

# Applicability of Montreal Process Criterion 1 – conservation of biological diversity – to rangeland sustainability

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## SUMMARY

Nine indicators of biodiversity conservation have been defined by the nations participating in the Montreal Process for assessing sustainability of temperate and boreal forests. Five of these indicators address compositional and spatial diversity of ecosystems; two address species diversity; and two are indirect measures of genetic diversity. Our objective was to evaluate their applicability for assessing biodiversity on rangeland ecosystems. In addition to assessing applicability, we also address whether data and methods exist to measure each indicator, and review research that is needed to improve implementation. In general, we found no ecological arguments for disqualifying any of the proposed indicators as applicable to rangelands. We did find, however, that unambiguous definitions, data, and methods were woefully lacking. Although some data exist for some indicators and some taxa, none of the indicators can be quantified in a thorough and rigorous manner at a national scale. Consequently, initial assessments of biodiversity on rangelands will have to be based on incomplete data. Research in the areas of definition clarification, inventory design, and testing of critical assumptions is necessary to conduct comprehensive, broad-scale assessments of biodiversity.

## INTRODUCTION

Many definitions of biodiversity have been proposed since its appearance in the literature more than 10 years ago. One of the more frequently cited definitions was offered by The Keystone Center (1991:6) as 'the variety of life and its processes' which encompasses 'the variety of living organisms, the genetic differences among them, and the communities and ecosystems in which they occur'. There is a growing recognition that maintaining this variety is critical to maintaining the goods and services that humans derive from ecosystems (Daily, 1997; Pimentel et

al., 1997). Thus, one of the fundamental goals emerging from the sustainable management paradigm is to use resources in ways that preserve the variety of ecosystems, species, and genes undiminished for future generations (Lubchenco et al., 1991; Meyer and Helfman, 1993; Reid et al., 1993).

Meeting this goal is made difficult by the rapid expansion of human activities and the attendant modification of natural ecosystems (Myers, 1997; Tilman, 1997). The intensification of land use activities to meet human needs has led to

dramatically elevated species extinction rates (Pimm *et al.*, 1995; Chapin *et al.*, 1998) and to much lower biodiversity within managed ecosystems (Rapport *et al.*, 1985). Because the pattern of decreasing diversity with increasing land use intensity appears consistently across systems, changes in biodiversity are invariably discussed as indicators of ecosystem health (Costanza, 1992) and integrity (Karr and Dudley, 1981; Karr, 1990).

The loss of biodiversity under land use intensification is a particularly relevant issue on rangelands because of their vulnerability to land use conversions. Most of the world's mesic rangelands have already been converted to agricultural land (Sala and Paruelo, 1997). The remaining rangelands are increasingly being recognized as reservoirs of biodiversity. For example, arid and semi-arid rangelands in South America have a greater number of mammal species, and more endemic taxa than Amazonian rainforest (Mares, 1992).

The nine indicators accepted by the Montreal Process countries for measuring biodiversity of temperate and boreal forests (see Coulombe, 1995; Canadian Forest Service, 1995) consider ecosystem, species, and genetic components of biodiversity. The purpose of this paper is to evaluate whether these are applicable and adequate for assessing the status biodiversity of rangelands. We also address whether adequate methods and data exist to measure the proposed biodiversity indicators, and summarize research that is needed to implement these indicators for rangeland ecosystems. Although we have drawn examples primarily from rangelands in the United States, this discussion is also broadly applicable in many other countries with extensive rangelands.

## ECOSYSTEM DIVERSITY

Although ecosystems are defined by their characteristic set of plants, animals, physical factors, and their interactions, ecosystem diversity is often measured by the kinds and amount of vegetation types that are found within a geographic area (Hunter, 1991). Often these classifications are hierarchical (see Bailey, 1996) with the broadest levels reflecting, perhaps, the interaction of climate and land form; finer levels may be based on specific edaphic conditions and

the successional and structural stages of vegetation. Assessing habitat suitability for individual plant and animal species inhabiting these ecosystems will require information at even finer scales (Morrison *et al.*, 1992).

In addition to simple measures of ecosystem composition, more complex attributes reflecting the spatial arrangement of land types qualify as measures of ecosystem diversity as well. Spatial attributes such as the degree of fragmentation reflect the dispersion of each ecosystem type across the landscape. The arrangement of ecosystem types affects important ecological processes such as the spread of disturbance or organism movement which are critical to maintaining ecosystem integrity (Saunders *et al.*, 1991).

### **Indicators 1 and 2: Extent of area by rangeland type (Indicator 1) and by successional stage (Indicator 2) relative to total rangeland area**

The simplest measure of ecosystem diversity is the amount of each rangeland type that occurs nationally. Assuming that rangelands can be defined unambiguously (Mitchell and Joyce, 2000), converting area estimates to the proportion of total rangeland area provides an easily interpreted description of rangeland composition. Under this approach, each rangeland type is considered to represent a separate ecosystem and is itself composed of a variety of ecosystem components (Bailey, 1996). The maintenance of sufficient area of each rangeland type is necessary to sustain the complex of ecosystem components (e.g. upland and lowland communities) and associated processes (e.g. hydrological, climatic, other disturbances) necessary to support the suite of species dependent on this complex. If sufficient area of each rangeland type is not maintained, these ecosystems are less likely to have the mix of successional stages necessary to support various species, may become more vulnerable to fragmentation effects, may be more susceptible to invasion by exotic species, or may be predisposed to catastrophic loss from fire or drought.

