortality rates, or effects of exotic diseases will need specific management focus in addition to the conditions provided by the ecosystem management measures.

An alternative use of the species level can be the development of conservation strategies for species of concern, especially in landscapes where complete ecosystem management implementation is not possible. In these situations, conservation strategies for those species of concern caused by habitat loss may address the greatest ecosystem representation needs even without the complete development of a coarse filter. Use of such conservation strategies should be viewed as a temporary action, as a focus on species of concern will not address habitat for all species, nor will it address ecosystem integrity.

<u>The Genetic Level</u>

The number of evolutionarily significant units (ESUs) for each species within a landscape is an important consideration. For most species, functional planning landscapes will contribute to only one evolutionary significant unit, but in some landscapes certain species may contain more. The genetic composition of a species, and its flow of genetic information among subpopulations and to future generations, should be within the historical range of variability. Genetic analysis can also indicate if any genetic bottleneck has occurred in the past that may threaten the future viability of a species, even with appropriate ecosystem characteristics and amounts being present. These types of questions can be addressed at the genetic level.

Selection of Appropriate Measures

The various hierarchical levels and the complexity of measures within each level make the identification of performance criteria a complex task. Yet, the situation is simplified by the fact that in most cases it is not necessary to address all levels and measures. For example, if landscape level measures are selected for a given ecosystem management initiative, they will define the range of ecosystems that could be considered. A few key ecosystems would probably stand out as most appropriate for ecosystem level measures. These ecosystems would then need to be evaluated to identify "essential ecosystem components" (Harwell et al. 1999) in order to identify the most important ecosystem level measures. If exotics are a major concern, a set of compositional and invasive species measures might be most appropriate. If acid rain is a significant concern, measures of biogeochemical cycling might be highlighted. At the species level, population viability of selected species could be assessed as a check of the representation of the coarse filter. Selecting a number of species to verify the coarse filter would be appropriate. If monitoring at the species level indicates that appropriate population interaction is occurring, then genetic measures such as heterozygosity may not be an issue. Isolated subpopulations of a species could be evaluated for their evolutionary significance.

Performance Measures for Highly Modified Landscapes

Areas outside the historical range of variability can be thought of as the matrix in which representative areas are embedded (Franklin 1990, 1993b). If managed appropriately, the matrix can facilitate processes that maintain the historical range of variability for areas that have the needed qualities for ecosystem representation. Conversely, management without regard to ecosystem considerations can create a hostile matrix that decreases the likelihood of meeting ecosystem management objectives. A hostile matrix may cause environmental conditions that are dangerous or intolerable for native organisms; export toxins, weeds, and sediments; and contribute to the degradation of ecosystem processes and loss of ecosystem components (for example through soil erosion). A favorable matrix does not export harmful substances, and may instead be a source of propagules of native organisms. A favorable matrix can perform some or all of the following functions:

- Providing habitat for some species of plants and animals. This function is enhanced by the provision of the structural habitat features required by native species.
- Allowing organisms to disperse or migrate through the matrix. Passage through the matrix is critical for processes such as interpatch colonization (Brown 1971, Weddell 1991) and augmentation of declining populations (Brown and Kodric-Brown 1977).
- Mimicking natural disturbances and promoting recovery after disturbances.

The degree to which modified ecosystems succeed in performing these functions can be measured with the same tools that are used to evaluate the performance of less modified ecosystems at the ecosystem and species levels.

Managers who are responsible for areas that are highly modified and cannot contribute to adequate ecological representation of ecosystems at the landscape level may nevertheless seek to manage in ways that contribute to ecosystem management objectives. Croplands, urban parks, golf courses, pastures, and similar areas fall in this category. Although these areas are clearly outside an ecosystem's historical range of variability and may exceed the thresholds at which restoration is normally possible, they can perform some valuable functions. The framework we have described above suggests how this can be done.

ECOSYSTEM MANAGEMENT PERFORMANCE MEASURES

Landscape Level Measures

Overview: What Are the Critical Questions at the Landscape Level?

At a landscape level, the critical question is: Are the ecosystems that comprise the coarse filter that characterizes the historical landscape adequately represented and appropriately arranged across the landscape? Another key question is: Are the disturbance regimes that resulted in historical structures, components, and processes functioning within the landscape, and at what scales? The two perspectives are connected by the fact that historical disturbance regimes played a pivotal role in determining ecosystem structure, function, composition, and pattern, and therefore resulted in the distribution and arrangement of ecosystems that prevailed in the past.

Performance Measures at the Landscape Level

Ecosystem Area (Adequate Ecological Representation with a Coarse Filter). Ecosystem area is an important performance measure for ecosystem management and ecological sustainability. Adequate ecological representation of ecosystems identified by a coarse filter is a performance measure that compares the area of the landscape currently occupied by each ecosystem to its extent under historical conditions and to a threshold.

To apply this coarse-filter framework, a comprehensive and practical coarse filter needs to be developed. This coarse filter should characterize the planning landscape in sufficient detail to identify a complete suite of ecosystems that will allow for ecosystem integrity and biological diversity to be maintained if all communities are adequately represented. If the classification of ecological communities lacks sufficient resolution, then a management plan might provide for each defined community and yet fail to provide for all species or processes. For example, if a forested landscape is broadly classified into structural stages, with one structural stage designated as old growth without regard to different types of old growth, then maintaining a potential threshold of a certain percentage of the forested landscape as old growth might fail to meet biodiversity objectives. If the landscape were mountainous and only high-elevation old growth was provided, then all species and ecosystem processes dependent on conditions in low-elevation old growth forests would be excluded, and the ecological objectives of ecosystem management and ecological sustainability would not be met. At the other extreme, a coarse filter at a very fine resolution could define the optimal habitat requirements of every species or the optimal conditions for all processes. Such a filter would most likely define a huge number of ecosystems and would be too complex to be managed effectively. Thus, the resolution of ecosystems in the coarse filter is a critical decision at the landscape level. The classification system for ecosystems must be fine enough to be biologically meaningful yet not so fine as to be infeasible to implement into a planning process.

To include enough of each ecosystem to provide for the ecological objectives, a planning landscape must be fairly large. One factor to consider is the area needed to provide sufficient amounts of each identified ecosystem throughout all of their historical successional dynamics to maintain species and processes linked to that ecosystem. Another factor to consider is that if a very large landscape is selected, then classifying ecosystems at an adequate resolution to differentiate their ecological features will result in a large number of ecosystems to track through an ecosystem management process (Haufler et al. 1999, Kernohan and Haufler 1999).

The coarse filter provides a classification framework for defining performance measures of ecosystem management and ecological sustainability at the landscape scale. Because ecological, social, and economic objectives are all to be considered, human influences will be an important component of the planning landscape. The question then becomes: How much of each ecosystem in the coarse filter is needed to meet ecosystem integrity and biological diversity objectives?

A properly defined coarse filter is one that delineates ecological sites occurring across a landscape that were subjected to similar historical disturbance regimes and supported a similar array of ecosystems through a disturbance response trajectory. In terrestrial systems, Daubenmire's (1968) habitat typing system is an example of a classification system that can be used in site delineation, with each habitat type or grouping having similar disturbance regimes and late successional or potential vegetation conditions. Habitat typing has been used for site characterization in a coarse filter in Idaho by Haufler et al. (1996, 1999) and at a slightly coarser scale for the Interior Columbia River Basin (Quigley and Arbelbide 1997). Based on this classification of ecological site complexity, temporal dynamics were then described by delineating stages within successional trajectories. Other classification systems or biophysical delineations of site complexity could be equally effective in defining and delineating ecological sites, as long as the influence of historical disturbance regimes was included in the classification system. The key point here is that an effective coarse filter for use at the landscape level of the representation of historical range of variability approach must integrate ecological site complexity with temporal delineation of ecosystems resulting from historical disturbance regimes.

Once a coarse filter has been identified, a threshold for representation must be selected. The amounts of each ecosystem present compared to the threshold level derived from the historical range of variability then become the performance measures at the landscape level. A sufficient amount of each ecosystem, at least to meet the threshold levels, needs to be distributed within the surrounding matrix and evaluated as to whether designated areas are ecologically functioning as needed to represent each ecosystem. While general rules for designating representation of the coarse filter are desirable, these must factor in such considerations as the historical rarity of the community being represented, and the types and severity of disturbances that influenced the ecosystem under historical disturbance regimes.

Spatial Configurations of Landscapes. A number of indices have been proposed for evaluating ecosystem integrity based on the spatial properties of landscape components (e.g. O'Neill et al. 1995, 1997, McGarigal and Marks 1995, Moyle and Randall 1996, 1998). These deal with properties that emerge at the landscape level (O'Neill et al. 1988), such as the size, shape, and arrangement of ecosystems. These properties, in turn, influence processes at the species level through their effects on movement among subpopulations, and habitat quality through their effects on the amount of habitat that is influenced by edges. FRAGSTATS, a spatial analysis program for quantifying landscape structure includes metrics that reflect properties such as patch size, density, shape, interspersion, and contagion (McGarigal and Marks 1995).

Landscape measures provide information on landscape level properties, such as edge and isolation, which are not apparent from data on ecosystem area alone. They are relatively easy to apply, especially in combination with geographic information systems. A disadvantage, however, is that they must be applied carefully (McGarigal and Marks 1995). They provide information on existing conditions but not on the ecological consequences of those conditions; therefore, they do not guide the selection of appropriate standards. In addition, landscape level metrics by themselves do not provide information on whether species and ecosystems are thriving. For this, as with other landscape level measures, assessments at the ecosystem, species, and genetic levels are required.

Although these metrics do not specifically incorporate information on historical variability, they can be used to evaluate impacts to landscapes resulting from changes in land use, diversions of surface water, and so on. When placed in a historical context, therefore, these indices can provide information on the degree to which current landscape conditions deviate from pre-impact situations. Spatial measures of landscapes such as quantification of edge are most meaningful when put in the context of change from landscape conditions produced under historical disturbance regimes (Sallabanks et al. 1999).

Ecosystem Level Measures

<u>Overview: What are the Critical Questions at the Ecosystem Level?</u>

The coarse filter described at the landscape level is used to define ecosystems and provide sufficient representation and configuration of these ecosystems. When applying performance measures for ecosystem management it is necessary to demarcate physical boundaries around which we can apply measures. Throughout this report, we will refer to two different physical components of ecosystems; the ecological site (abiotic factors that characterize the ability of areas to support similar plant and animal communities) and the stand or reach (characterized by the existing plant and animal communities). We further define ecosystems by the processes (temporal dynamics) affecting them. Stand (terrestrial or semi-terrestrial) and reach (aquatic), or other similar descriptors, refer to an existing biologically homogeneous unit, whereas site refers to the inherent ecological potential of a given area (e.g., as conceptualized by such classification as habitat types for forested ecosystems). These ecosystem components (e.g., stand, reach) can be described by their composition, structure, and function as well as by processes affecting them. The measures at the ecosystem level are therefore defined by these descriptors.

Ecosystem level measures address the question of what are the appropriate compositions, structures, and functions of each ecosystem for it to be considered as representing that ecosystem at the landscape level. Ecosystem level measures define the acceptable range of conditions for any stand or reach in a landscape to qualify as suitable for contributing to the amount needed for adequate ecological representation (i.e., the coarse filter). Therefore, historical range of variability must be estimated for selected measures at the ecosystem level to determine if a stand or reach contributes to adequate ecological representation of that particular ecosystem. In addition, ecosystem level measures may describe areas outside the historical range of variability. These communities may serve as evaluation units of matrix conditions (Franklin 1990, 1993b).

<u>Performance Measures at the Ecosystem Level</u>

To function in the hierarchical framework presented in this volume, ecosystem measures must describe the limits of an ecosystem to ensure adequate representation at the landscape level. Because ecosystems are defined by the interaction of biotic and abiotic factors, it may be necessary to consider several measures (i.e., composition, structure, function, and process). Likewise, it may be necessary to estimate several parameters within one measure to accurately assess ecosystem management and ecological sustainability at the ecosystem level. For example, plant species diversity can be estimated as a parameter of ecosystem composition for both current conditions and historical range of variability. The diversity index for each time period may be similar; however, current diversity may reflect an increase in exotic species. This difference may go undetected unless another parameter, e.g., a ratio of exotic to native species, was estimated as well. Although we will give examples of parameters estimated from data for each measure, actual implementation may warrant combinations of several parameters across a variety of measures. Conversely, with increased knowledge of ecological relationships, managers may find that measures of one ecosystem component are adequate indicators of other ecosystem components.

Ecosystem Composition. Ecosystem composition under historical disturbance regimes was determined by a complex set of interacting environmental factors such as climate and soil, competing species, and the type and regularity of disturbances. Effective measures of ecosystem composition describe the absolute or relative abundance of species or groups of species on a site. Because identifying all organisms in an ecosystem is rarely possible, generally organisms in a given taxa (e.g., birds, mammals) are measured or a species guild is used. Therefore, composition is often measured as richness (i.e., diversity) or relative abundance of species or groups of species.

A variety of indices for quantifying the similarity of biotic communities exist (see Morrison et al. 1992) including species richness, Odum's similarity measure (1950) and Kendall's tau coefficient (adopted by Ghent 1963). Such diversity indices reflect community composition as measured through species richness, equitability, and sometimes density (Morrison et al. 1992). Diversity indices are useful parameters of community composition when they can be compared to an index of historical conditions. Rule sets must be applied to judge comparisons of this type. For example, to determine if existing composition for a particular stand or reach is within the historical range of variability, an appropriate rule might be one standard deviation around the mean historical diversity index across stands. By estimating both existing and historical conditions and invoking this simple rule, the existing stand is assessed as to whether or not it can contribute to adequate ecological representation.

Diversity indices may not be affected by changes in species composition. For example, if an exotic species replaced a native species, most diversity indices would not reflect this change. Therefore, it is important to estimate a variety of parameters and use several measures when evaluating performance measures for ecosystem management or ecological sustainability. To continue the above example, a manager may suspect that an invasion of exotic species has taken over the ecosystem under investigation. Therefore, another parameter to consider would be the ratio of exotics to native species. Native species are those known or expected to have occurred in the stand or reach under historical conditions. If the proportion of exotics were at an acceptable level (e.g., less than 10% of the importance value for plants in the stand), then the stand might be deemed suitable, in terms of this measure, to qualify as representative.

For aquatic ecosystems, composition of aquatic macroinvertebrates might be used as a compositional measure. Various biotic integrity indices have been developed (Box 3-1). For these to work as ecosystem management performance measures, they must be evaluated relative to similar indices under historical conditions. This generally requires comparisons to reference areas, as historical range of variability for such indices may be impossible to derive. It is important that reference areas be identified that span as much of the range of the ecosystems that occurred under historical disturbance regimes as possible.

Ecosystem Structure. Ecosystem structure includes the presence and arrangement of physical structures in three-dimensional space. These biotic structures can include features such as large organic debris and pool to riffle ratio in aquatic systems, and stem density and diameter of live and dead trees or coarse wood debris in terrestrial ecosystems (Harmon et al. 1986). Structural features furnish microhabitats for a variety of organisms by providing substrates or cover used for feeding, breeding, resting, traveling, or hiding. Patch dynamics within some ecosystems are important in providing horizontal structure, such as tree gaps in mature northern hardwood forests (Bormann and Likens 1979), or the ratio of water to emergent vegetation in some wetlands (Schroeder 1982, Short 1984, 1985). Thus, ecosystem structure has important influences on species abundance and diversity. To use structural features as performance measures each parameter (e.g., volume of organic debris) must be estimated under current conditions and for historical range of variability.

