Performance Measures for Ecosystem Management and Ecological Sustainability

THE WILDLIFE SOCIETY
Technical Review 02-1
2002
PERFORMANCE MEASURES FOR ECOSYSTEM MANAGEMENT
AND ECOCLOGICAL SUSTAINABILITY

The Wildlife Society

Members of The Technical Committee on Performance Measures for Ecosystem Management

Jonathan B. Haufler, Chair
Ecosystem Management Research Institute
210 Borderlands
P.O. Box 717
Seeley Lake, MT 59868

Richard K. Baydack
Natural Resource Institute
University of Manitoba
430 Dysart Road
Winnipeg, Manitoba
Canada R3T 2N2

Henry Campa, III
Department of Fisheries and Wildlife
Michigan State University
East Lansing, MI 48824-1222

Brian J. Kernohan
Ecosystem Management Research Institute
2010 Curtis Circle
Boise, ID 83705

Craig Miller
Department of Fish and Wildlife Resources
University of Idaho
Moscow, ID 83844

L. J. O'Neil
U.S. Army Corps of Engineers Waterways Experiment Station
3909 Halls Ferry Road
Vicksburg, MS 39180-6199

Lisette Waits
Department of Fish and Wildlife Resources
University of Idaho
Moscow, ID 83844

Edited by William M. Healy
Foreword

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The Wildlife Society
5410 Grosvenor Lane, Suite 200
Bethesda, MD 20814
(301) 897-9770
Fax: (301) 530-2471


Acknowledgments

Numerous people have contributed to the preparation of this report, and their help is greatly appreciated. Tom Franklin was instrumental in helping form this committee and in supporting its efforts through a long process. Harry Hodgdon provided valuable support and assistance to the committee. TWS Council provided support, advice, and comments, and we especially thank Dianna Hallett and Jerry Kobriger for their reviews of a draft of this report. Chris Risbrubt, Larry Vangilder, and Monica Schwalbach as well as one anonymous reviewer all contributed to the report. Bertie Weddell and Gary Skiba contributed to the committee's work. Final copyediting and layout were performed by The Wildlife Society editorial staff. We thank all for their support, constructive input, and ideas.

Cover: GIS 3-D map of Admiralty Island, Alaska, courtesy of Atterbury Consultants, Beaverton, Oregon.
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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
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.
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 absence of supportive data (Simberloff 1998). For this reason, it is 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 economic objectives with the ecological, the strategic approach must consider the social and economic objectives.

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

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<th>Philosophy</th>
<th>Method of application</th>
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<td>Bioreserve</td>
<td>Human effects have led to loss of biodiversity. Conservation of biodiversity is best achieved by minimizing human activities across a system of core reserve areas with surrounding buffers and corridor connections.</td>
<td>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.</td>
</tr>
<tr>
<td>Coarse filter—habitat diversity</td>
<td>If a diversity of habitat conditions can be maintained across a planning landscape, then biodiversity will be maintained.</td>
<td>Identify different successional conditions, or other indicators of temporal dynamics, and assure that all successional conditions are provided across the landscape.</td>
</tr>
<tr>
<td>Coarse filter—historical range of variability</td>
<td>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.</td>
<td>Determine historical disturbance regimes and manage landscape to stay within the historical range of variability of those disturbances.</td>
</tr>
<tr>
<td>Coarse filter—historical range of variability-based</td>
<td>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.</td>
<td>Determine complex of conditions produced by historical disturbance regimes, and manage to maintain representation of this full complex of conditions.</td>
</tr>
<tr>
<td>Fine filter</td>
<td>Species are the basic units of biodiversity, so if all species can be maintained, biodiversity will be maintained.</td>
<td>Develop approaches that will account for the viability of all species. May use guilds, life forms, umbrella species, indicator species, or other such approaches.</td>
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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.

The Landscape Level
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.

The Ecosystem Level
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.

The Species Level
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.

The Genetic Level
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

Overview: What are the Critical Questions at the Ecosystem Level?
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).

Performance Measures at the Ecosystem Level
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.

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 Lichvar 1995).

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 CO₂ 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, Furbishs loosewort (*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.

**Links Between the Species Level and Other Levels in the Hierarchy**

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**

**Overview: What Are the Critical Questions at the Genetic Level?**

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*) (Colman et al. 1998); growth rate, survival, and fecundity in the Sonoran topominnow (*Poeciliopsis* spp.) (Quattro and Vrijenhook 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 (Colman 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 1992, 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).


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 Strobeck 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 unparentally 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 (Sialis 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). 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.

Links Between the Genetic Level and Other Levels in the Hierarchy

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...

<table>
<thead>
<tr>
<th>Vegetation Growth Stages</th>
<th>Moist Fir</th>
<th>Rich, Moist Fir</th>
<th>Wet Fir/ Ash/Cedar</th>
<th>Wet Fir/ Cedar</th>
<th>Poor, Wet Spruce</th>
</tr>
</thead>
<tbody>
<tr>
<td>Seeding/Sapling</td>
<td>5-9%</td>
<td>5-9%</td>
<td>5-9%</td>
<td>5-8%</td>
<td>18-32%</td>
</tr>
<tr>
<td>Small tree</td>
<td>12-20%</td>
<td>12-20%</td>
<td>8-14%</td>
<td>12-19%</td>
<td></td>
</tr>
<tr>
<td>Shade Intolerant Species</td>
<td>Medium tree</td>
<td>7-10%</td>
<td>7-10%</td>
<td>14-18%</td>
<td>13-17%</td>
</tr>
<tr>
<td>Large tree</td>
<td>3-5%</td>
<td>3-5%</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Small tree</td>
<td>1-2%</td>
<td>1-3%</td>
<td>7-9%</td>
<td>6-8%</td>
<td>15-23%</td>
</tr>
<tr>
<td>Medium tree</td>
<td>Shade Tolerant Species</td>
<td>10-12%</td>
<td>17-18%</td>
<td>19-20%</td>
<td>17%</td>
</tr>
<tr>
<td>Large tree</td>
<td>6%</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Old growth</td>
<td>25-51%</td>
<td>24-29%</td>
<td>20-42%</td>
<td>19-42%</td>
<td>22-46%</td>
</tr>
</tbody>
</table>

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

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.
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 evolutionarily 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 Clemente 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 collaborative 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


Noss, R. F. 1990. Indicators for monitoring biodiversity: a hierarchical
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.
Timbers Fire Ecology Center Conference. Tall Timbers Research Station, Tallahassee, Florida, USA.


The Wildlife Society is the association of wildlife professionals dedicated to excellence in wildlife stewardship through science and education. The goals of The Wildlife Society are to: develop and maintain professional standards for wildlife research and management; enhance knowledge and technical capabilities of wildlife managers; advance professional stewardship of wildlife resources and their habitats; advocate use of sound biological information for wildlife policy and management decisions; and increase public awareness and appreciation of wildlife management. The Wildlife Society, founded in 1937, is a nonprofit organization whose members include research scientists, educators, resource managers, administrators, communications specialists, conservation law enforcement officers, and students from more than 70 countries.