Ecological processes and the species associated with those processes within a rangeland type are affected by vegetative composition and structural

features. Many species are dependent on one or more successional or structural stage, and all stages should be present with sufficient area and proper juxtaposition to support these species. In human terms, the rangeland successional stages present in an area influence livestock productive capacity, the suitability of the habitat for wildlife and other species, and the rangeland's aesthetic and recreational value.

### Applicability of indicator

Although Indicator 1 is applicable for rangelands at a national level, a current assessment of rangeland types relative to the total rangeland acreage does not account for the significant losses that have occurred historically. In the United States, more than half of those ecosystems determined to be critically endangered (> 98% of the areal extent of the ecosystem has been lost or ecologically degraded) were grasslands and an additional 24% were shrublands (Noss *et al.*, 1995). For example, less than 4% of the tallgrass prairie of the eastern Great Plains of the United States remains, making this the most altered major ecosystem in North America (Samson and Knopf, 1994). Therefore, for rangeland types such as the tallgrass prairie, future trends should be viewed in the context of their already endangered status and not just the simple proportion of remaining rangeland.

Problems with the applicability and interpretation of successional data, combined with an inconsistent approach to measuring successional stages, impede the implementation of Indicator 2 on rangelands. Traditionally, rangeland specialists have estimated the successional state or ecological status of a particular rangeland type by measuring the degree to which current plant species composition compares with the composition expected under the climax or potential natural community (National Research Council, 1994). However, some scientists have questioned the validity of the concept of a single, definable, and predictable climax plant community for all rangelands. Rangeland succession may follow multiple pathways, and the outcome community may be strongly influenced by factors such as the amount and timing of precipitation (Westoby *et al.*, 1989; Friedel, 1991).

### Data availability

Documenting trends in the area of rangeland types is, and will continue to be, hindered by the absence of a generally accepted classification of ecosystem types (see Losos, 1993). Certainly this state of affairs is not for the lack of intellectual effort. There are many 'ecosystem' classifications that have been proposed and implemented. The problem is that ecologists cannot agree on the fundamental elements of a comprehensive classification system that would permit unambiguous communication among conservation scientists (Orians, 1993). The lack of a comprehensive classification system notwithstanding, multi-agency efforts in the United States such as the Multi-Resolution Land Characteristics (MRLC) Consortium are focusing on developing technologies to facilitate national-level vegetation assessments. The goal of MRLC is to generate 30-m resolution land cover data based on both coarse (Advanced Very High Resolution Radiometer [AVHRR]) and medium resolution (Landsat Thematic Mapper [TM]) satellite imagery and field data (Loveland and Shaw, 1996). MRLC also incorporates the North American Landscape Characterization (NALC) project, which consists of landsat 60-m multispectral (MSS) data acquired in the years 1973, 1986, and 1991 (Lunetta and Sturdevant, 1993).

We are aware of only one point-based inventory, the National Resources Inventory (NRI), that could contribute to estimation of change in rangeland ecosystems and permits an estimation of acres of rangeland in various successional stages of development. The NRI is a longitudinal survey designed to assess conditions and trends of soil, water, and related natural resources on non-federal lands throughout the United States (Nusser and Goebel, 1997). Of particular relevance to ecosystem diversity is the estimation of land area in various use and cover classes including rangelands. In addition to being only a partial inventory of the United States land base, another weakness of the NRI with respect to these indicators is that the data collected do not lend themselves to an unambiguous assignment to specific rangeland types and successional stages.

### Research needs

The absence of nationwide maps of pre-settlement

and current vegetation, combined with the lack of comprehensive nationwide monitoring of rangeland types and successional stages, point out the need to develop a functional ecosystem classification and standardized methodology for assessing rangeland successional stages. The range science community also needs to develop criteria for determining when the amount of land area remaining in any given ecosystem type threatens its existence as a functioning ecological entity. There is a growing recognition that ecosystem behaviour can change abruptly in response to some change in the environment - a pattern termed a critical threshold (Turner and Gardner, 1991). Ecosystem destruction, or the loss of land in a particular category, is one environmental change that has been associated with threshold behaviour (Anderen, 1994; Fahrig, 1998). Interpreting when ecosystems can sustainably withstand further area reductions, or when successional processes are not reversible (West, 1999), will require knowledge of when critical thresholds are being approached.

**Indicators 3 and 4: Extent of area by rangeland type (Indicator 3) and by successional stage (Indicator 4) in protected categories as defined by the International Union for Conservation of Nature and Natural Resources (IUCN) or other classification systems**

A common strategy to protect a nation's biological resources is the establishment of parks, refuges, wilderness areas, or other nature reserves that are managed to conserve biodiversity. The protected categories recognized by the IUCN (1994) include: strict nature reserve, wilderness, national park, national monument, habitat/species management area, protected landscape/seascape, and managed resource protected area. This form of biodiversity protection assumes that if good examples of most rangeland types are protected then protection is also offered to the full range of species they contain, which is perhaps most important for those species about which we know the least, including bacteria, fungi, and invertebrates (Noss, 1987; Hunter, 1991; Pressey et al., 1993, Pressey, 1994).