Box 3-1. Indices of Integrity.

Several ecosystem level indices of biological integrity have been developed. These are synthetic approaches which integrate measures of several parameters into a single metric that reflects the integrity of an ecosystem. The concept of integrity, "the capability of supporting and maintaining a balanced, integrated, adaptive community of organisms having a species composition, diversity, and functional organization comparable to that of natural habitat of the region" (Karr and Dudley 1981), was developed with reference to aquatic systems. However, a variety of indices of integrity has been developed for both aquatic and terrestrial community assessments (Karr 1991, see review in Morrison et al. 1992). To meet the need for assessment of biological parameters, indices that use a variety of metrics reflecting community properties were developed. The resulting indices of biotic integrity are used to detect environmental changes.

The principal advantages of indices of biologic integrity are: (1) biological communities integrate the effects of a variety of stresses over time, because they combine measures of several different community attributes, (2) routine monitoring of biological communities is relatively inexpensive compared to monitoring stressors such as contaminants, (3) indices of integrity are based on easily defined ecological relationships, (4) indices of integrity combine information from structural, compositional, and functional parameters and facilitate quantitative comparison of different settings in terms of a single metric. The disadvantages of indices of integrity are: (1) they must be tailored to specific regional settings, (2) they may depend on the taxonomic expertise of the investigators, (3) they do not provide information on the mechanisms responsible for impairment, and (4) they have not been developed or tested relative to historical range of variability.

The best-known bioassessment index for aquatic communities is Karr's IBI, which uses three classes of fish community parameters: species richness and composition, trophic composition, and fish abundance and condition (Karr 1991). The Ohio EPA (1988) and Plafkin et al. (1989) developed indices of biotic integrity based on benthic invertebrate communities. An example of an index of biotic integrity designed for use in terrestrial situations is the index of floristic integrity developed for northern Ohio (Andreas and Lichvar1995).

In stream reaches, the amount of woody debris and the pool to riffle ratio over a given length of reach can be measures of structural complexity. As with biotic indices, these comparisons to historical range of variability may need to be made in reference areas and relative to the stage of temporal response to disturbance. The challenge is to recognize that a full suite of reference areas are needed to span the range of historical disturbance regimes to properly represent the range of ecosystems in the coarse filter for any given site. Where these goals cannot be achieved, there will be significantly higher risks to meeting the ecological objectives.

Ecosystem Functions. Ecosystems operate as a unit through nutrient cycling and energy flow. Therefore, ecosystem function can be considered the "driver" of ecosystem composition and structure. Ecosystem functions such as decomposition often dictate presence or absence of species, succession or development of vegetation, and the interaction among biotic and abiotic components of ecosystems. Function-related measures ensure that ecosystems "look right" and function appropriately to ensure conservation of biological diversity and ecosystem integrity. Lugo et al. (1999) described ecosystem processes and functions.

Physical processes such as sedimentation and deposition that move matter, and processes such as photosynthesis and nitrogen fixation in which inorganic substances are converted to organic forms are parameters that can be estimated to describe ecosystem functions. Because data on past rates of ecological processes are usually difficult to obtain, differences between current and historical energy and nutrient cycling are frequently inferred from comparisons with reference sites (Scott 1993). If reference areas are available, the processes of interest can be compared to the reference site to assess whether or not processes involving the conversion of inorganic materials to organic forms or physical processes are outside the historical range of variability. For example, reference rates of nitrogen cycling will likely come from reference sites. However, caution should be exercised to ensure that outside influences (e.g., atmospheric deposition of nitrogen, acid rain) are not confounding the estimated rates. Maurer et al. (1999) documented changes in the carbon balance of beech-spruce model ecosystems because of elevated levels of atmospheric CO_2 and increased nitrogen deposition. Such broad scale effects make it difficult to delineate appropriate reference sites for understanding historical range of variability for functional measures. Where reference sites are not available, performance measures may need to be based on models of physical processes.

Interactions among species, such as predation, parasitism, and herbivory, as well as mutualistic interactions, such as seed dispersal, nitrogen fixation, and pollination are appropriate parameters for describing ecosystem functions related to species interactions. For example, parasitism rates can increase because of pollution, disturbance regimes, or habitat fragmentation. Thus, parasitism rate may be a useful parameter to compare to historical conditions. Data on parasitism rates can be collected in conjunction with other information on population productivity. The rate of predation on bird nests can be estimated (Hartley and Hunter 1998). The historical range of variability for nest predation rates is rarely known, but reference conditions can be used to evaluate predation and parasitism.

Ecosystem Processes. Ecosystem level processes include historical disturbance regimes associated with fire, wind, and flood, insect and disease outbreaks, and more gradual changes due to succession, climate variation, and geomorphic processes (White et al. 1999). Disturbance has been defined as "any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment" (White and Pickett 1985). Ranges of variability for community composition, structure, and function were defined by historical disturbance regimes. Therefore, an important measure to consider when assessing ecosystems is the type of disturbance impacting the ecosystem and whether or not it is within the historical range of variability. Disturbance processes can operate over large areas and affect the size, shape, and configuration of ecosystems. Disturbance regimes vary geographically, and by topographic position and substrate (see White et al. 1999 for listing). For any specific site, the type, frequency, extent, and intensity of disturbance should be estimated under both current conditions and historically.

At the ecosystem level, it is important to determine if processes are operating as they did in the past. Two types of disturbances need to be identified. Major disturbances shift the ecosystem from one type to another. Major disturbance is a primary driver of the historical range of variability of the coarse filter (at the landscape level). For example, fire may return mature lodgepole pine (*Pinus contorta)* stands burned on a 100–300 year return interval (Crane and Fisher 1986) to a grass/forb stage of development. Similarly, a major flood event may scour a stream, creating a new, recently disturbed ecosystem in a reach that previously represented a relatively aggraded ecosystem. These types of disturbance relate to the type of ecosystem being considered for representation within the coarse filter. For example, the mature lodgepole pine stand would be evaluated relative to its composition, structure, and function (as compared to the historical range of variability). Once burned, the resulting grass/forb community would be evaluated as to whether it meets the historical range of variability criteria for inclusion as a grass/forb community for this particular type of ecological site.

Similarly, a stream reach that is in an aggraded condition may have a particular pool to riffle ratio, certain amount of large woody debris, and certain cobble embeddedness. These measures, in comparison to historical range of variability, would determine if this reach could contribute to adequate ecological representation. If a major flood event affected this stream reach, it would change the reach from an aggraded ecosystem to an early disturbance ecosystem, with a new set of measures to compare to appropriate historical range of variability levels.

Other disturbances function in order to maintain ecosystem condition. For example, frequent understory burns in many longleaf pine (*Pinus palustris*) communities (Carroll et al. 1999) or western ponderosa pine (*Pinus ponderosa)* ecosystems (Covington and Moore 1994a,b) are essential to maintaining the composition, structure, and function of these ecosystems within historical range of variability. Similarly, insects and disease, ice damage, and wind throw are normally within ecosystem dynamics for many old growth ecosystems (Bormann and Likens 1979, Spies and Turner 1999). For these ecosystems, the type, frequency, and intensity of disturbance events may be valuable ecosystem level performance indicators. For streams, current hydrological regimes for a particular stream reach can be compared to historical range of variability using long-term stream flow records. This method was applied to the Roanoke River in North Carolina to assess the degree of hydrologic alteration caused by dams (Richter et al. 1996). A comparison of daily USGS stream flow measurements going back to 1913 revealed that high and especially low pulses are shorter and occurred more often under current conditions than under historical conditions.

Ecosystem level measures are dependent on the temporal scale used in defining a reference historical range of variability. Gradual changes due to climate variation and geomorphic processes generally operated on timeframes longer than the 200 to 400 year interval we suggest for evaluating the historical range of variability of performance measures for ecosystem management or ecological sustainability. However, understanding these longer-term changes allow for the reference time period for historical range of variability to be evaluated relative to longer term past or future conditions.

Links Between the Ecosystem Level and Other Levels in the Hierarchy

Ecosystems form the elements of the coarse filter, and the plant and animal communities of an ecosystem are composed of populations and species. For these reasons, ecosystem level assessments seek to determine whether critical components are present at appropriate levels and whether processes are functioning to maintain biological diversity and ecosystem integrity. Comparisons of these features with historical conditions serve as a reference against which the contributions of ecosystems to adequate ecological representation can be gauged.

Ecosystems are linked to the other levels of the management hierarchy. At the landscape level, managers assess whether ecosystems are present in adequate amounts and appropriate configurations to maintain biodiversity and ecosystem integrity. At the same time, assessments of species diversity and genetic diversity are necessary to evaluate whether the conservation of ecosystems is actually succeeding in conserving biodiversity at the species and genetic levels. Furthermore, species occurrences and genetic interactions across landscapes are tied to the mix of types and spacing of ecosystems.

Species Level Measures

Overview: What are the Critical Questions at the Species Level?

A primary question at the species level is whether adequate ecological representation is providing for acceptable levels of risk to viability of species. Answering this question involves determining which species maintained viable populations within a landscape under an historical range of viability, and assessing whether viable populations of a particular species will be maintained under desired future landscape conditions. This section provides a summary of measures that can be used to compare species viability under current versus historical landscape conditions.

For historically viable species, standards for maintaining minimum viable population sizes will need to be set. Managers may be interested in developing these standards for threatened and endangered species, species of special concern, or focal species. For species that were not viable prior to major human impacts, no further consideration may be necessary, as their contribution to ecological relationships within a landscape over time has been minimal. Exceptions may occur where the viability of a species that historically occurred in a neighboring landscape is presently compromised in that landscape, so contributions from adjoining landscapes may be needed, even where the species may not have been viable under historical range of variability. Ecosystem management may not provide for viability for all species that were historically viable in a landscape, although that is a desired objective for ecosystem management. Some species may be extinct. Restoring populations of others may not be economically, socially, or ecologically feasible. For example, large, wild carnivores may not be compatible with dense human development because of conflicts with people and livestock. The ecological consequences of these decisions, however, remain. Species that have been extirpated from a region, or have become rare, may have played important ecological roles in the past.

As managers attempt to conserve species, a management question may be identifying the number of evolutionary significant units that exist for each species in the landscape of interest. Identifying subpopulations that are evolutionary significant units associated with the population of a species may be essential for meeting ecosystem management objectives because each evolutionary significant unit may require different management strategies to maintain its viability.

Criteria for Selecting Species to be Monitored

Species are good indicators of a number of biodiversity objectives, and can also indicate some trends or conditions in ecosystems. For example, species have been used as indicators to monitor chemical or physical changes in the environment and to indicate the fate of other species (Landres et al. 1988, Simberloff 1998). Use of species as for environmental assays assumes their abundance or condition is correlated with physical or chemical variables (Spellerberg 1995). Examples of this type of indicator are lichens as indicators of air pollution and benthic macroinvertebrates to indicate stream pollution (Ohio EPA 1988, Plafkin et al. 1989). A considerable body of empirical evidence supports the use of indicator species as environmental assays. Species used as indicators of the status of other species should be chosen on the basis of evidence that their relative abundance is correlated with habitat suitability or population trends of the other species. Species that are monitored for reasons such as their threatened status or charismatic appeal should not automatically be assumed to represent the status of other species (Simberloff 1998). Landres et al. (1988) challenged the assumption that population responses of guild members change in parallel fashion and concluded that if it is necessary to use indicators as “surrogates for population trends of other species...such use...must be justified by research on populations of the species involved, over an extensive area and time. Since managers must often choose indicator species in the absence of supportive data, these designations should be considered hypotheses in need of further testing.”

Haufler et al. (1996) recommended criteria for selecting species that can be used for assessing if a coarse filter is providing a desired range of ecosystem types across a landscape to meet ecosystem management objectives, including the maintenance of habitat for threatened and endangered species or species of interest. These criteria include: (1) species that rely on ecosystem types that have undergone major ecological changes, (2) species with stenotopic habitat requirements for certain ecosystem types, (3) species with relatively large home ranges and requirements for specific ecosystem types, and (4) species that would use the extreme ranges of historically occurring ecosystem types.

Species selection for ecosystem types, within a landscape, should be based on their ecological requirements for specific conditions. As a result of having specific requirements, fluctuations in species abundance should track management practices or natural disturbances within the ecosystems they represent. This criterion for species selection is extremely important and may require a literature review on the habitat requirements of a species or a scientific investigation on the habitat relationships of a species. If the relative abundance of an indicator species for an ecosystem type does not vary because of major successional changes or after a severe perturbation, managers should reassess their selection of species being monitored. In contrast, if the relative abundance of the indicator species selected for an ecosystem type is fluctuating beyond their historical range of variability, managers should be concerned that there may be other ecosystem level changes occurring beyond the historical range of variability.

The species selected for assessment may also be based on legislative mandates (i.e., threatened and endangered species), conservation concern, or of special interest. In all of these cases, fluctuations in the abundance of a species should not occur beyond the threshold required to maintain viable populations. In addition, where managers observe an increase in the number of threatened, endangered, or species of conservation concern within a specific ecosystem type, the ecological changes causing these shifts in species abundance should be identified.

Performance Measures at the Species Level

We describe 5 types of performance measures for evaluating species and population responses to management practices. These include: 1) viability analysis of species in landscapes 2) occurrence and distribution of species within representative ecosystems, 3) population measures and comparisons, 4) population continuity, and 5) functional measures.

At the species level of organization, the following data are available to address the specific measures: (1) species occurrence, (2) species abundance, (2) dispersion, (3) population structure (e.g., sex and age ratios), (4) demographic processes (e.g., recruitment, mortality, survivorship), and (5) habitat attributes. Data on the presence or absence of species and populations are the easiest to obtain but the least useful for conserving species and meeting ecosystem management objectives. Lancia et al. (1994) and Cooperrider et al. (1986) reviewed a variety of population measurement techniques. Hayek and Buzas (1997) discussed methods for quantifying population measures such as density, relative abundance, species distributions and occurrence, and relationships between density and occurrence. Gros et al. (1996) evaluated several methods of estimating density or relative abundance. Litvaitis et al. (1994) reviewed a range of techniques that have been used to measure vertebrate habitat use. Morrison et al. (1992) reviewed theoretical models (e.g. habitat suitability indices) and empirical (e.g., field-based) modeling approaches that have been used extensively by natural resource managers to evaluate wildlife responses to changes in habitat conditions.

Population Parameters. Population Viability Assessment (PVA) and Sensitivity Analysis are used to predict the possible fate of populations and assign each fate a probability (e.g., Murphy et al. 1990, McCullough 1996, Nantel et al. 1996, Hanski and Gilpin 1997). Reed et al. (1988) provided a discussion of the population parameters that need to be quantified or estimated to use a PVA model.