*Applicability of indicators*

There is evidence that protection of key areas has helped sustain some species, including a few that are critically endangered (World Resources Institute, 1992). Unfortunately, in spite of a five-fold increase in the number and extent of protected areas between 1950 and 1990 (IUCN, 1990), the average rate of species extinction increased during the same time period (Myers, 1979). The failure of this protection policy to conserve biodiversity is partially attributed to the fact that many such areas were established for purposes other than biodiversity conservation (Franklin, 1993; Pimm and Lawton, 1998). Park boundaries often follow political lines instead of ecological boundaries, and are often too small to conserve intact ecosystems, which makes them more vulnerable to factors that erode biodiversity from inside (Shafer, 1990) and outside of the park's boundaries (Western, 1989). Past land uses, improper management, lack of support from local residents (World Resources Institute, 1992), and exotic invasions (Usher et al., 1988) are all factors that can make the maintenance of biodiversity in preserves difficult. Furthermore, failure to maintain biodiversity within protected reserves may also stem from inadequate consideration of the processes that have shaped the pattern of rangeland types across the landscape (see Joyce et al., 2000). This is particularly important in many rangeland ecosystems due to the strong role of disturbances such as herbivory and fire in shaping the life history of plants and animals over evolutionary time. If ecological processes are not considered in the management of protected areas then there is a risk that critical disturbance regimes will be disrupted and biodiversity will be lost over time (McNeely, 1994a). The effectiveness of future preserves in conserving biodiversity (and therefore the applicability of these indicators) will likely be enhanced if these factors are taken into account in their selection and management (Franklin, 1993).

*Data availability*

Given the dependence of these indicators on an agreed-upon classification of ecosystem types, it should not be surprising that no single

hensive data source exists to assess the current representation of rangeland ecosystem types within the existing network of conservation lands in the United States. Apart from efforts to partially assess ecosystem representation in protected areas of the United States (Crumpacker *et al.*, 1988), the Gap Analysis Project (administered by the US Geological Survey [Scott *et al.*, 1993]), the Natural Heritage Data Center Network (originally established by The Nature Conservancy [Jenkins, 1985]), and the Research Natural Areas program (administered by the US Forest Service [Ryan *et al.*, 1994]) have the potential to collectively provide a nationally comprehensive perspective on ecosystem conservation. The recently initiated Gap Analysis Program uses state or regional maps of vegetation to determine if there are vegetation types that are inadequately represented in areas currently managed for biodiversity protection (Scott *et al.*, 1993). However, because this programme has been implemented state-by-state, these assessments may lack consistency due to varying ecosystem classification. Therefore, there is a need to adopt consistent methodology before a meaningful national assessment is possible.

### Research needs

Although the establishment of reserves is a common strategy for biological conservation, the total area receiving protection within any one country is usually small. McNeely (1994) estimated that only about 3% of the terrestrial landbase worldwide received strict protection (IUCN protection category I). Increasing competition among alternative land uses can only limit the opportunities for extending reserve networks in the future. Consequently, when there is choice over which areas to add to which protection status, that decision should be informed and in some sense optimal (Pressey *et al.*, 1993). We do not yet know how to allocate limited conservation resources in a way that assures comprehensive protection of ecosystem types (Flather *et al.*, 1997). Nor do we fully understand what degree of protection is needed to sustain various elements, and what mechanisms are involved in whether or not protection of a given rangeland type will sustain viable populations of dependent species.

### Indicator 5: Fragmentation of rangeland types

When ecosystems are fragmented many aspects of habitat configuration can change simultaneously. In general, there is a net reduction in the amount of habitat, a shift toward smaller habitat patch sizes, an increase in the amount of edge habitats, and an increased distance among remaining patches (Opdam, 1991). Decades of research has identified many ecological processes that are affected by habitat fragmentation including: limiting dispersal, interfering with pollination, increasing the likelihood of exotic species invasion, decreasing the spread of natural disturbance agents (e.g. fire), reducing food supplies, and elevating predation rates (Saunders *et al.*, 1991; Arenz and Joern, 1996; Steinauer and Collins, 1996; Robinson, 1998). In addition, a decrease in regional-level connectivity of rangelands could hinder the adaptation of species to climate changes (Peters, 1992).

The alteration of these processes by fragmentation ultimately affects the survival of plant and animal species that inhabit fragmented ecosystems. It is this concern for species survival that has resulted in the ecosystem fragmentation issue being perceived as the principal threat to the viability of most species in temperate climates (Wilcove *et al.*, 1986). Evidence is mounting that fragmentation of natural habitats poses serious survival problems for certain types of species: those that are initially rare or dependent on specialized pollinators (Leach and Givnish, 1996); those that have large home range requirements, such as large carnivores; those that do poorly near ecological edges; and those that have poor dispersal abilities and become marooned on isolated fragments (see Morrison *et al.*, 1992).

### Applicability of indicator

Although many rangeland ecosystems throughout the United States have been severely fragmented since settlement, it is not clear what the impact has been on the ability of fragmented rangelands to retain biodiversity. One reason for this uncertainty is the fact that most fragmentation research has focused on forested ecosystems. The effect of habitat fragmentation on rangeland communities has received comparatively little

attention despite significant losses of rangeland habitats in some regions. Furthermore, the difference between rangelands and other land uses (e.g. improved pasture, cultivation) may not be as ecologically distinct as forest habitats are from other land uses surrounding forest fragments (Herkert, 1994). Consequently, grassland species might respond to habitat fragmentation differently than do forest species.

Although the fragmentation of rangelands into smaller and more dispersed remnant patches will most certainly disrupt many ecological processes, fragmentation per se does not unequivocally lead to ecosystem degradation. A common prediction for fragmented systems is that population persistence of obligate habitat specialists is lower in more fragmented landscapes. However, species persistence is also affected by environmental disturbances (e.g. fire, extreme weather, disease) that can have spatially extensive impacts on populations. There is evidence for some ecosystems that the disruption of these disturbances is more responsible for the loss of species than the fragmentation itself (Leach and Givnish, 1996). Furthermore, by spreading the risk of environmental disturbances among subdivided populations, population persistence may actually increase under fragmentation (Fahrig and Paloheimo, 1988; Hof and Flather, 1996). The interpretation of fragmentation measures must thus be couched within a framework that considers the expected heterogeneity in different rangeland ecosystems as determined by the natural disturbance regimes that have shaped species life histories.

#### Data availability

Data on the size, shape, and dispersion of rangeland ecosystems will likely come from remotely sensed images that will be interpreted into maps of landscape structure. Although point-based inventories can provide estimates of total area in different rangeland ecosystem types and some coarse measures of ecosystem arrangement (Gustafson, 1998), spatially explicit categorical maps are required to fully characterize fragmentation patterns. Several national-level programmes may be refined for broad-scale assessments of ecosystem fragmentation. The

earliest of these programmes was the US Geological Survey, Geographic Information Retrieval and Analysis System (GIRAS) (Mitchell et al., 1977; USDI, Geological Survey, 1987). High-altitude aerial photographs were used to digitize land use and land cover data to 1:250,000 base maps for the entire United States. Because this programme only provides a cross-sectional depiction of landscape structure, trends in fragmentation cannot be estimated. The MRLC consortium (see Indicator 1) shows some promise in providing data useful in assessing fragmentation effects. But, the applicability of both GIRAS and MRLC for assessing fragmentation effects is limited by the coarse land cover classification used. The Anderson et al. (1976) land use and land cover scheme only distinguishes herbaceous, shrub and brush, and mixed rangeland ecosystems.

#### Research needs

Quantifying the size and arrangement of rangeland ecosystems as an indicator of fragmentation assumes that such measures are readily interpretable in terms of their relevance to, and impact on, assessing biodiversity. Since most fragmentation research has focused on forest ecosystems, there is a critical need to extend similar studies into rangelands. As noted by Lubchenco et al. (1991), there is a need for research that will provide insights into how landscape patterns (including fragmentation) affect species population dynamics, dispersal, and diversity. There is also a need to refine the use of remotely sensed satellite imagery to quantify rangeland fragmentation such that rangeland types and the specific agents of fragmentation (e.g. intensive land uses, roads, concentrations of exotic species) can be identified.

#### SPECIES Diversity

Species diversity is the variety of organisms found in a particular location; it varies spatially and temporally, and its interpretation is affected by the extent of the area over which it is measured. Because one of the most widespread signs of ecosystem stress is a reduction in species diversity

(Rapport et al., 1985), diversity measures already have a long history of use in assessing ecosystem well being (Magurran, 1988). Furthermore, diversity has been linked conceptually to notions of system stability, resistance, and recovery (Tilman and Downing, 1996, Solbrig, 1991) and therefore has relevance to environmental sustainability (Goodland, 1995).

Although the concept of diversity is straightforward, its measurement is contentious (Huston, 1994). The difficulty with quantifying diversity is related to the fact that it addresses two components - a simple count of species present in a given area, and the relative abundance of those species. In deriving a composite measure of diversity, ecologists have proposed numerous indices that weight these two components differently. It is the sheer number of indices and the logic for combining the two components into a single index that has fuelled the conflict over how to best measure this attribute of species assemblages (Hurlbert, 1971). To a certain extent the Montreal Process indicators have avoided some of this controversy by defining separate indicators that address these two components independently; species richness is addressed in Indicator 6 (discussed below), while abundance patterns are addressed in Indicator 9 (discussed as a surrogate measure of genetic diversity).

### **Indicator 6: The number of rangeland-dependent species**

A simple count of rangeland-dependent species is the most basic and easily understood measure of diversity. The simplicity of species counts results in a high level of intuitive appeal, and avoids the controversy surrounding the interpretation of more complex diversity indices (Magurran, 1988). However, there is some concern that a count of species at the national level may be insensitive to ecosystem change and therefore difficult to interpret with respect to conservation of biodiversity.