Because it is difficult and costly to obtain data on the population dynamics for many species, a habitat-based approach to setting minimum viable population standards has been recommended by Roloff and Haufler (1997). This approach links population viability analysis and information on habitat requirements of species to allow measures of habitat quality and quantity to be used as relative indicators of population size.

Information on changes in species occurrence within their historical ecosystems provides a species assessment of a properly functioning ecosystem. If an ecosystem historically supported a species, but does not at the present, then investigations of causative factors might reveal changes in ecosystem characteristics, such as structure or nutrient cycling, that have made the ecosystem unattractive to the species.

Information on the density and relative abundance of species in existing ecosystem types is more difficult to obtain than information on species occurrence especially for historical conditions. Historical archives often document only the presence or absence of species or, if information on abundance is included, it is general and qualitative rather than quantitative and specific. Nevertheless, if such data can be obtained, comparisons of species relative abundance under current and historical conditions are extremely useful for conserving species.

If direct census information for a species is not available, indirect indices of abundance may be gleaned from historical records. For example, Elton and Nicolson (1942) analyzed Hudson's Bay Company records for a period of over 200 years. Using the number of traded Canada lynx (*Lynx canadensis*) furs as an index to population size, they concluded that lynx populations were highly variable and that these variations followed a predictable 10-year cycle. Such analyses are valuable, but the assumptions on which they are based should be recognized. Elton and Nicholson's analysis assumed that the number of traded furs was correlated with population size; thus, it ignored factors such as economic conditions that might influence trapping effort.

Evaluating sex ratios and age structure of some species, predominately large vertebrates, are common metrics that wildlife managers use to evaluate selected dynamics of populations generally in response to specific human activities. However, understanding the sex or age structure of a population under historical range of variability can be important reference information for evaluating existing conditions, population potential, and population threats. Unfortunately, such information is usually not available. Often it may only be estimated from relatively intact reference populations.

Survival rates and productivity of a species throughout its range are important metrics to describe elements of population dynamics (Johnson 1994). For example, for different populations of a species to survive they must achieve some threshold density. Unfortunately, wildlife managers are uncertain about the absolute thresholds required for most species or what the historical range of variability of these were.

Where habitat quality is variable, productivity will be higher in "good" habitat than in "poor" habitat. Habitat in which reproduction exceeds mortality acts as sources of individuals that disperse into poorer habitat, or sinks (Pulliam 1988). From the standpoint of conservation, sources are extremely important (Pulliam 1988). Critical habitat for a species is likely to occur where a species is most productive, and not necessarily where it is most common. Evaluating a species status in terms of source areas and sink areas within a landscape, both for historical and current conditions, can be very insightful in determining a species long term potential.

Population Continuity. In addition to evaluating a population's response to habitat patches, some populations may exist in discontinuous distributions consisting of subpopulations. It is important to evaluate whether a population was arranged in a similar manner under historical range of variability, or whether this condition has been created by human alterations to the species habitat. Understanding the abilities of a population to interact spatially is one of the greatest challenges for landscape planning. Failing to evaluate spatial interactions and capabilities of populations under historical conditions is one of the most common shortcomings of many population analyses. If habitat losses are isolating patches of habitat in ways that exceed the species' dispersal capabilities, serious consequences to the population can be inferred. In these cases, the projected amounts *and* distributions of representative ecosystems will need to be evaluated for their effects on species viability.

Data on habitat-specific demography and movements of individuals among populations are difficult and time-consuming to obtain. Obtaining data on population dynamics under historical conditions is especially challenging. Care must be taken that sampling data are adequate to reflect current and past distributions; otherwise, "holes" in distribution patterns may not represent true absences (Cutler 1991).

Data on past extinction rates and colonization rates among habitat patches have been inferred from comparisons of fossil and contemporary distribution patterns. For example, fossil distribution patterns of small, terrestrial, boreal mammals in patches of montane habitat in the Great Basin suggest that rates of movement between patches of high elevation habitat are extremely low for this group whereas extinctions are not uncommon (Patterson 1984, Grayson 1987, Grayson and Livingston 1993). Metapopulation approaches may have relevance to spatial analyses of some populations (McCullough 1996, Hanski and Gilpin 1997). For example, the endangered herb, Furbish lousewort (*Pedicularis furbishiae*), exists in subpopulations living in ephemeral riverbank habitat patches created by periodic flooding (Menges 1990).

Functional Measures. Herbivore-habitat interactions are an example of a process that can be measured at several levels of biological organization to examine what effects species may have on the functions associated with different ecosystem types. Herbivores can create disturbance regimes beyond the historical range of variability especially where human activity has altered habitats or reduced predator numbers. In this case, habitat conditions may be impaired for herbivores and other wildlife species, such as songbirds (Raymer 1996) and successional trajectories may be altered. Numerous wildlife managers in the north central region of the United States are concerned about herbivore induced changes in forest ecosystems in the face of historically high white-tailed deer (*Odocoileus virginianus*) numbers and browsing intensities.

Ecologists have also become concerned with recent declines in many neotropical migrant songbird populations (e.g., Robbins et al. 1992, Herkert et al. 1996). One potential limiting factor for such species may be nest parasitism. The ecological relationships that facilitate cowbird parasitism can be evaluated at the ecosystem and the species level. At the ecosystem level, parasitism rates of nests within selected ecosystem types can be compared to estimates of parasitism under the historical range of variability. At the species level, parasitism effects on population viability can be assessed by monitoring the nesting success of species of conservation concern. The species of conservation concern monitored for nesting success should represent a range of ecosystem types if ecosystem level monitoring is desired.

<u>Links Between the Species Level and Other Levels in the Hierarchy</u>

Species assessments can provide information that contributes to the conservation of specific components of biodiversity, but this information is most useful if it is linked to the other hierarchical levels. Species can serve as checks on the adequacy of representation of the coarse filter. A properly functioning coarse filter should provide for viability of native species in the landscape of interest. Additionally, species can serve as indicators that reflect the integrity of the ecosystems within a landscape. Each ecosystem may be considered functional if a range of indicator species is present within the ecosystem. Finally, a species assessment can allow managers to estimate the minimum habitat or population parameters required for a population to be viable and help develop specific conservation strategies for the species of interest.

Genetic Level Measures

<u>Overview: What Are the Critical Questions at the Genetic Level?</u>

The genetic level is the finest scale in the ecological hierarchy. Three basic components define and determine the genetic realm of biodiversity. The first is the spatial arrangement of genetic diversity in a landscape. The second is the dynamic movement of genetic material across the landscape (i.e. gene flow). The third is the movement of genetic material across generations. This component involves the loss and gain of genetic diversity, plus the change in distribution and frequency of alleles (variants of a gene) over time. These 3 components of genetic diversity are fundamental to the process of evolution. A measure of ecosystem integrity is whether a landscape will retain its evolutionary heritage and allow the continuation of processes that created its biological diversity (Angermeier and Karr 1994, Moore et al. 1999). From a genetic perspective, this implies that ecosystem managers should strive to maintain important patterns and levels of genetic variation and to preserve driving processes of evolution such as: gene flow, isolation, speciation, and colonization (Smith et al. 1993). With time, natural processes will change the spatial arrangement of genetic variation across the landscape. Therefore, the goal is not to freeze the patterns of variation, but to maintain appropriate patterns by preserving the processes that shape and change them.

One central concept of this report is the measurement of ecosystem performance against a historical context. When attempting to establish historical references for levels, patterns, and processes that characterize genetic variation, there are several potential sources of information. Historical genetic references can be established when a large number of museum specimens (e.g., >15) exist from each of one or more populations (Mundy et al. 1997, Bouzat et al. 1998, Nielsen et al. 1999). Often, museum specimens for the taxa of interest will not be available. In this situation, populations that remain relatively unimpacted can be evaluated to estimate “natural” genetic levels, patterns, and processes (Avise 1994). For some ecosystems and for some species, relatively unimpacted populations no longer exist. Comparisons with less closely related populations can still be informative, but the accuracy of reference data based on such comparisons becomes increasingly uncertain. In some cases, when genetic variation is lost it may be irretrievable on time scales reasonable to management. Assuming the loss is a result of anthropogenic impact, the goal will often be to conserve what remains, and the reference must be established from modern samples. In other cases, genetic variation will have been lost from sub-populations largely because of isolation and fragmentation. Returning historical levels of gene flow will be a powerful tool for reestablishing historical patterns and levels of genetic variation.

Genomes can be extremely sensitive to perturbations in the landscape. Herein lies one of their greatest values for ecosystem management. Six groups of questions can be evaluated to determine if the genetic components of the landscape are within the historical range of variability: (1) Is the level of genetic diversity lower than the historical range of variability and if so, are low levels of genetic diversity affecting the viability of populations? (2) What was the historical range of variability in gene flow levels and patterns? Do current levels of gene flow fall within the historical range of variability? (3) What is the historical range of variability for the presence and degree of hybridization, and do current hybridization levels fall within this historical range of variability? (4) Are there evolutionarily distinct populations within the planning landscape? What is the evolutionary distinctiveness of populations in the managed landscape compared to other populations of the species outside the landscape? (5) Does the mating system differ from that observed in other landscapes, and does it change over time? (6) Is there genetic evidence of a population decline or bottleneck?

The 6 groups of specific questions outlined above highlight the wide range of contributions that genetic evaluation and monitoring can make to conservation and ecosystem management (Mace et al. 1996). However, we do not wish to suggest that addressing each question will be required to accomplish ecosystem management goals. The extent to which genetic investigation and monitoring can be incorporated into ecosystem management will depend on resources and priorities. Regardless, managers should be aware of basic genetic characteristics of healthy ecosystems and how to achieve them.

Criteria for Selecting Taxa to be Monitored

Ideally, managers should evaluate multiple species representing distinct taxonomic groups and ecological niches. In reality, managers will never have the resources available to study and monitor genetic diversity in all or even a significant proportion of a landscape's taxa. Therefore, managers must choose to focus on specific taxa. While no single species can be a surrogate for the landscape, some species will be far more informative than others. We suggest that species in the following categories are good targets for genetic study and monitoring:

- *Species at risk*: Small populations are likely to be a central concern to ecosystem managers for several reasons. When a species is rare in a landscape because of its sensitivity to some form of ecological degradation, it may be useful as an indicator of ecological integrity.
- *Species with limited dispersal abilities*: Species which cannot disperse effectively across the matrix between patches of suitable habitat are more likely to suffer the negative effects of isolation and display important genetic substructuring across the landscape (Avise et al. 1987).
- *Species that exist in spatially substructured populations*: The movement of individuals among habitat patches is a critical process in sustaining a metapopulation. In the modern landscape, extensive habitat fragmentation has occurred in many places and even species that formally existed as continuous populations have been forced into spatially substructured populations (Hanski 1998).

Performance Measures at the Genetic Level

The genetic measures in this section provide specific ways of obtaining ecologically relevant information with molecular data. Within each measure is a discussion of how genetic data can be gathered and used to address the questions outlined previously. A detailed description and explanation of genetic methods and genetic markers is beyond the scope of this document and the reader is referred to reviews by Avise (1994), Cruzan (1998), and Parker et al. (1998).

Genetic Diversity Levels and Population Viability. Genetic diversity is one commonly used genetic performance measure, because loss of genetic diversity can increase the probability of extinction of small populations (Allendorf and Leary 1986, Gilpin and Soulé 1986). The relative importance of genetic diversity to a species' or population's health and persistence remains an enigmatic and contentious issue. Points of contention include questions of how accurately variation at neutral markers represents variation at loci affecting fitness, how often and directly the genetic variation affects the fitness of individuals and how individual fitness affects population viability (Lande 1988, Caro and Laurenson 1994). Nevertheless, correlations between various fitness traits and genetic diversity have been demonstrated for multiple taxa. Examples include growth rate in the coot clam, *Mulinia lateralis* (Koehn et al. 1988); birth weight and neonatal survival of harbor seals (*Phoca vitulina*) (Coltman et al. 1998); growth rate, survival, and fecundity in the Sonoran topominnow (*Poeciliopsis* spp.) (Quattro and Vrijenhoek 1989); fecundity in the greater prairie chicken (*Tympanuchus cupido*) (Westemeier et al. 1998); sperm quality in Indian lions (O'Brien and Evermann 1988) and parasite resistance in Soay sheep (Coltman et al. 1999).

There are 4 main mechanisms that can lead to the loss of genetic diversity in populations: 1) founder effect, 2) demographic bottleneck, 3) isolation and genetic drift, and 4) inbreeding (Hartl and Clark 1989). If managers suspect that any of these 4 mechanisms may be reducing genetic diversity and potentially increasing the extinction risk of one or more taxa, then selected estimators can be used to test this hypothesis, and ideally, contrasted with historical levels of variation.

Historical and Current Levels of Gene Flow. Gene flow is the transfer of genetic material among populations. The degree of gene flow between 2 populations ranges from an extreme of complete isolation and no gene flow to extensive exchange that genetically homogenizes 2 populations. Some populations and species have existed for long periods of time in complete isolation, and the appropriate management goal for such populations would be to prevent human-induced gene flow. Other species with high dispersal abilities, such as wolves (*Canis lupus*), coyotes (*Canis latrans*), and migratory birds, historically have high levels of gene flow and low levels of population structure (Avise and Aquadro 1982, Avise et al. 1987, Wayne et al. 1990, 1992, Avise 1992, 1994). An appropriate management goal for such species would be to retain habitats or suitable matrix conditions that allow for movements that would preserve historical gene flow levels and patterns. When the habitat necessary for migration no longer exists, managers will have to consider restoring historical gene flow levels and patterns artificially by moving individuals between populations.

Four main indirect measures indicate average levels of gene flow over evolutionary time:

1) *F*-statistics: This group of estimators indicates the degree of population structure and can be used to estimate the number of migrants per generation (*Nm*) between populations.
2) Private alleles analysis: Slatkin (1985) developed a gene flow and *Nm* estimator based on the number of private alleles (alleles found only in one population).
3) Genetic distance methods: Genetic distance methods give an index of the degree of differentiation between pairs of populations (or taxa).
4) Phylogenetic analysis: Evaluating gene flow using phylogenetics requires knowledge of the phylogeny of nonrecombining segments of DNA (Hillis et al. 1996).

In addition to these indirect measures of gene flow, various direct measures are also available. For animals, standard mark–recapture methods and radiotracking can be used to detect current migrants (Wilson et al. 1996). Genetic fingerprinting of samples (hair, scat, feathers) collected non-invasively can also be used in a mark–recapture approach with the advantage that sampling can be done without handling or disturbing the animals (Kohn and Wayne 1997, Kohn et al. 1999, Taberlet et al. 1999, Woods et al. 1999). The assignment test is another genetic method that can be used to detect recent migrants when populations are genetically distinct and significant population substructure exists (Paetkau et al. 1995, Waser and Strobceck 1998). The main drawback of these approaches is that they only demonstrate that the individuals are migrating and do not indicate whether the migrating individual has bred or will breed. To determine if migrant individuals are breeding, genetic analyses can be performed to determine paternity and maternity of offspring (Chakraborty et al. 1988, Craighead et al. 1995, Girman et al. 1997, Cruzan 1998). If no data exist on potential migrants, relatedness statistics can also be calculated to determine if a mating individual has genetic material very different from other individuals within the population (Queller and Goodnight 1989, Queller et al. 1993).