#### **Applicability of indicator**

There is little argument that a count of rangeland-dependent species is a fundamental and applicable attribute of overall biodiversity,

assuming that 'dependent' is defined as those species that obtain at least a portion of their life-history requirements from rangelands. However, we have two concerns about this indicator that relate primarily to its measurement and interpretation.

First, the indicator implies that a single estimate of the species count will be used to assess species richness. As noted by Huston (1994) the total species richness within an area can be difficult, if not impossible, to interpret. Pooling species counts across taxonomic units ignores the ecological differences that exist among species groups and therefore obscures the different mechanisms causing changes in species counts. At a minimum, species counts should be estimated by taxonomic classes for animals and by life forms for plants, or species that share a similar ecological function (such as pollinators and grazers) (West, 1993).

Second, the count of rangeland-dependent species can change under two conditions. Species can become extinct within the country, or exotic species can invade and become established in the species pool. Species extinctions can occur over extremely long periods of time (Tilman et al., 1994) and invasive species populations may remain small and undetected for long periods before a sudden explosive range expansion (Hobbs and Humphries, 1995). Therefore, there is a concern that a simple monitoring of species counts will not be sensitive to changes in ecosystems that presage an erosion of biological diversity. These concerns highlight the need to interpret indicators of biodiversity as an integrated group.

#### **Data availability**

Monitoring species richness over large geographic areas is particularly difficult (Lubchenco et al., 1991). Although it is not surprising that we lack basic inventory information on such obscure species as mites, nematodes, fungi, and bacteria, it is surprising that we generally lack geographically comprehensive and readily accessible data on species distributions for most other taxa as well. Much of the information that could support a national investigation of species richness patterns is restricted to a subset of well-studied taxa and

even this information is not readily available, being widely dispersed among individual investigators, museum records, and government agencies (Brown and Roughgarden, 1990). Some estimates of the number of species associated with rangeland ecosystems do exist (see Flather *et al.*, 1999), but these estimates are based on a mixture of known and hypothesized habitat associations rather than a statistically designed inventory. Estimates of species counts based on habitat associations are known to be inaccurate (Flather *et al.*, 1997) and therefore represent a weaker alternative to estimates derived from actual inventories.

Gap analysis (Scott *et al.*, 1993) is an example of a programme in the United States that has been designed to synthesize existing biodiversity surveys. Basic species distribution information for terrestrial vertebrates and butterflies is being compiled and comes from two sources: point location data on species from such sources as museum records, and predicted distributions from habitat association models. The basic distributional information being collected by the Gap Analysis Program, once completed, will be a valuable data source for documenting species distributions for the United States. However, because the majority of the species distribution data are derived from habitat association models, interpretation of species richness changes over time will have to consider the uncertainty associated with these predictions.

One of the few inventory-based sources for species richness data is the North American Breeding Bird Survey (BBS). The BBS provides information on the presence of bird species at a continental scale. The survey was initiated in 1966 and consists of > 4000 roadside routes located on secondary roads throughout the United States and southern Canada (for details see Droege, 1990). Based on these data, estimates of bird species richness for a given geographic area can be derived. The simplest estimate of bird species richness is the count of birds observed. However, inventories of species presence rarely detect all species in an area (Thompson *et al.*, 1998). Consequently, there is an unknown proportion of species that go unobserved during the inventory process. Recent research is now developing analysis approaches that permit estimates of total species richness, and their associated variances, based on capture-recapture theory (Boulinier *et al.*, 1998, Nichols *et al.*, 1998).

## Research needs

Although biologists recognize that it is currently unfeasible to fully account for the world's biodiversity (Solbrig, 1991), they also recognize that an extensive taxonomically-specific inventory programme for monitoring changes in species richness, even if designed for only a subset of taxa, is essential to documenting spatial and temporal patterns of richness. Although recent efforts have extended BBS-type survey design to amphibians (see the North American Amphibian Monitoring Program, <http://www.im.nbs.gov/amphibs.html>), there is a critical need to develop surveys that will, at a minimum, characterize species richness for other vertebrates, butterflies, and plants (National Research Council, 1992). Concurrent with survey design research, there is a need to develop analysis approaches that will permit tenable estimates of species richness. Recent applications of capture-recapture theory to estimate breeding bird richness local (Boulinier *et al.*, 1998) needs to be extended to other taxa and across broader geographic scales.

### **Indicator 7: The status (rare, threatened, endangered, or extinct) of rangeland-dependent species at risk of not maintaining viable breeding populations, as determined by legislation or scientific assessment**

This indicator is a companion to Indicator 6 because it provides information on those species which are rare, formally listed as threatened or endangered, or extinct. By tracking the conservation status of species on this list, relative improvement or degradation to biodiversity can be gauged by the number and composition of species in each status category. Interpretation of changes to the status lists will require the adoption of consistent criteria used to identify those species that are at risk of not maintaining viable populations.

#### Applicability of indicator

The intent of this indicator is to monitor species at risk of not maintaining viable breeding populations. However, at this point, we lack both

the data and methodology for almost all species to adequately assess population viability. Determining population viability is complex involving detailed information of population demographics, the spatial arrangement of populations on the landscape, and consideration of stochastic events that critically affect species persistence (see Beissinger and Westphal, 1998). In addition, there are no guidelines on what constitutes a valid assessment of population viability and such analyses can be burdened with severe assumptions (Boyce, 1992).

Relying on official lists of species determined to be at risk based on legislative assessment can underestimate the number of species that are actually at risk of extinction. The rate at which species appear on legislated lists of endangerment is often more sensitive to changes in law, budget, bureaucratic process, and listing policy than the biological status of the particular species itself (Langner and Flather, 1994). The formation of a candidate list, which includes species being considered for legal listing, partially offsets that underestimate. Trends in the number of rare species may provide an early warning system for identifying endangerment patterns of the future (Flather *et al.*, 1998). The interpretability of this indicator would be enhanced if the data were summarized as the proportion of species in each taxon, in each status category, relative to the total number of species in that taxonomic group.

### *Data availability*

The World Conservation Monitoring Centre (<http://www.wcmc.org.uk/species/data/index.html>) maintains the IUCN Red List of threatened species by country. The current data base includes animals (including invertebrates) and plants; however, they are not summarized by habitat association. This database will provide a good foundation for developing the list of species of concern in each country, which can be used to identify rangeland-dependent species by incorporating habitat association information provided by other sources. For US species, databases maintained by the US Fish and Wildlife Service and The Nature Conservancy will be valuable resources for identifying those species that are dependent on rangelands (Jenkins, 1988).

### *Research needs*

This indicator points out the need for research designed to refine our ability to assess population viability for species of concern. Central to the issue of population viability is the need for a better understanding of the causes of rarity and the role of stochastic processes in both dooming and rescuing rare species. Further, there is a critical need to quantify thresholds for species and ecosystem persistence. This knowledge, combined with an analysis of trends in candidate species can be used to develop a better 'early warning' system whereby additional listings would become less likely.

## **GENETIC DIVERSITY**

Genetic diversity measures the variability of genes among individuals in a species or population. A species' capacity to evolve depends on sufficient genetic diversity to maintain immediate fitness and adaptability to changing environmental conditions (Schonewald-Cox *et al.*, 1983). Concern about genetic diversity is most serious for populations that are either naturally small and isolated, or populations that have become so because of changes in their environment (see Falk and Holsinger, 1991). Genetic diversity issues may be more profound in rangelands than other systems, due to the highly developed ecotypic differentiation common to many rangeland ecosystems (Risser, 1988). As human population pressures increase, more species may face situations where their genome is likely to become simpler (Soule and Mills, 1998). Genetic simplicity can reduce population viability in a number of ways. Low genetic variability can increase the chance expression of deleterious genes that reduce survival, fertility, or physiological vigor (Wright, 1977). Moreover, loss of genetic diversity could constrain evolutionary flexibility (Primack, 1993) and the ability of populations to respond to environmental changes brought on by climate change, the conversion of natural vegetation to intensive land uses, or competition from exotic species. Unfortunately, genetic diversity is difficult to estimate directly over broad geographic scales for more than a very few species (Smith and Rhodes, 1992) - a fact that likely led the Montreal Process members to select species distribution

and abundance as surrogate measures for evaluating genetic diversity.

### **Indicator 8: Number of rangeland-dependent species that occupy a small portion of their former range**

The geographic ranges of species are constantly fluctuating in response to phenomena such as glaciation, climate fluctuation, vegetation migration, predation, or interspecific competition (MacArthur, 1972). Species that currently occupy only a small portion of their former range have undoubtedly lost genetic variation (Soule and Mills, 1998). The high cost of directly measuring genetic markers makes analysis of range maps an attractive alternative to identifying species where genetic diversity may be declining.

#### *Applicability of indicator*

Because range size is a surrogate for genetic diversity, its applicability as an indicator of biodiversity is conditional on research that establishes a link between range reduction and genetic structure. Of particular importance is the need to specify a general definition of what constitutes a 'small portion' of a species' range. The meaning of 'small' is dependent on the initial distribution of the species. Species that are characterized as having naturally restrictive ranges, as may occur with relic populations or species with very specific habitat requirements, may not tolerate the same relative range reduction as could be tolerated by species that are widely distributed. 'Small' might therefore be defined as 90% of the existing range for a relic population, or as low as 20% for a species that is currently widely distributed. Finally, current species distributions should be compared to some historical standard (e.g. pre-settlement range maps in the United States). Granted, such maps are not available for many species, and historical standards may be difficult to define in some countries (see Angelstam, 1996), but without considering past losses, reductions in genetic viability may be inaccurately assessed.