Presence and Degree of Hybridization. Hybridization between closely related taxa is a serious and commonly overlooked threat to biodiversity (Rhymer and Simberloff 1996). The prevalence of exotics as a measure of ecosystem integrity has been discussed under ecosystem level measures. An extension of this measure is to ask if the exotic species are impacting the ecosystem by hybridizing with native species. For example, hybridization between the introduced brook trout (*Salvelinus fontinalis*) and the native bull trout (*S. confluentus*) creates a significant reproductive sink for the less numerous bull trout (Leary et al. 1993).

A second cause of hybridization involves habitat modifications that bring 2 formerly isolated species into contact. For example, 2 species of native tree frogs in Alabama (*Hyla cinerea* and *H. gratiosa*) are isolated by mating behaviors associated with different structural components of ponds. Loss of emergent vegetation due to disturbance results in a breakdown in the reproductive barrier (Avise 1994). The extent of hybridization in plants may be even greater than in animals, where reproductive barriers are generally less stringent (Soltis and Gitzendanner 1999).

Under historical conditions, hybridization with true exotics should have been essentially zero. It may or may not be possible to determine the historical range of variability of hybridization in cases where habitat modification has broken down reproductive barriers, depending on the quality of historical data. Where they exist, reference areas can be used to estimate the historical range of variability of hybridization. For example, hybridization between *H. cinerea* and *H. gratiosa* occurs but is rare at unimpacted ponds compared with impacted sites (Avise 1994).

Detecting hybrids involves determining distinctive genetic signatures for species so that hybrids genetic signatures can be identified (Avise 1994, Hughes 1998). The direction of hybridization can be studied as well, using molecular markers that are uniparentally inherited such as mitochondrial DNA and Y chromosome loci in animals and chloroplast DNA in plants (Avise 1994).

Evolutionary Distinctiveness. An evolutionary tree that describes the genealogical relationships that unite taxa is known as a phylogeny. Phylogeography is the process of mapping the phylogeny of individuals within a species on the landscape and provides managers with a powerful tool for conserving the evolutionary heritage of species (Avise 1987, Avise et al. 1987, Avise 1989, Avise 1992, Avise 1998). Practically speaking, the manager asks which populations are the most valuable in terms of preserving the genetic diversity of the species.

When a population is subdivided into 2 and kept relatively isolated over generations, allele frequencies in the 2 populations begin to diverge. Moritz (1994) suggested that when these frequencies become significantly different, the 2 populations constitute separate management units and should be managed independently. When a large number of generations have passed with very little exchange, allele frequency differences will be significant, and every individual in both populations will be more closely related to other individuals in the same population than to individuals in the other populations (a condition called reciprocal monophyly). Moritz (1994) suggested that such populations constitute separate evolutionary significant units (ESUs).

In mapping patterns of mitochondrial DNA diversity in the canyon treefrog (*Hyla arenicolor*) in the Southwest United States, Barber (1999) found 3 highly divergent evolutionary lineages that occupy distinct geographic regions. In fact, 1 of the lineages found in the Grand Canyon differs from the others by an astounding 13% and is more closely related to another species (*H. eximia*) than to other lineages within *H. arenicolor*. In general, conserving representative populations of each ESU should be the highest priority, followed by conserving representative populations of each management unit.

Because species in the same community have often been subject to similar climatic and geologic (biogeographic) forces, they may share similar phylogeographic patterns. Comparative phylogeography is the overlaying of multiple species' phylogenies on the landscape (Avise 1992, Moritz and Bermingham 1998, Moritz and Faith 1998). When there is a strong concordance among distinct types of taxa, it is likely than many unstudied taxa will have the same basic phylogenetic pattern. In this way, areas of especially high evolutionary value may be identified.

Phylogenetic distinctiveness at the depth of ESUs is classically determined by reconstructing phylogenetic trees with sequence data from mitochondrial and nuclear DNA or allozymes (Waples 1991, Moritz 1994, Waples 1995). A finer scale resolution, to define management units for example, can be gained with allele frequency data (Moritz 1994). The techniques used for phylogeny estimation and phylogeography are beyond the scope of this report; Avise (1994), Hillis et al. (1996), and Molecular Ecology (1998) provided good overviews of the subject.

Evaluation of Mating Systems. The study of mating systems focuses on ways individuals obtain mates, the number of individuals with which they mate, and how long mates stay together. Modern genetic techniques are providing new insights into studies of mating systems due to their high resolution and accuracy (Hughes 1998). Recently a number of presumably monogamous species were redefined as polygamous using the increased resolution of genetic methods. These included eastern bluebird (*Sialia sialis*) (Gowaty and Karlin 1984), red-winged black bird (*Agelaius phoeniceus*) (Gibbs et al. 1990), and alpine marmot (*Marmota marmota*) (Goossens et al. 1998). For plants and other organisms capable of self-fertilization, genetic analysis provides a statistical method for estimating selfing and outcrossing rates (reviewed in Schemske and Lande 1985).

Mating patterns and systems often correlate with ecological factors and may change as environmental conditions are altered. In the red-winged blackbird, population density is significantly associated with decreased monogamy (Gibbs et al. 1990). The degree of monogamy was also associated with habitat quality in the alpine marmot (Goossens et al. 1998). Other environmental conditions that may alter mating systems are: a) hunting pressure that alters the sex ratio or dominance hierarchy of a population or b) a contraction of a critical resource that causes individuals to cluster during the breeding season. Thus, evaluation of mating systems is another potentially useful measure of ecosystem integrity.

Maternity, paternity, and relatedness analyses are used to evaluate and characterize mating systems. These analyses generally involve combining field observations with DNA multilocus fingerprint data to infer genetic relationships.

Population Trends and Bottlenecks. Monitoring population trends, and especially detecting drastic declines, will be important for managing focal species. When a population is reduced to a small number of breeders (bottlenecked), the allele frequencies between generations shift dramatically, creating a detectable genetic signal. Additionally, non-invasive genetic sampling can be used in conjunction with DNA fingerprinting to get minimum and mark–recapture population estimates (Woods et al 1999, Kohn et al 1999).

Another role of genetic census methods is in detecting cryptic bottlenecks, where the population size does not crash, but only a small number of individuals are contributing to the gene pool of the next generation. This is most common in highly fecund species like fish and amphibians and in species with a dominance hierarchy that limits breeding to a small number of individuals.

The use of DNA fingerprinting to estimate population size and trend is very similar to capture-based census methods, except that an individual's DNA, in the form of hair, scat, etc., is captured instead of the individual. Recent population estimates of brown bears (*Ursus arctos*), coyotes (*Canis latrans*), and cougars (*Puma concolor*) demonstrate some advantages of the approach (Kohn et al. 1999, Woods et al. 1999, Ernest et al. 2000).

Several genetic methods have been developed specifically for detecting population bottlenecks. The simplest approach is to monitor levels of heterozygosity across generations because heterozygosity will decline as the effective population size shrinks. However, the decline in heterozygosity is generally not drastic, and thus this approach is not powerful enough to be useful except in detecting severe contractions (Allendorf and Leary 1986, Luikart et al. 1998). More powerful approaches include evaluating: 1) allele frequencies over time (Luikart et al. 1999, Waples 1989), 2) the number of rare alleles (Allendorf 1986, Luikart et al. 1998), and 3) disruptions in the equilibrium between genetic drift and mutation (Cornuet and Luikart 1996, Luikart and Cornuet 1998). All 4 methods become far more powerful when highly variable codominant markers are used (e.g. microsatellites), sample sizes are at least 30, and bottlenecks are relatively severe.

<u>Links Between the Genetic Level and Other Levels in the Hierarchy</u>

The genetic level is closely linked to the species level. In fact, most of the genetic measures discussed are actually genetic properties of populations or groups of populations. For example, the evolutionary distinctiveness of a population compared to the species as a whole is property of that population, and historical levels of gene flow between populations were a characteristic of that assemblage of populations. Thus, the nested nature of species within ecosystems is not logically equivalent to the way genetic variation is a property of populations and species. The genetic level has been separated from the species level in this report largely to maintain methodological clarity. Managers will choose focal taxa at the species level to monitor and evaluate the genetic level of the hierarchy. In addition, accurately addressing questions at the genetic level is dependent upon collection of samples at the landscape scale. Many genetic measures can be used to evaluate the effectiveness of the spatial distribution of populations that are responding to the arrangement of ecosystems at the landscape level. Thus, even at this finest level of biological organization, linkages exist across all the other organizational levels.

Genetic methods, such as non-invasive genetic sampling (Taberlet et al. 1999), can be used to collect data for performance measures at other levels of the hierarchy. Several of the genetic and species level performance measures are nearly synonymous. In fact, for some bird and mammalian species, all of the performance measures listed at the species level could be evaluated with genetic methods alone. For example, hair, feces, and feathers can be collected and the DNA can be used to determine: 1) presence/absence of species, 2) geographic range of species, 3) the abundance of species in different ecosystems, 4) sex-ratio within species, 5) the degree of immigration and emigration, and 6) population continuity. In other instances, the genetic performance measures provide a greater degree of resolution than that provided by the species level. They ask: How well do species, community, and landscape measures correlate with genetic performance indicators?

APPLICATIONS OF PERFORMANCE MEASURES

Use of Performance Measures at the Landscape, Ecosystem, and Species Levels: Ecosystem Management in Northern Minnesota

The full application of performance measures for ecosystem management at all levels of the organizational hierarchy requires that an appropriate ecosystem management process be in place. Boise Cascade Corporation (BCC) initiated an Ecosystem Management Demonstration Project in northern Minnesota. The Ecosystem Management Project was designed to allow BCC to function effectively while addressing regional biodiversity concerns and to demonstrate approaches and methodologies that can meet the objectives of ecosystem management in a flexible, sustainable manner. This project was an example of the application of performance measures ranging from the landscape level to the species level. The project was modeled after the process described by Haufler et al. (1996, 1999).

Boise Cascade's project delineated a landscape that corresponded to the section level as described by the National Hierarchy of Ecological Units (Cleland et al. 1997). The 2.5-million-hectare Northern Minnesota and Ontario Peatlands Section (NMOPS), as described by McNab and Avers (1994), represented an appropriate landscape for ecosystem management in northern Minnesota. Within this landscape, information on historical disturbance regimes and resulting conditions was sampled, derived, or obtained. The fire history of the landscape had not been described in any detail; however, Marschner (1974) compiled and mapped vegetation information obtained from U.S. General Land Office survey notes for the period 1850–1905. A summary of historical vegetation types (Marschner 1974) within the landscape described a landscape dominated by conifer bogs and swamps and seral aspen-birch (*Populus tremuloides-Betula papyrifera*) stands succeeding to conifer communities.

Landscape Level: Comparing Adequate Ecological Representation to Existing Conditions

Once the landscape was delineated, an ecosystem diversity matrix was used to quantify and describe ecological complexity across multiple land ownerships within the NMOPS (Kernohan et al. 1999) (Fig. 4). The ecosystem diversity matrix for the NMOPS reflected both the potential natural vegetation of a site (habitat types, *sensu* Daubenmire [1968]), and the existing vegetation (vegetation growth stage described in terms of shade tolerance). The combination of vegetation growth stages and habitat type classes creates ecological units, which are represented as cells in the ecosystem diversity matrix. The ecosystem diversity matrix was section-specific (thus, it was unique to NMOPS) and represented the range of ecological units (i.e., ecosystems) on all ownerships within the section. The ecosystem diversity matrix provided the framework for a description of historical disturbance regimes, existing landscape conditions, conditions required to support biodiversity, potential future landscape conditions, and a classification scheme for species assessments (Haufler et al. 1996).

The ecosystem diversity matrix was used to describe existing conditions in the NMOPS landscape by classifying current vegetation growth stages from stand inventory data and by modeling habitat type classes from general landscape attributes such as surficial geology, landform, and hydrography. Using information about the historical disturbance regimes operating on the landscape, the area of a given ecological unit in the ecosystem diversity matrix under historical conditions was estimated (Frelich 1998) (Fig. 4). For example, the rich, moist fir community included 9 vegetation growth stages including shrubs and seedlings, shade-tolerant and intolerant saplings, small trees, and medium trees and shade-intolerant large trees (aspen and balsam fir, (*Abies balsamea*)). The rich, moist fir community was found to occupy approximately 189,876 hectares of the landscape, and historically, the shade tolerant medium tree stage made up 17–18% of this community. Thus, under historical conditions this stage or ecological unit occupied up to 18% of 189,876 hectares, or an estimated 34,178 hectares (Fig. 4). This represented reference conditions in amounts of this ecological unit.

Once historical conditions across the landscape were quantified, they were used as a reference point from which threshold levels for specific ecological units were calculated. Adequate ecological representation was considered a threshold set at 10% of the maximum of the range of historical conditions. Therefore, adequate ecological representation for the rich, moist fir; medium tree tolerant ecological unit would be met by maintaining 3,418 hectares (i.e., 10% of 34,178 hectares) across the landscape (Fig. 5). A specific landscape level measure would be to compare adequate ecological representation to existing acres of each ecological unit within the landscape. To continue the above example, the rich, moist fir; medium tree tolerant ecological unit currently occupies 7,431 hectares across the landscape. When the existing amount of this ecological unit is compared to adequate ecological representation, the landscape is above

Historical Range of Variability
Ecosystem Diversity Matrix (excerpt)

Vegetation Growth Stages	Habitat Type Classes: Moist Fir	Rich, Moist Fir	Wet Fir/ Ash/Cedar	Wet Fir/ Cedar	Poor, Wet Spruce
Seedling/Sapling	5-9%	5-9%	5-9%	5-8%	18-32%
Small tree	12-20%	12-20%	8-14%	12-19%	
Shade Intolerant Species → Medium tree	7-10%	7-10%	14-18%	13-17%	
Large tree	3-5%	3-5%			
Small tree	1-2%	1-3%	7-9%	6-8%	15-23%
Medium tree ← *Shade Tolerant Species*	10-12%	17-18%	19-20%	17%	21-23%
Large tree	6%				
Old growth	25-51%	24-29%	20-42%	19-42%	22-46%

Figure 4. Partial historical range of variability ecosystem diversity matrix for the Northern Minnesota and Ontario Peatlands landscape of northern Minnesota. Primary axes of the ecosystem diversity matrix describe site potential as depicted by habitat type classes and temporal stand dynamics depicted by vegetation growth stages. The intersection of both axes represents ecological units across the entire landscape. Percentages represent the range of each ecological unit by habitat type class historically occurring on the landscape.

Adequate Ecological Representation
Ecosystem Diversity Matrix (excerpt)

	Habitat Type Classes				
Vegetation Growth Stages	Moist Fir	Rich, Moist Fir	Wet Fir/ Ash/Cedar	Wet Fir/ Cedar	Poor, Wet Spruce
Seedling/Sapling	343	1,709	437	295	4,313
Small tree	762	3,798	679	623	
Shade Intolerant Species → Medium tree	381	1,899	873	557	
Large tree	190	950			
Small tree	76	570	437	262	3,100
Medium tree ← *Shade Tolerant Species*	457	3,418	970	557	3,100
Large tree	228				
Old growth	1,943	9,304	2,038	1,377	6,200
Total area in class (ha)	38,090	189,876	48,510	32,775	134,777

Figure 5. Partial adequate ecological representation ecosystem diversity matrix for the Northern Minnesota and Ontario Peatlands landscape of northern Minnesota. Values, in hectares, represent 10% of the maximum historical range of variability for each ecological unit. Ecological units without a value did not occur historically.

this threshold level (Fig. 6), so that this particular ecosystem would not be identified as one of high restoration need.

Ecosystem Level: Assessing Ecological Unit Composition and Function

Ecosystem level performance measures assess whether or not stands within the landscape contribute to adequate ecological representation. In order for stands to contribute to adequate ecological representation, the existing conditions of an ecological unit should correspond to the historical range of variability of that ecological unit with regard to composition, structure, and function. Each ecological unit in the ecosystem diversity matrix was characterized through comprehensive vegetation sampling. Variables collected included species, diameter, height of all live trees and snags, percent canopy and understory cover by species, presence and description of coarse woody debris, and vertical strata by life form. Using information on existing conditions (e.g., diameter distribution), an ecological unit can be described and compared to expected historical conditions. For example, in the large tree, tolerant, rich, moist fir ecological unit, the mean number of large snags per hectare historically may have been 7 snags per hectare distributed in a clumped pattern. An appropriate ecosystem level measure would be to compare the existing number of snags per acre and their distribution within the ecological unit. If existing conditions were found to have 2 snags per hectare arranged in a random distribution, then the large tree, rich moist fir ecological unit would not be within the historical range of variability for this ecosystem structural characteristic. Restoration efforts may then focus on developing more snags, in clumped arrangements.

Species Level: Habitat Potential Models Based on Habitat Quality and Quantity

Species-specific assessments were conducted to assess whether or not minimum habitat requirements were being met for pileated woodpecker (*Dryocopus pileatus)* and ruffed grouse (*Bonasa umbellus)*, thus providing species-level performance measures. These 2 species were selected because of their known habitat requirements and the different successional stages the 2 species need. As a landscape level measure, habitat and home ranges can be used to assess population viability for individual species across the landscape, thus providing a check against adequate ecological representation (Roloff and Haufler 1997). For these 2 species, the number and quality of individual home ranges could be mapped for the landscape based on projected conditions including the estimated amounts of each ecological unit for adequate ecological representation.

Applying Performance Measures

This project was designed to conserve biological diversity and ecosystem integrity by providing an appropriate mix of ecosystems across the planning landscape. The objective of the habitat potential modeling was to check the coarse filter approach and provide a means of assessing performance measures at the species level. Three primary scales were used including the planning landscape (<2 million hectares), species home range (5–100's hectares), and the ecological unit (10–20 hectares). In addition, temporal scales addressed included historical time frames (300 years), the landscape planning cycle (100 years), and monitoring intervals (5 year cycles). Performance measures included adequate ecological representation at the landscape level, ecological unit composition, structure, and function at the ecosystem level, and habitat quality and quantity by home range for 2 species at the species level. Additional performance measures at all levels of biological diversity could be added to strengthen the evaluation of ecosystem management and ecological sustainability.

Example of Ecosystem Management Linkage at the Ecosystem Level: Southwestern Ponderosa Pine Restoration

Ecologists can make significant contributions to ecosystem management at the level of the ecosystem, even without having a larger landscape assessment. In many landscapes, ecosystems that have been subjected to substantial alteration or conversion are already known. Examples include long leaf pine ecosystems in the Southeastern United States, most prairie ecosystems across the Great Plains, and low elevation forest ecosystems in the Rocky Mountains. Covington et al. (1999) described how restoration at the ecosystem level could be approached relative to a reference to historical range of variability. This example describes how ecosystem ecologists in the Southwestern United States have identified ponderosa pine forests as ecosystems in need of restoration, and the types of research and management that can be conducted at the ecosystem level to address these concerns. Covington and Moore (1994a,b) and Covington et al. (1999) described the changes that have occurred in ponderosa pine ecosystems in northern Arizona because of grazing and fire exclusion. They discussed the effects of these changes on the current disturbances operating within existing ecosystems as compared to the historical range of variability. Moore et al. (1999) described how they established 4 restoration trials to demonstrate and evaluate methods for restoring functional ponderosa pine ecosystems. They felt that such efforts were critical to maintain what they termed were evolutionary habitats that would continue to allow evolutionary processes for species that utilized ponderosa pine ecosystems.

Based on work by Swetnam and Baisan (1996) and others, Moore et al. (1999) and Covington et al. (1999) quantitatively described historical disturbance regimes for southwestern ponderosa pine, detailing a historical range of variability of high frequency, low-intensity fires over the last 300–500 years. They also described how this changed with Anglo-American settlement. Further, they described ecosystem composition and structure under historical ranges of variability, and how this has been altered in existing conditions, with much higher fuel loads and dramatically different fire regimes with current fires more infrequent and severe. They described both overstory and understory conditions.

With this knowledge of historical range of variability and the differences in existing ecosystem conditions, Covington et al. (1997, 1999) described a process to restore functional ponderosa pine ecosystems. In addition to composition and structure, Kaye and Hart (1998) reported on nutrient cycling in response to restoration efforts. The restoration trials described by Moore et al. (1999) documented a successful return to ecosystem conditions resembling those reported to have occurred under historical disturbance regimes.

Similar descriptions of needs in ponderosa pine ecosystems in other landscapes in the Inland West have been reported (Agee 1993, Crane and Fisher 1986, Steele et al.1986, Everett et al. 2000). Harrod et al. (1998) modeled snag densities and distributions under historical ranges of variability in ponderosa pine forests in Washington State. They provided an understanding of the abundance and role of snags under historical conditions, which can provide insights to the needs of species that depended on these ecosystems.

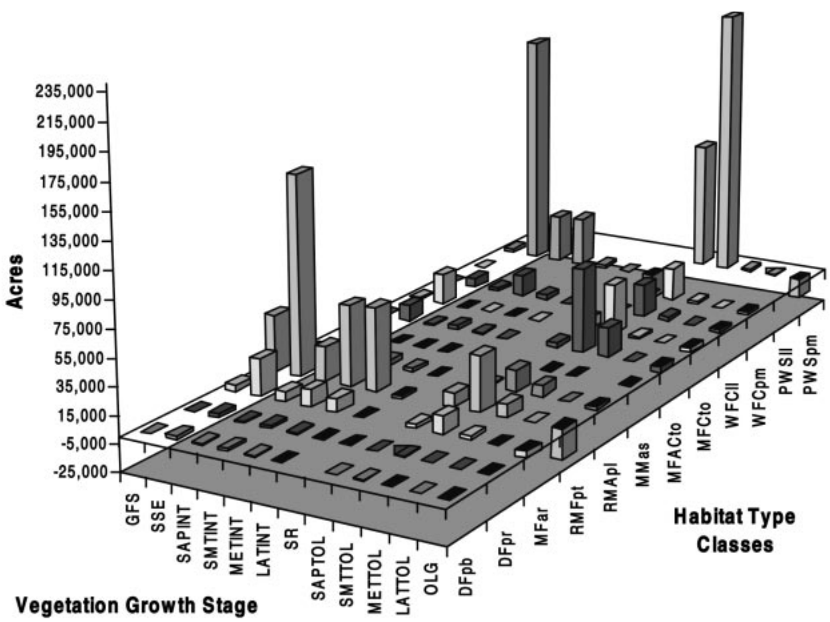

Figure 6. Difference between the amount of each ecological unit existing within the Northern Minnesota and Ontario Peatlands landscape currently and adequate ecological representation calculated as 10% of the maximum historical range of variability. A positive difference identifies ecological units that are currently above adequate ecological representation where a negative difference identifies those ecological units currently below the threshold. Rows in the matrix are the vegetation growth stages: GFS (grass/forb/seedling stage), SSE (shrub/seedling stage), SAPINT (saplings with intolerant species), SMTINT (small trees with intolerant species), METINT (medium trees with intolerant species), LATINT (large trees with intolerant species), SR (self-replacing stand with intolerant species), SAPTOL (saplings with tolerant species), METTOL (medium trees with tolerant species, LATTOL (large trees with tolerant species), OLG (old growth). The columns of the matrix are the habitat type classes: DFpb (Dry fir, jack pine), DFpr (Dry fir, red pine), MFar (Moist fir, red maple), RMFpt (Rich, moist fir, aspen), RMApl (Rich moist ash, balsam poplar), MMas (Wet maple, silver maple), MFACto (Wet fir/ash/cedar, cedar), MFCto (Wet fir/cedar, cedar), WFCll (Very wet fir/cedar, tamarack), WFCpm (Very wet fir/cedar, spruce), PWSll (Poor, very wet spruce, tamarack), PWSpm (Poor, very wet spruce, spruce).

These examples demonstrate the significant contributions and efforts to ecosystem management that can occur at the ecosystem level. While major ecosystem management contributions can occur at the ecosystem level alone, questions concerning how much restoration may be needed in a landscape, and what spatial arrangement of restoration efforts will provide the best results require additional information and assessment at the landscape level. Further, ecosystem level efforts can also make significant contributions to the needs of species, and to genetic level objectives.

Example of Ecosystem Management Linkage at the Species Level: Managing for Kirtland's Warbler (*Dendroica kirtlandii*)

A primary focus of many wildlife management activities is to maintain viable populations of species. These actions become critical for threatened and endangered species or candidate species. Often this task becomes problematic due to limited biological data, the characteristics of the required habitat, and the migratory status of the species. Yet, managers addressing species needs can contribute significantly to ecosystem management initiatives. Maintaining and enhancing the status of a single species, or multiple species, can contribute to broader ecosystem management objectives. If the species has been limited by a loss of suitable habitat, then obviously some types of ecosystems that previously occurred have been lost. These ecosystems would undoubtedly be a focus for restoration at the ecosystem and landscape levels. By addressing the needs of a declining species, the loss of the broader ecosystem may also be addressed. Thus, while not addressing the full range of ecosystems, declining species may indicate those ecosystems most in need of attention.

In this example, we discuss conservation efforts for the Kirtland's warbler, a neotropical migratory bird species that is dependent on early successional stages of jack pine (*Pinus banksiana*) in the northern region of Michigan's lower peninsula. We used this species as an example since it portrays several management interests. For example, how do managers conserve a species that has relatively specialized and limited habitat and has been threatened by nest parasitism by the brown-headed cowbird (*Molothrus ater*) (Ryel 1981).

The management objective for the Kirtland's warbler, as stated in the Recovery Plan, is to "reestablish a self-sustaining Kirtland's warbler population throughout its known range at a minimum level of 1,000 pairs" (Kirtland's Warbler Recovery Team 1985). Meeting this management objective will allow the species to be removed from the Endangered Species List.

Managers responsible for conserving the Kirtland's warbler will need to stratify their efforts into wintering versus the breeding area because of the difficulties of making management decisions across international boundaries and the need to assess the historical range of variability within the unique ecosystems required by the species in each respective area. We will limit our discussion to the breeding range.

Kirtland's warblers require a specific set of habitat conditions, that of young (5–23 year old) jack pine produced by stand replacing fire (Nelson and Buech 1996, Probst and Weinrich 1993), where a majority (73%) of males identified in censuses have been found (Probst and Weinrich 1993). Although jack pine areas disturbed by fire provide the most suitable habitat conditions for the Kirtland's warbler, jack pine types not disturbed by fire also may provide less suitable warbler habitat. For example, Probst and Weinrich (1993) documented that a few Kirtland's warbler males were also found in habitat conditions such as plantations (11%) or in harvested, unburned jack pine stands that have regenerated (16%).

Because stand age is a critical nesting habitat attribute for Kirtland's warbler, managers must quantify availability of suitable nesting habitat. Five age classes span Kirtland's warbler habitat conditions pre- and post-occupation. These include: pre-occupation (<8-years-old), growth (8–11-years-old), level stage (12–17-years-old), decline (18–21-years-old), and post-occupation (>22-years-old) (Marshall et al. 1998). Having an understanding of the current amounts and distributions of jack pine age classes is critical for forest planning to provide quality nesting sites.

With this information, population and habitat thresholds can be established. This requires estimates of what constitutes a viable population (1,000 pairs) for the Kirtland's warbler, and the amount of habitat required to support this population size. Specifically, what minimum proportion of the planning landscape needs to be in suitable habitat conditions at a given time for the warbler to persist, how should this habitat be distributed, and how can the historical disturbances be restored to help provide threshold habitat conditions. If managers are going to be effective in meeting population and habitat management objectives for a species, it is essential that these types of thresholds be clearly established and periodically evaluated.

To aid in maintaining a viable Kirtland's warbler population, managers should understand how many evolutionary significant units occur within the breeding habitat. In this case, Kirtland's warblers appear to be only 1 evolutionary significant unit. However, evaluation of the population's heterozygosity may be desirable to insure that a genetic bottleneck has not occurred when the population dropped to low numbers.

Species management can contribute to larger ecosystem management efforts. The decline of the Kirtland's warbler highlighted landscape changes that had occurred due to alteration of historical disturbance regimes and landscape patterns. The warbler, a stenotopic species, served as an excellent indicator of early successional jack pine communities. Meeting warbler viability goals should help address adequate ecological representation thresholds of these specific ecosystems. Thus, a species focus can make significant contributions to ecosystem management efforts even without an overall landscape assessment and coarse filter development.

Example of Ecosystem Management Linkage at the Genetic Level: Use of Museum Specimens to Investigate Historical Levels of Genetic Diversity and Gene Flow in Brown Bears

Several studies have employed museum specimens as a source of genetic information to examine evolutionary relationships among taxa and assess the degree of past anthropogenic impact. Most studies have focused on rare or endangered species. Examples that have yielded information directly applicable to management include the greater prairie chicken (Bouzat et al. 1998), the northern hairy nosed wombat (*Lasiorhinus krefftii*) (Taylor et al. 1994), the San Clamente Island loggerhead shrike (*Lanius ludovicianus mearnsi*) (Mundy et al. 1997), and the Laysan duck (*Anas laysanensis*) (Cooper 1996). We provide an example of current work by Waits and Miller using museum specimens of grizzly bears from Yellowstone to help guide the long-term management of this population.

Brown bears (regionally referred to as grizzly bears) are adaptable creatures with a historical range extending across Europe, Asia, and the western half of North America. Primarily due to human extermination, the brown bear in North America has been extirpated from approximately 98% of its historical range south of the Canadian border. All extant populations south of the 49th parallel are connected to a larger population north of the border except the population in the Yellowstone Ecosystem, which has been isolated since around 1910. Brown bears in this region were noticeably reduced by early hunters and trappers. Between the turn of the century and 1971, bears were concentrated because of the extensive garbage feeding that occurred in the park. With the closure of the dumps around 1970, human–bear conflicts increased and, as a consequence, the population declined from 250–310 in the 1960s to between 136–200 in the mid-1970s (Craighead et al. 1995). The population was protected under the Endangered Species Act in 1976 and has grown since to a current size of between 400 and 800 individuals.