#### *Data availability*

Assessing the extent to which a species occupies a

restricted portion of its former range requires independent estimates of historic and current geographic range— data that are lacking for many rangeland-dependent species. For some species, past ranges can be estimated from historic journals, naturalist reports, or trapping records; pollen studies can provide historic information for plants; and for some species historic distributions can be inferred from information known about the distribution of their associated plant community. However, none of these data have been consolidated from these diverse sources into a central and readily accessible database. The status of data to estimate current geographic ranges of species is not appreciably different. For many vertebrates, published natural history accounts at a continental scale (e.g. Chapman and Feldhamer, 1982) represent a valuable, yet taxonomically dispersed, source of information on species distributions. For other taxa, standard monitoring systems have been developed (e.g. North American Breeding Bird Survey [Droege, 1990]) or are being designed (e.g. see the North American Amphibian Monitoring Program, <http://www.im.nbs.gov/amphibs.html>). Finally, as discussed in Indicator 6 (number of rangeland-dependent species), the Gap Analysis Program project is in the process of consolidating distributional information on species from diverse sources including museum records and knowledge of species vegetation association patterns (Scott *et al*, 1993) to support prediction of the current ranges of some species in the United States.

#### *Research needs*

Reliable interpretations of trends in this indicator depend on quantifying the relationship between the current extent of a species' range (relative to its former range) and genetic variability. This relationship will not only vary among species (Soule and Mills, 1998), but we also suspect that it will vary with geographic arrangement of extant populations. Range collapse to a single core distribution will likely be characterized by a greater reduction of genetic variation than if a range contracts in a dispersed fashion with several relict populations. The developing methods of spatial statistics associated with geographical population analysis will be vital to specifying standard

protocols for estimating relative area of range occupancy and geographic range fragmentation (see Maurer, 1994). These fundamental measures of geographic range structure, coupled with independent estimates of genetic variation, could then be used to empirically derive the relationship between changes in a species' range and genetic diversity.

### **Indicator 9: Population levels of representative species from diverse habitats monitored across their range**

There are many rangeland-dependent species that rely on some particular type of vegetative structure (e.g. residual cover for nesting prairie chickens [*Tympanuchus cupido*]), range vegetation association (e.g. the association of sage grouse [*Centrocercus urophasianus*] with sagebrush [*Artemisia* spp.]), or ecological process (e.g. fire-dependent species of the tallgrass prairie). These species may also be associated with other species that are dependent on similar conditions. This indicator makes two key assumptions: (1) it assumes that genetic diversity can be tracked by monitoring population levels, and (2) since it is not feasible to monitor all species, it assumes that monitoring populations levels of representative species will allow us to understand population responses of related species.

#### *Applicability of indicator*

As with Indicator 8, a direct link between population levels and genetic diversity has not been quantified for very many, if any, species. Although researchers have simulated the erosion of genetic variation for varying population sizes (e.g. Lacy, 1987), there are few empirical estimates of the rate at which genetic diversity is lost or gained as a function of changing population levels (but see Westemeier *et al.*, 1998). Equally important to an evaluation of how applicable this indicator is to an assessment of rangeland biodiversity is the veracity of using a subset of representative species to monitor the biota as a whole. Using the status of a subset of species to represent others in the community is commonly practiced and recommended in biodiversity conservation issues because basic inventory data

are so sparse (Raven and Wilson, 1992). Unfortunately, tests of this assumption to date do not support its general applicability (Flather *et al.*, 1997, van Jaarsveld *et al.*, 1998).

Even if this indicator proves to be a poor indicator of genetic diversity, it may still be a useful indicator of species diversity. As discussed earlier, species diversity is composed of two components - species richness and relative abundance. Indicator 6 monitors changes in species richness and Indicator 9 monitors changes in species abundance. Since changes in species abundances are a more sensitive measure of environmental stress than species counts alone (Kempton, 1979), this indicator has the potential to provide an early signal of biodiversity degradation.

#### *Data availability*

In the United States, population data for potential representative species at the national level are restricted primarily to game species and breeding birds. Population trends are available for more species of birds than for any other taxon because of the North American Breeding Bird Survey (BBS) (Droege, 1990). The BBS is administered by the Biological Resources Division of the US Geological Survey and has been conducted annually since 1966. The survey provides population trend estimates for more than 420 species whose primary breeding range occurs in the United States and southern Canada.

#### *Research needs*

The paucity of population data for taxa other than game animals or breeding birds points out the need to develop methodologies to monitor long-term trends in other vertebrate, invertebrate, and plant taxa. In the absence of a standardized methodology to monitor population levels of these life forms, it will be impossible to evaluate the relationship between population levels and genetic variability across a diverse taxonomic set, let alone the population viability of these groups.

Apart from developing a suite of monitoring protocols for a diverse set of taxa, an equally important research task is evaluating the veracity of using the abundance of representative species

to reflect population changes in other taxa. Although early indications caution against indiscriminate use of representative species, an unequivocal assessment has been hindered by the absence of a complete biotic inventory for any nation. In addition, there may be ecological circumstances where the use of representative species may be tenable (Flather *et al.*, 1997), and certain attributes of some species may make them more likely to reflect the status of other species (e.g. species that play a vital role in ecosystem function [Westman, 1990; West, 1993]).