Paetkau et al. (1997) studied levels of genetic variation in extant brown bear populations from around North America using 8 microsatellite loci. At 55% heterozygosity, the Yellowstone population has significantly less genetic variation (69%) than the population in the North Continental Divide Ecosystem (NCDE) located several hundred kilometers north, populations in the southern Canadian Rockies (65%), or the large imbedded population in Alaska and Canada (75%). Historical accounts, museum specimens, and habitat considerations all suggest that there was gene flow in and out of Yellowstone. There is, therefore, no obvious reason why the bears of Yellowstone should have historically had lower levels of genetic variation. This led Paetkau et al. (1997) to hypothesize that the Yellowstone population once had considerably higher levels of genetic variation that it lost as a consequence of isolation and/or bottlenecking. If this scenario were accurate, a loss of 10–20% heterozygosity within a century would be serious cause for concern. Though the population appears to be stable or increasing now, stressors on the population are expected to continue increasing (e.g. decline of important food sources such as whitebark pine (*Pinus albicaulis*) seeds and cutthroat trout (*Oncorhynchus clarki*), as well as continued loss of habitat to development). There is empirical evidence of inbreeding depression in captive brown bears (Laikre et al. 1996), and population genetic theory generally predicts that recently bottlenecked populations are more likely to suffer the negative effects of loss of genetic variation than populations that have adapted to such a condition.

There are approximately 175 Yellowstone grizzly bear museum specimens from the late 1800s through the early 1970s. Using these as a source of genetic material, Waits and Miller are working to track levels of genetic variation in Yellowstone across time to address the questions: Were historical levels of genetic variation greater than modern levels? If they were, how rapidly and severely have they declined and what historical events caused these declines? This information can then be used to define an appropriate threshold for recovery of genetic diversity in the Yellowstone population.

If significant levels of genetic variation have been lost, how shall they be restored? The practical solution is to facilitate gene flow between the historically connected Yellowstone and the NCDE populations. In the current political and cultural landscapes, this movement will necessarily be artificial. How many individuals should be moved? The level of genetic differentiation between the modern NCDE and Yellowstone populations suggests there were between 0.5 and 2 migrants per generation (Waits and Paetkau, unpublished data). However, if recent isolation and bottlenecking in the Yellowstone population have caused an accelerated divergence from NCDE, then these estimates are expected to be lower than the long-term evolutionary average. Using the genetic data from the historical population, we aim to estimate pre-impact levels of genetic exchange. This figure will be especially useful for establishing long-term management objectives for gene flow once the Yellowstone population has returned to its historical range of genetic variation.

SUMMARY

This report has described a hierarchical approach for performance measures for the ecological objectives of ecosystem management. While tackling the entire set of measures at all levels of the hierarchy may seem to be a daunting task, if we are to fully address the objectives of maintaining and enhancing biological diversity and ecosystem integrity, we need to implement ecosystem management and assess its success with a full array of performance measures. These ecological objectives are the cornerstone of ecological sustainability, so establishing a hierarchical framework of performance measures is a critical first step in assuring long term sustainability. However, the report also attempted to show how significant contributions to ecosystem management can be made even when addressing only 1 level of the hierarchy. We think that it is critical for natural resource managers to initiate collaborative ecosystem management efforts that will allow for implementation of ecosystem management across all levels of the hierarchy. Ecosystem management will require new levels of cooperative efforts across disciplines and across agencies, organizations, industries, and landowners. It will also require managers to step out of traditional roles and views and embrace new approaches including the review and understanding of new types of data and information. Ecosystem management offers the best solutions to many of today's complex natural resource management problems including managing in an ecologically sustainable manner. This report has been prepared with the goal of enhancing the implementation of effective ecosystem management.

LITERATURE CITED

Agee, J. K. 1993. Fire ecology of Pacific Northwest forests. Island Press, Washington, D.C., USA.

Allendorf, F. W. 1986. Genetic drift and the loss of alleles versus heterozygosity. Zoo Biology 5:181–190.

Allendorf, F. W., and R. F. Leary. 1986. Heterozygosity and fitness in natural populations of animals, Pages 57–76 *in* M. Soulé, editor. Conservation biology: the science of scarcity and diversity. Sinauer Associates Inc, Sunderland, Massachusetts, USA.

Almendinger, J. C. 1996. Minnesota's bearing tree database. Minnesota DNR Natural Heritage Information System, Section of Ecological Services. Mimeograph, St. Paul, MN, USA.

Andreas, B., and R. Lichvar. 1995. A floristic quality assessment system for northern Ohio. Wetlands Research Program Technical Report WRP-DE-8. U.S. Army Corps of Engineers, Waterways Experiment Station, Vicksburg, Mississippi, USA.

Angermeier, P. L., and J. R. Karr. 1994. Biological integrity versus biological diversity as policy directives. BioScience 44:690–697.

Avise, J. C. 1987. Identification and interpretation of mitochondrial DNA stocks in marine species. Pages105–136 *in* H. Kumpf and E. L. Nakamura, editors. Proceedings of the stock identification workshop. N.O.A.A., Panama City.

Avise, J. C. 1989. A role for molecular genetics in the recognition and conservation of endangered species. Trends in Ecology and Evolution 4:279–281.

Avise, J. C. 1992. Molecular population structure and the biogeographic history of a regional fauna: a case history with lessons for conservation biology. Oikos 63:62–76.

Avise, J. C. 1994. Molecular markers, natural history and evolution. Chapman and Hall, New York, USA.

Avise, J. C. 1998. The history and purview of phylogeography: a personal reflection. Molecular Ecology 7:371–379.

Avise, J. C., and C. F. Aquadro. 1982. A comparative summary of genetic distances in the vertebrate. Evolutionary Biology 15:51–185.

Avise, J. C., J. Arnold, R. M. Ball, E. Bermingham, T. Lamb, J. E. Neigel, C. A. Reed, and N. C. Saunders. 1987. Intraspecific phylogeography: the mitochondrial DNA bridge between population genetics and systematics. Annual Review of Ecology and Systematics 18:489–522.

Barber, P. H. 1999. Phylogeography of the canyon treefrog, *Hyla arenicolor* (Cope) based on mitochondrial DNA sequence data. Molecular Ecology 8:547–562.

Bonnicksen, T. M., M. K. Anderson, H. T. Lewis, C. E. Kay, and R. Knudson. 1999. Native American influences on the development of forest ecosystems. Pages 439–470 *in* R. C. Szaro, N. C. Johnson, W. T. Sexton, and A. J. Malk, editors. Ecological stewardship: a common reference for ecosystem management, Volume II. Elsevier Science, Ltd., Oxford, UK.

Bormann, F. H., and G. E. 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, USA.

Bouzat, J., H. Lewin, and K. Paige. 1998. The ghost of genetic diversity past: historical DNA analysis of the Greater Prairie Chicken. American Naturalist 152:1–6.

Brown, J. H. 1971. Mammals on mountaintops: noninsular biogeography. American Naturalist 105:467–478.

Brown, J. H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effects of immigration on extinction. Ecology 58:445–449.

Canham, C. D., and O. L. Loucks. 1984. Catastrophic windthrow in the presettlement forests of Wisconsin. Ecology 65:803–809.

Caro, T. M., and M. K. Laurenson. 1994. Ecological and genetic factors in conservation—a cautionary tale. Science 183:1748–1752.

Carpenter, C. A., W. N. Busch, D. T. Cleland, J. Gallegos, R. Harris, R. Holm, C. Topik, and A. Williamson. 1999. The use of ecological classification in management. Pages 395–430 *in* R. C. Szaro, N. C. Johnson, W. T. Sexton, and A. J. Malk, editors. Ecological stewardship: a common reference for ecosystem management, Volume II. Elsevier Science, Ltd., Oxford, UK.

Carroll, R., J. Belnap, B. Breckenridge, and G. Meffe. 1999. Ecosystem sustainability and condition. Pages 583–598 *in* R. C. Szaro, N. C. Johnson, W. T. Sexton, and A. J. Malk, editors. Ecological stewardship: a common reference for ecosystem management, Volume II. Elsevier Science, Ltd., Oxford, UK.

Chakraborty, R., T. R. Meagher, P. E. Smouse. 1988. Parentage analysis with genetic markers in natural populations. I. The expected proportion of offspring with unambiguous paternity. Genetics 118:527–536.

Christensen, N. L., A. M. Bartuska, J. H. Brown, S. Carpenter, C. D'Antonio, R. Francis, J. F. Franklin, J. A. MacMahon, R. F. Noss, and D. J. Parsons. 1996. The report of the Ecological Society of America committee on the scientific basis for ecosystem management. Ecological Applications 6:665–691.

Clark, J. S. 1988. Effect of climate change on fire regimes in northwestern Minnesota. Nature 334:233–235.

Cleland, T. D., P. E. Avers, W. H. McNab, M. E. Jensen, R. G. Bailey, T. King, and W. E. Russell. 1997. National hierarchical framework of ecological units. Pages 181–200 *in* M. S. Boyce and A. Haney, editors. Ecosystem management: applications for sustainable forest and wildlife resources. Yale University Press, London, UK.

Coltman, D. W., W. D. Bowen, and J. M. Wright. 1998. Birth weight and neonatal survival of harbour seal pups are positively correlated with genetic variation measured by microsatellites. Proceedings of the Royal Society of London Series B 265:803–809.

Coltman, D., J. Pilkington, J. Smith, and J. Pemberton. 1999. Parasite-mediated selection against inbred Soay sheep in a free-living, island population. Evolution 53:1259–1267.

Cooper, A., J. Rhymer, and H. F. James. 1996. Ancient DNA and island endemics. Nature 381:484

Cooperrider, A. Y., R. J. Boyd, and H. R. Stuart. 1986. Inventory and monitoring of wildlife habitat. United States Bureau of Land Management Service Center, Denver, Colorado, USA.

Cornuet, J. M., and G. Luikart. 1996. Description and power analysis of two tests for detecting recent population bottlenecks from allele frequency data. Genetics 144:2001–2014.

Cortner, H. J., J. C. Gordon, P. G. Risser, D. E. Teeguarden, and J. W. Thomas. 1999. Ecosystem management: evolving model for stewardship of the nation's natural resources. Pages 3- 20 *in* R. C. Szaro, N. C. Johnson, W. T. Sexton, and A. J. Malk, editors. Ecological stewardship: a common reference for ecosystem management, Volume II. Elsevier Science, Ltd., Oxford, UK.

Covington, W. W., P. Z. Fule, M. M. Moore, S. C. Hart, T. E. Kolb, J. N. Mast, S. S. Sackett, and M. R. Wagner. 1997. Restoration of ecosystem health in ponderosa pine forests of the Southwest. Journal of Forestry 95:23–29.

Covington, W. W., and M. M. Moore. 1994a. Southwestern ponderosa forest structure and resource conditions: changes since Anglo-American settlement. Journal of Forestry 92:39–47.

Covington, W. W., and M. M. Moore. 1994b. Postsettlement changes in natural fire regimes and forest structure: ecological restoration of old-growth ponderosa pine forests. Journal of Sustainable Forestry 2:153–181.

Covington, W., W. A. Niering, E. Starkeky, and J. Walker. 1999. Ecosystem restoration and management: scientific principles and concepts. Pages 599–617 *in* R. C. Szaro, N. C. Johnson, W. T. Sexton, and A. J. Malk, editors. Ecological stewardship: a common reference for ecosystem management, Volume II. Elsevier Science, Ltd., Oxford, UK.

Craighead, L., D. Paetkau, H. V. Reynolds, E. R. Vyse, and C. Strobeck. 1995. Microsatellite analysis of paternity and reproduction in Arctic grizzly bears. Journal of Heredity 86:55–261.

Crane, M. F., and W.C. Fischer. 1986. Fire ecology of the forest habitat types of central Idaho. United States Forest Service General Technical Report INT-218.

Cruzan, M. 1998. Genetic markers in plant evolutionary ecology. Ecology 79:400–412.

Cutler, A. 1991. Nested faunas and extinction in fragmented habitats. Conservation Biology 5:496–505.

Dahms, C. W., and B. W. Geils, technical editors**.** 1997. An assessment of forest ecosystem health in the Southwest. United States Forest Service General Technical Report RM-295.

Daubenmire, R. 1968. Plant communities: A textbook of plant synecology. Harper and Row, New York, USA.

Elton, C. and M. Nicolson. 1942. The ten-year cycle in numbers of the lynx in Canada. Journal of Animal Ecology 11:215–244.

Engstrom, R. T., S. Gilbert, M. L. Hunter, Jr., D. Merriwether, G. J. Nowacki, and P. Spencer. 1999. Practical applications of disturbance ecology to natural resource management. Pages 313–330 *in* R. C. Szaro, N. C. Johnson, W. T. Sexton, and A. J. Malk, editors. Ecological stewardship: a common reference for ecosystem management, Volume II. Elsevier Science, Ltd., Oxford, UK.

Ernest, H., M. Penedo, B. May, M. Syvanen, and W. Boyce. 2000. Molecular tracking of mountain lions in the Yosemite Valley region in California: genetic analysis using microsatellites and faecal DNA. Molecular Ecology 9:433–442.

Everett, R. L., R. Schellhaas, D. Keenum, D. Spurbeck, and P. Ohlson. 2000. Fire history in the ponderosa pine/Douglas-fir forests on the east slope of the Washington Cascades. Forest Ecology and Management 129:207–225.

Foster, D. R. 1988. Species and stand response to catastrophic wind in central New England, USA. Journal of Ecology 76:135–151.

Franklin, J. F. 1990. Biological legacies: A critical management concept from Mount St. Helen's. Transactions of the North American Wildlife and Natural Resources Conference 55:216–219.

Franklin, J. F. 1993a. Preserving biodiversity: Species, ecosystems, or landscapes? Ecological Applications 3:202–205.

Franklin, J. F. 1993b. The fundamentals of ecosystem management with applications in the Pacific Northwest. Pages 127–144 *in* G. H. Aplet, N. Johnson, J. T. Olson, and V. A. Sample, editors. Defining sustainable forestry. Island Press, Washington, D.C., USA.

Frelich, L. E. 1998. Representing historical conditions in an ecosystem diversity matrix for the Northern Minnesota Peatlands section. Unpublished Report. Boise Cascade Corporation.

Gaines, W. L., R. J. Harrod, and J. F. Lehmkuhl. 1999. Monitoring biodiversity: quantification and interpretation. United States Forest Service General Technical Report PNW-443.

Galatowitsch, S. M. 1990. Using the original land survey notes to reconstruct presettlement landscapes in the American West. Great Basin Naturalist 50:181–191.

Ghent, A. W. 1963. Kendall's "tau" coefficient as an index of similarity in comparisions of plant and animal communities. Canadian Entomologist 95:568–575.

Gibbs, H., P. Weatherhead, P. Boag, B. White, L. Tabak, et al. 1990. Realized reproductive success of polygynous red-winged blackbirds revealed by DNA markers. Science 250:1394–1397.

Gilpin, M. E., and M. E. Soulé. 1986. Minimum viable populations: processes of species extinction. Pages 19–34 *in* M. Soulé, editor. Conservation biology: the science of scarcity and diversity. Sinauer Associates Inc, Sunderland, Massachusetts, USA.

Girman, D. J., M. G. Mills, E. Geffen, and R. K. Wayne. 1997. A molecular genetic analysis of social structure, dispersal, and interpack relationships of the African wild dog (*Lycaon pictus*). Behavioral Ecology and Sociobiology 40:187–198.

Goodman, S. W. 1994. Implementation of ecosystem management in the Department of Defense. Memorandum from the Office of the Under Secretary of Defense.

Goossens, B., L. Graziani, L. P. Waits, E. Farand, S. Magnolon, J. Coulton, M. C. Bel, P. Taberlet, and D. Allaine. 1998. Extra-pair paternity in the monogamous Alpine marmot revealed by nuclear DNA microsatellite analysis. Behavioral Ecology and Sociobiology 43:281–288.

Gowaty, P., and A. Karlin. 1984. Multiple paternity and paternity in single broods of apparently monogamous eastern bluebirds (*Sialia sialis*). Behavioral Ecology and Sociobiology 15:91–95.

Grayson, D. K. 1987. The biogeographic history of small mammals in the Great Basin: Observation on the last 20,000 years. Journal of Mammalogy 68:359–375.

Grayson, D. K., and S. D. Livingston. 1993. Missing mammals on Great Basin Mountains: Holocene extinctions and inadequate knowledge. Conservation Biology 7:527–532.

Gros, P. M., M. J. Kelly, and T. M. Caro. 1996. Estimating carnivore densities for conservation purposes: indirect methods compared to baseline demographic data. Oikos 77:197–206.

Grumbine, R. E. 1994. What is ecosystem management? Conservation Biology 8:27–38.

Hansen, A., and J. Rotella. 1999. Abiotic factors. Pages 161–209 *in* M. L. Hunter, Jr., editor. Maintaining biodiversity in forest ecosystems. Cambridge University Press, Cambridge, UK.

Hanski, I. 1998. Metapopulation dynamics. Nature 396:41–49.

Hanski, I. A., and M. E. Gilpin, editors**.** 1997. Metapopulation biology: ecology, genetics, and evolution. Academic Press, San Diego, California, USA.

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, Jr., and K. W. Cummins. 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research 15:133–302.

Harrod, R. J., W. L. Gaines, W. E. Hartl, and A. Camp. 1998. Estimating historical snag density in dry forests east of the Cascade Range. United States Forest Service General Technical Report PNW-428.

Hartl, D., and A. Clark. 1989. Principles of population genetics. Sinauer Associates Inc, Sunderland, Massachusetts, USA.

Hartley, M. J., and M. L. Hunter. 1998. A metaanalysis of forest cover, edge effects, and artificial nest predation rates. Conservation Biology 12: 465–69.

Harwell, M. A., V. Myers, T. Young, A. Bartuska, N. Gassman, J. H. Gentile, C. C. Harwell, S. Appelbaum, J. Barko, B. Causey, C. Johnson, A. McLean, R. Smola, P. Templet, and S. Tosini. 1999. A framework for an ecosystem management report card. BioScience 49:543–556.

Hastings, J. R., and R. M. Turner. 1965. The changing mile: An ecological study of vegetation change with time in the lower mile of an arid and semiarid region. University of Arizona Press, Tucson, USA.

Haufler, J. B. 1994. An ecological framework for forest planning for forest health. Journal of Sustainable Forestry 2:307–16.

Haufler, J. B. 1999a. Strategies for conserving terrestrial biodiversity. Pages 17–30 *in* Baydack, R. K., H. Campa, III, and J. B. Haufler, editors. Practical approaches to the conservation of biological diversity. Island Press, Washington, D.C., USA.

Haufler, J. B. 1999b. Contrasting approaches for the conservation of biological diversity. Pages 219–232 *in* Baydack, R. K., H. Campa, III, and J. B. Haufler, editors. Practical approaches to the conservation of biological diversity. Island Press, Washington, D.C., USA.

Haufler, J. B. 2000. Ecosystem management: from rhetoric to reality. Transactions of the North American Wildlife and Natural Resources Conference 65:11–33.

Haufler, J. B., C. M. Mehl, and G. J. Roloff. 1996. Using a coarse-filter approach with species assessment for ecosystem management. Wildlife Society Bulletin 24:200–208.

Haufler, J. B., C. M. Mehl, and G. J. Roloff. 1999. Conserving biological diversity using a coarse filter approach with a species assessment. Pages 107–125 *in* Baydack, R. K., H. Campa, III, and J. B. Haufler, editors. Practical approaches to the conservation of biological diversity. Island Press, Washington, D.C., USA.

Hayek, L. C., and M. A. Buzas. 1997. Surveying natural populations. Columbia University Press, New York, USA.

Heinselman, M. L. 1973. Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. Quaternary Research 3:329–382.

Herkert, J. R., D. W. Sample, and R. E. Warner. 1996. Management of midwestern grassland birds. United States Forest Service General Technical Report NC-187.

Hilderbrand, G. V., S. D. Farley, C. T. Robbins, T. A. Hanley, K. Titus, and C. Servheen. 1996. Use of stable isotopes to determine diets of living and extinct bears. Canadian Journal of Zoology 74:2080–2088.

Hillis, D., C. Moritz, and B. Mable. 1996. Molecular systematics. Sinauer Associates Inc, Sunderland, Massachusetts, USA.

Holling, C. S., and G. K. Meffe. 1996. Command and control and the pathology of natural resource management. Conservation Biology 10:328–337.

Hughes, C. 1998. Integrating molecular techniques with field methods in studies of social behavior: a revolution results. Ecology 79:383–399.

Hunsaker, C. T., and D. E. Carpenter. 1990. Environmental monitoring and assessment program: Ecological indicators. United States Environmental Protection Agency EPA/600/3–90/060.

Ives, R. L. 1942. The beaver-meadow complex. Journal of Geomorphology 5:191–203.

Jacoby, M. E., G. V. Hilderbrand, C. Servheen, C. C. Schwartz, S. M. Arthur, T. A. Hanley, C. T. Robbins, and R. Michener. 1999. Trophic relations of brown and black bears in several western North American ecosystems. Journal of Wildlife Management 63:921–929.

Johnson, D. H. 1994. Population analysis. Pages 419–444 *in* T. A. Bookhout, editor. Research and management techniques for wildlife and habitat. The Wildlife Society, Bethesda, Maryland, USA.

Karr, J. R. 1991. Biological integrity: A long-neglected aspect of water resource management. Ecological Applications 1:66–84.

Karr, J. R. and D. R. Dudley. 1981. Ecological perspective on water quality goals. Environmental Management 5:55–68.

Kaufmann, M. R., R. T. Graham, D. A. Boyce, Jr., W. H. Moir, L. Perry, R. T. Reynolds, **R. Bassett, P. Mehlhop, C. B. Edminster, W. M. Block, and P. S. Corn.** 1994. An ecological basis for ecosystem management. United States Forest Service General Technical Report RM-246.

Kaye, J. P., and S. C. Hart. 1998. Ecological restoration alters nitrogen transformations in a ponderosa pine-bunchgrass ecosystem. Ecological Applications 8:1052–1060.

Kenna, J. G., G. R. Robinson, Jr., B. Pell, M. A. Thompson, and J. McNeel. 1999. Ecosystem restoration: a manager's perspective. Pages 619–676 *in* R. C. Szaro, N. C. Johnson, W. T. Sexton, and A. J. Malk, editors. Ecological stewardship: a common reference for ecosystem management, Volume II. Elsevier Science, Ltd., Oxford, UK.

Kernohan, B. J., and J. B. Haufler. 1999. Implementation of an effective process for the conservation of biological diversity. Pages 233–249 *in* R. K. Baydack, H. Campa, III, and J. B. Haufler, editors. Practical approaches to the conservation of biological diversity. Island Press, Washington, D.C., USA.

Kernohan, B. J., J. Kotar, K. Dunning, and J. B. Haufler. 1999. Ecosystem diversity matrix for the Northern Minnesota and Ontario Peatlands landscape: Technical manual. Unpublished Report. Boise Cascade Corporation.

Keystone Center. 1996. The Keystone national policy dialogue on ecosystem management: final report. The Keystone Center, Keystone, Colorado, USA.

Kirtland's Warbler Recovery Team. 1985. Kirtland's Warbler recovery plan. United States Fish and Wildlife Service. Twin Cities, Minnesota, USA.

Knight, D. H. 1987. Parasites, lightening, and the vegetation mosaic in wilderness landscapes. Pages 61–80 *in* M. G. Turner, editor. Landscape heterogeneity and disturbance. Springer-Verlag, New York, USA.

Koehn, R., W. Diehl, and T. Scott. 1988. The differential contribution by individual enzymes of glycolysis and protein catabolism to the relationship between heterozygosity and growth rate in the coot clam, *Mulinia lateralis*. Genetics 118:121–130.

Kohn, M. H., and R. K. Wayne. 1997. Facts from feces revisited. Trends in Ecology and Evolution 12:223–227.

Kohn, M. H., E. C. York, D. A. Kamradt, G. Haught, R. M. Sauvajot, and R. K. Wayne. 1999. Estimating population size by genotyping faeces. Proceedings of the Royal Society of Biological Sciences London Series B 266:657–663

Laikre, L., R. Andren, H. O. Larsson, and N. Ryman. 1996. Inbreeding depression in brown bears. Biological Conservation 76:69–72.

Lamberti, G. A., S. V. Gregory, L. R. Ashkenas, R. C. Wildman, and K. M. S. Moore. 1991. Stream ecosystem recovery following a catastrophic debris flow. Canadian Journal of Fisheries and Aquatic Science 48:196–208.

Lancia, R. A., J. D. Nichols, and K. H. Pollack. 1994. Estimating the number of animals in wildlife populations. Pages 215–253 *in* T. A. Bookhout, editor. Research and management techniques for wildlife and habitat. The Wildlife Society, Bethesda, Maryland, USA.

Lande, R. 1988. Genetics and demography in biological conservation. Science 241:1455–1460.

Landres, P. B., J. Verner, and J. W. Thomas. 1988. Ecological use of vertebrate indicator species: A critique. Conservation Biology 2:316–328.

Landres, P. B., P. Morgan, and F. J. Swanson. 1999. Evaluating the utility of natural variability concepts in managing ecological systems. Ecological Applications 9:1179–1188.

Leary, R. F., F. W. Allendorf , and S. H. Forbes. 1993. Conservation genetics of bull trout in the Columbia and Klamath River drainages. Conservation Biology 7:857–865.

Litvaitis, J. A., K. Titus, and E. M. Anderson. 1994. Measuring vertebrate use of terrestrial habitats and foods. Pages 254–275 *in* T. A. Bookhout, editor. Research and management techniques for wildlife and habitats. The Wildlife Society, Bethesda, Maryland, USA.

Lugo, A. E., J. S. Baron, T. P. Frost, T. W. Cundy, and P. Dittberner. 1999. Ecosystem processes and functioning. Pages 219–254 *in* R. C. Szaro, N. C. Johnson, W. T. Sexton, and A. J. Malk, editors. Ecological stewardship: a common reference for ecosystem management, Volume II. Elsevier Science, Ltd., Oxford, UK.

Luikart, G., and J. M. Cornuet. 1998. Empirical evaluation of a test for identifying recently bottlenecked populations from allele frequency data. Conservation Biology 12:228–237.

Luikart, G., J. M. Cornuet, and F. W. Allendorf. 1999. Temporal changes in allele frequencies provide estimates of population bottleneck size. Conservation Biology 13:523–530.

Luikart, G., W. B. Sherwin, B. M. Steele, and F. W. Allendorf. 1998. Usefulness of molecular markers for detecting population bottlenecks via monitoring genetic change. Molecular Ecology 7:963–974.

MacCleery, D. W., and D. C. Le Master. 1999. The historical foundation and the evolving context for natural resource management on Federal lands. Pages 517–556 *in* R. C. Szaro, N. C. Johnson, W. T. Sexton, and A. J. Malk, editors. Ecological stewardship: a common reference for ecosystem management, Volume II. Elsevier Science, Ltd., Oxford, UK.

Mace, G. M., T. B. Smith, M. W. Bruford, and R. K. Wayne. 1996. An overview of the issues. Pages 3–21 *in* T. B. Smith and R. K. Wayne, editors. Molecular genetic approaches in conservation. Oxford University Press, Oxford, UK.

Marschner, F. J. 1974. Original vegetation of Minnesota. United States Forest Service. North Central Forest Experiment Station, St. Paul, Minnesota, USA.

Marshall, E., R. Haight, and F. R. Homans. 1998. Incorporating environmental uncertainty into species management decisions: Kirtland's warbler habitat management as a case study. Conservation Biology 12:975–985.

Maurer, S., P. Egli, D. Spinnler, and C. Korner. 1999. Carbon and water fluxes in Beech-Spruce model ecosystems in response to long-term exposure to atmospheric CO_2 enrichment and increased nitrogen deposition. Functional Ecology 13:748–755.

McCullough, D. R., editor**.** 1996. Metapopulations and wildlife conservation. Island Press. Washington, D.C., USA.

McGarigal, K., and B. J. Marks. 1995. FRAGSTATS: Spatial pattern analysis program for quantifying landscape structure. United States Forest Service General Technical Report PNW-351.

McNab, W. H, and P. E. Avers. 1994. Ecological subregions of the United States: section descriptions. United States Forest Service Administrative Publication WO-WSA-5.

Meffe, G. K., and C. R. Carroll. 1997. Principles of conservation biology. Sinauer Associates, Sunderland, Massachusetts, USA.

Menges, E. S. 1990. Population viability analysis for an endangered plant. Conservation Biology 4:52–62.

Millar, C. I., and W. B. Woolfenden. 1999. The role of climate change in interpreting historic variability. Ecological Applications 9:1207–1216.

Molecular Ecology. 1998. Molecular Ecology 7(4).

Moore, M. M., W. W. Covington, and P. Z. Fulé. 1999. Reference conditions and ecological restoration: A southwestern ponderosa pine perspective. Ecological Applications 9:1266–1277.

Morgan, P., G. H. Aplet, J. B. Haufler, H. C. Humphries, M. M. Moore, and W. D. Wilson. 1994. Historical range of variability: A useful tool for evaluating ecosystem change. Journal of Sustainable Forestry 2:87–112.

Moritz, C. 1994. Defining "evolutionarily significant units" for conservation. Trends in Ecology and Evolution 9:373–375.

Moritz, C., and D. Faith. 1998. Comparative phylogeography and the identification of genetically divergent areas for conservation. Molecular Ecology 7:419–429.

Moritz, C., and E. Bermingham. 1998. Comparative phylogeography: concepts and applications. Molecular Ecology 7:367–369.

Morrison, M. L., B. G. Marcot, and R. W. Mannan. 1992. Wildlife-habitat relationships concepts and applications. University of Wisconsin Press, Madison, USA.

Moyle, P. B., and P. J. Randall. 1996. Biotic integrity of watersheds. Pages 975–985 *in* Sierra Nevada Ecosystem Report to Congress, Vol. II, Assessments and scientific basis for management options. University of California, Davis, Wildland Resources Center Report 37.

Moyle, P. B., and P. J. Randall. 1998. Evaluating biotic integrity of watersheds in the Sierra Nevada, California. Conservation Biology 12:1318–1326.

Mueller-Dombois, E., and H. Ellenberg. 1974. Aims and methods of vegetation ecology. John Wiley and Sons, New York, USA.

Mundy, N., C. Winchell, T. Burr, and D. Woodruff. 1997. Microsatellite variation and microevolution in the critically endangered San Clemente Island loggerhead shrike (*Lanius ludovicianus mearnsi*). Proceedings of the Royal Society of London Series B 264:869–875.

Murphy, D. D., K. E. Freas, and S. B. Weiss. 1990. An environment-metapopulation approach to population viability analysis for a threatened invertebrate. Conservation Biology 4:41–51.

Nantel, P., D. Gagnon, and A. Nault. 1996. Population viability analysis of American ginseng and wild leek harvested in stochastic environments. Conservation Biology 10:608–621.

Nelson, M. D., and R. R. Buech. 1996. A test of 3 models of Kirtland's warbler habitat suitability. Wildlife Society Bulletin 24:89–97.

Nielsen, E., M. Hansen, and V. Loeschcke. 1999. Genetic variation in time and space: microsatellite analysis of extinct and extant populations of Atlantic salmon. Evolution 53:261–268.

Noss, R. F. 1987. From plant communities to landscapes in conservation inventories: A look at the Nature Conservancy (USA). Biological Conservation 41:11–37.

Noss, R. F. 1990. Indicators for monitoring biodiversity: a hierarchical approach. Conservation Biology 4:355–364.

O'Brien, S., and J. Evermann. 1988. Interactive influence of infectious disease and genetic diversity in natural populations. Trends in Ecology and Evolution 3:86–96.

O'Neill, R. V., C. T. Hunsaker, D. Jones, J. M. Klopatek, V. H. Dale, M. G. Turner, R. H. Gardner, and R. Graham. 1995. Sustainability at landscape and regional scales: The biogeophysical foundations. Pages 137–143 *in* M. Munasinghe and W. Shearer, editors. Sustainability at landscape and regional scales. United Nations University, Washington, D.C., USA.

O'Neill, R. V., C. T. Hunsaker, K. B. Jones, K. H. Riitters, J. D. Wickham, P. M. Schwartz, I. A. Goodman, B. L. Jackson, and W. S. Baillargeon. 1997. Monitoring environmental quality at the landscape scale. BioScience 47:513–519.

O'Neill, R. V., J. R. Krummel, R. H. Gardner, G. Sugihara, B. Jackson, D. L. DeAngelis, B. T. Milne, M. G. Turner, B. Zygmunt, S. W. Christensen, V. H. Dale, and R. L. Graham. 1988. Indices of landscape pattern. Landscape Ecology 1:153–162.

Odum, E. P. 1950. Bird population of the Highlands (North Carolina) Plateau in relation to plant succession and avian invasion. Ecology 31:587–605.

Odum, E. P., editor**.** 1971. Fundamentals of ecology. Saunders, Philadelphia, Pennsylvania, USA.

Ohio EPA. 1988. Biological criteria for the protection of aquatic life. Ohio Environmental Protection Agency, Division of Water Quality Monitoring and Assessment, Surface Water Section, Columbus, USA.

Paetkau, D., L. P. Waits, P. L. Clarkson, L. Craighead, and C. Strobeck. 1997. An empirical evaluation of genetic distance statistics using microsatellite data from bear (Ursidae) populations. Genetics 147:1943–1957.

Paetkau, D., W. Calvert, I. Stirling, and C. Strobeck. 1995. Microsatellite analysis of population structure in Canadian polar bears. Molecular Ecology 4:347–354.

Parker, P. G., A. A. Snow, M. D. Schug, G. C. Booton, and P. A. Fuerst. 1998. What molecules can tell us about populations: choosing and using a molecular marker. Ecology 79:361–382.

Patterson, B. D. 1984. Mammalian extinction and biogeography in the southern Rocky Mountains. Pages 247–293 *in* M. H. Nitecki, editor. Extinction. University of Chicago Press, Chicago, Illinois, USA.

Periman, R. D., C. Reid, M. K. Zweifel, G. McVicker, and D. Huff. 1999. Human influences on the development of North American landscapes: applications for ecosystem management. Pages 471–492 *in* R. C. Szaro, N. C. Johnson, W. T. Sexton, and A. J. Malk, editors. Ecological stewardship: a common reference for ecosystem management, Volume II. Elsevier Science, Ltd., Oxford, UK.

Plafkin, J. L., M. T. Barbour, K. D. Porter, S. K. Gross, and R. M. Hughes. 1989. Rapid bioassessment protocols for use in streams and rivers: Benthic macroinvertebrates, and fish. United States Environmental Protection Agency EPA/444/4–89–001.

Poff, N. L ., and J. V. Ward. 1989. Implications of streamflow variability and predictability for lotic community structure: A regional analysis of streamflow patterns. Canadian Journal of Aquatic Sciences 46:1805–1818.

Poff, N. L., J. D. Allan, M. B. Bain, J. R. Karr, B. D. Richter, R. E. Sparks, and J. C. Stromberg. 1997. The natural flow regime. BioScience 47:769–784.

Propst, J. R., and J. Weinrich. 1993. Relating Kirtland's warbler population to changing landscape composition and structure. Landscape Ecology 8:257–271.

Pulliam, H. R. 1988. Sources, sinks and population regulation. American Naturalist 132:652–661.

Quattro, J., and R. Vrijenhoek. 1989. Fitness differences among remnant populations of the endangered Sonoran topminnow. Science 245:976–978.

Queller, D. C., J. E. Strassmann, and C. R. Hughes. 1993. Microsatellites and kinship. Trends in Ecology and Evolution 8:285–288.

Queller, D., and K. Goodnight. 1989. Estimating relatedness using genetics markers. Evolution 43:258–275.

Quigley, T. M., and S. J. Arbelbide, editors**.** 1997. An assessment of ecosystem components in the interior Columbia Basin and portions of the Klamath and Great Basins. United States Forest Service General Technical Report PNW-405.

Raymer, D. F. 1996. Current and long-term effects of ungulate browsing on aspen stand characteristics in northern lower Michigan. M. S. Thesis. Michigan State University. East Lansing, USA.

Reed, J. M., P. D. Walters, and J. R. Doerr. 1988. Minimum viable population size of the red-cockaded woodpecker. Journal of Wildlife Management 52:385–91.

Rhymer, J., and D. Simberloff. 1996. Extinction by hybridization and introgression. Annual Review of Ecology and Systematics 27:83–109.

Richter, B. D., J. V. Baumgartner, J. Powell, and D. P. Braun. 1996. A method for assessing hydrologic alteration within ecosystems. Conservation Biology 10:1163–1174.

Richter, B. D., J. V. Baumgartner, J. Powell, and D. P. Braun. 1997. How much water does a river need? Freshwater Biology 37:231–239.

Robbins, C. S., J. R. Sauer, and B. G. Peterjohn. 1992. Population trends and management opportunities for neotropical migrants. Pages 17–23 *in* D. M. Finch, and P. W. Stangel, editors. Status and management of neotropical migratory birds. United States Forest Service General Technical Report RM-229.

Roloff, G. J., and J. B. Haufler. 1997. Establishing population viability planning objectives based on habitat potentials. Wildlife Society Bulletin 25:895–905.

Ryel, L. A. 1981. Population change in the Kirtland's warbler. Jack-Pine Warbler 59:77–90.

Sallabanks, R., P. J. Heglund, J. B. Haufler, B. A. Gilbert, and W. Wall. 1999. Forest fragmentation of the Inland West: issues, definitions and potential study approaches for forest birds. Pages 187–199 *in* J. A. Rochelle, L. A. Lehmann, and J. Wisniewski, editors. Forest fragmentation: wildlife and management implications. Brill, Leiden, Netherlands.

Schemske, D., and R. Lande. 1985. The evolution of self-fertilization and inbreeding depression in plants. II. Empirical observations. Evolution 39:41–52.

Schowalter, T. D. 1985. Adaptations of insects to disturbance. Pages 235–252 *in* S. T. A. Pickett and P. S. White, editors. The ecology of natural disturbance and patch dynamics. Academic Press, New York, USA.

Schroeder, R. L. 1982. Habitat suitability index models: Yellow-headed blackbird. U.S. Fish and Wildlife Service Biological Report FWS-OBS-82/10.26.

Scott, J. M. 1993. Gap analysis: a geographic approach to protection of biological diversity. Wildlife Monographs 123.

Short, H. L. 1984. Habitat suitability index models: Western grebe. United States Fish and Wildlife Service FWS/OBS-82/10.69.

Short, H. L. 1985. Habitat suitability index models: Red-winged blackbird. United States Fish and Wildlife Service Biological Report 82(10.95).

Simberloff, D. 1998. Flagships, umbrellas, and keystones: Is single-species management passé in the landscape era? Biological Conservation 83:247–257.

Skovlin, J. M., and J. W. Thomas. 1995. Interpreting long-term trends in Blue Mountain ecosystems from repeat photography. United States Forest Service Research Paper PNW-315.

Slatkin, M. 1985. Rare alleles as indicators of gene flow. Evolution 39:53–65.

Sloan, J. P. 1998. Historical density and stand structure of an old-growth forest in the Boise Basin in central Idaho. Pages 258–266 *in* L. A. Brennan, and T. L. Pruden, editors. Fire in ecosystem management: shifting the paradigm from suppression to prescription. Proceedings of the 20th Tall

Timbers Fire Ecology Center Conference. Tall Timbers Research Station, Tallahassee, Florida, USA.

Smith, T. B., M. W. Bruford, and R. K. Wayne. 1993. The preservation of process: the missing element of conservation programs. Biodiversity Letters 1:164–167.

Soltis, P. S., and M. A. Gitzendanner. 1999. Molecular systematics and the conservation of rare species. Conservation Biology 13:471–483.

Spellerberg, I. F. 1995. Monitoring ecological change. Cambridge University Press, Cambridge, UK.

Spies, T., and M. Turner. 1999. Dynamic forest mosaics. Pages 95–160 *in* M. L. Hunter, Jr., editor. Maintaining biodiversity in forest ecosystems. Cambridge University Press, Cambridge, UK.

Stanford, J. A., J. V. Ward, W. J. Liss, C. A. Frissell, R. N. Williams, J. A. Lichatowich, and C. C. Coutant. 1996. A general protocol for restoration of regulated rivers. Regulated Rivers, Research and Management 12:391–413.

Steele, R. R. 1994. The role of succession in forest health. Journal of Sustainable Forestry 2:183–190.

Steele, R., S. F. Arno, and K. Deier-Hayes. 1986. Wildfire patterns change in central Idaho's ponderosa pine-Douglas-fir forest. Western Journal of Applied Forestry 1:16–18.

Swanson, F. J., and C. T. Dyrness. 1975. Impact of clear-cutting and road construction on soil erosion by landslides in the western Cascade Range, Oregon. Geology 10:393–396.

Swanson, F. J., J. A. Jones, D. O. Wallin, and J. H. Cissel. 1993. Natural variability: Implications for ecosystem management. Pages 89–103 *in* M. E. Jensen and P. S. Bourgeron, editors. Ecosystem management: principles and applications. Vol. II. Eastside forest ecosystem health assessment. United States Forest Service, Pacific Northwest Research Station, Forestry Sciences Laboratory, Wenatchee, WA.

Swetnam, T. W. and A. M. Lynch. 1993. Multicentury, regional-scale patterns of western spruce budworm epidemics. Ecological Monographs 63:399–424.

Swetnam, T. W. and C. H. Baisan. 1996. Historical fire regime patterns in the southwestern United States since AD 1700. Pages 11–36 *in* C. D. Allen, technical editor. Fire effects in southwestern forests: Proceedings of the second La Mesa fire symposium. United States Forest Service General Technical Report RM-286.

Swetnam, T. W., C. D. Allen, and J. L. Betancourt. 1999. Applied historical ecology: using the past to manage the future. Ecological Applications 9:1189–1206.

Taberlet, P., L. P. Waits, and G. Luikart. 1999. Noninvasive genetic sampling: look before you leap. Trends in Ecology and Evolution 14:323–327.

Taylor, A. C., W. B. Sherwin and R. K. Wayne. 1994. Genetic variation of microsatellite loci in a bottlenecked secies: the northern hairy-nosed wombat. Molecular Ecology 3:277–290.

The Nature Conservancy. 1982. Natural heritage program operations manual. The Nature Conservancy. Arlington, Virginia, USA.

Waples, R. 1991. Pacific salmon, *Orcorhynchus* spp. and the definition of "species" under the Endangered Species Act. Marine Fisheries Review 53:11–22.

Waples, R. 1995. Evolutionarily significant units and the conservation of biological diversity under the Endangered Species Act. Pages 8–27 *in* J. Nielsen, editor. Evolution and the aquatic ecosystem: defining unique units in population conservation. American Fisheries Society, Bethesda, Maryland, USA.

Waples, R. S. 1989. A generalized approach for estimating effective population size from temporal changes in allele frequency. Genetics 121:379–391.

Waser, P. M., and C. Strobceck. 1998. Genetic signatures of interpopulation dispersal. Trends in Ecology and Evolution 13:43–44.

Wayne, R. K., A. Meyer, and N. Lehman. 1990. Large sequence divergence among mitochondrial DNA genotypes within populations of Eastern African black-backed jackals. Proceedings of the National Academy of Sciences 87:1772–1776.

Wayne, R. K., N. Lehman, M. W. Allard, and R. L. Honeycutt. 1992. Mitochondrial DNA variability of the gray wolf: genetic consequences of population decline and habitat fragmentation. Conservation Biology 6:559–569.

Weddell, B. J. 1991. Dispersal and movements of Columbian ground squirrels (*Spermophilus columbianus* (Ord)): are habitat patches like islands? Journal of Biogeography 18:385–394.

Westemeier, R. L., J. D. Brawn, S. A. Simpson, T. L. Esker, R. W. Jansen, J. W. Walk, E. L. Kershner, J. L. Bouzat, and K. N. Paige. 1998. Tracking the long-term decline and recovery of an isolated population. Science 282:1695–1698.

White, P. S., and S. T. A. Pickett. 1985. Natural disturbance and patch dynamics: An introduction. Pages 3–13 *in* S. T. A. Pickett and P. S. White, editors. The ecology of natural disturbance and patch dynamics. Academic Press, San Diego, California, USA.

White, P. S., J. Harrod, W. H. Romme, and J. Betancourt. 1999. Disturbance and temporal dynamics. Pages 281–312 *in* R. C. Szaro, N. C. Johnson, W. T. Sexton, and A. J. Malk, editors. Ecological stewardship: a common reference for ecosystem management, Volume II. Elsevier Science, Oxford, UK.

Whittaker, R. H. 1970. Communities and ecosystems. Macmillan Company, London, UK

Wilson, D., F. Cole, J. Nichols, R. Rundran, and M. Foster. 1996. Measuring and monitoring biological diversity: standard methods for mammals. Smithsonian Institution Press, Washington D.C., USA.

Woods, J. G., D. Paetkau, D. Lewis, B. N. McLellan, M. Proctor, and C. Storbeck. 1999. Genetic tagging free-ranging black and brown bears. Wildlife Society Bulletin 27:616–627.

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