## CONCLUSION

The nine indicators of biodiversity defined by the signatory nations participating in the Montreal Process were proposed as a mechanism for monitoring sustainable management of temperate and boreal forests at a national level. We found little evidence that would disqualify these indicators as being potentially useful for assessing biodiversity on rangelands. Although these indicators are generally applicable to rangeland systems, their use to thoroughly assess biodiversity at a national scale is most severely constrained by the lack of an agreed upon system to classify rangeland ecosystem types and successional stages, and by the absence of consistent monitoring strategies for collecting information on rangeland types and representative species. Of the extant data sources in the United States, there was no set that would collectively permit a complete measurement of any of the nine indicators as defined by the Montreal Process countries. Consequently, evaluating the status of biodiversity will have to rely on partial and incomplete information until nationally consistent inventory and monitoring systems are designed to provide the desired data sets.

Given an agreed upon classification system and monitoring protocols, the analysis and interpretation of these biodiversity indicators is dependent on a consistent understanding and application of the indicators. Of utmost importance is an agreed upon standard for comparison. For example, if we compare the current acreage of rangeland types relative to 20 years ago, the trajectory of change is quite different from that identified by a comparison of the current acreage with pre-settlement

figures. Failing to account for past losses will dramatically change our assessment of the degree to which we are conserving biodiversity.

In addition to adapting and customizing inventories of biodiversity indicators, research is also needed to address three themes. First, there is a critical need to understand the dynamics of indicators and when they signify a trajectory toward or away from conserving biodiversity. There is growing evidence that many biological systems exhibit threshold behaviour – thresholds that may be used to signal critical shifts in resource management activities. Whether thresholds exist for any or all of these national-scale indicators is a critical question that research must address if indicator dynamics are to be interpreted effectively. Second, there is a need to better understand the influence of landscape dynamics (including fragmentation) and stochastic events on the population viability of rangeland-dependent species. This knowledge is needed to develop conservation strategies and to better understand mechanisms involved when protection fails. Lastly, research needs to test those assumptions that are critical to evaluations of biodiversity conservation. In several cases, indicators have been defined as surrogate measures for an attribute that is difficult to monitor directly. For example, indicators of genetic diversity are based solely on indirect measures. Unfortunately, our current understanding of ecological systems does not provide definitive support for the use of these surrogates to assess the status of biodiversity at a national scale.

We emphasize that our conclusion about the applicability of these indicators to monitor biodiversity is preliminary. None of these indicators have been tested extensively by any nation for either rangeland or forest ecosystems. These indicators should be treated as hypotheses subject to rejection and modification as data become available. Moreover, these indicators are inherently correlated (ecosystems affect populations, and populations in turn affect genetic variability and species assemblages). Consequently, interpreting these indicators individually will not lead to an unambiguous assessment of biodiversity. Therefore, there is a need to establish analysis protocols for integrating the information among indicators within and across the sustainability criteria established by the Montreal Process.

## REFERENCES

- Anderson, J.R., Hardy, E.E., Roach, J.T. and Winner, R.E. (1976). *A Land Use and Land Cover-Classification System for Use with Remote Sensor Data*, 28 pp. US Department of the Interior, Geological Survey, Geological Survey Professional Paper 964. (Washington, DC)
- Andren, H. (1994). Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos*, 71, 355-66
- Angelstam, T. (1996). The ghost of forest past-natural disturbance regimes as a basis for reconstruction of biologically diverse forests in Europe. In DeGraaf, R.M. and Miller, R.I. (eds) *Conservation of Faunal Diversity in Forested Landscapes*, pp. 287-337. (New York: Chapman and Hall)
- Arenz, C.L. and Joern, A. (1996). Prairie legacies - invertebrates. In Samson, F.B. and Knopf, F.L. (eds) *Prairie Conservation: Preserving North America's Most Endangered Ecosystem*, pp. 91-109. (Washington, DC: Island Press)
- Bailey, R.G. (1996). *Ecosystem Geography*. (New York: Springer-Verlag)
- Beissinger, S.R. and Westphal, M.I. (1998). On the use of demographic models of population viability in endangered species management. *Journal of Wildlife Management*, 62, 821-41
- Boulinier, T., Nichols, J.D., Sauer, J.R., Hines, J.E. and Pollock, K.H. (1998). Estimating species richness: the importance of heterogeneity in species detectability. *Ecology*, 79, 1018-28
- Boyce, M.S. (1992). Population viability analysis. *Annual Review of Ecology and Systematics*, 23, 481-506
- Brown, J.H. and Roughgarden, J. (1990). Ecology for a changing earth. *Ecological Society Bulletin*, 71, 173-88
- Canadian Forest Service (1995). *Criteria and Indicators for the Conservation and Sustainable Management of Temperate and Boreal Forests: the Montreal Process*. (Hull, Quebec: Minister of Supply and Services Canada)
- Chapin, F.S., Sala, O.E., Burke, I.C., Grime, J.P., Hooper, D.U., Lauenroth, W.K., Lombard, A., Mooney, H.A., Mosier, A.R., Naeem, S., Pacala, S.W., Roy, J., Steffen, W.L. and Tilman, D. (1998). Ecosystem consequences of changing biodiversity. *BioScience*, 48, 45-52
- Chapman, J.A. and Feldhamer, G.A. (eds) (1982). *Wild Mammals of North America: Biology, Management, and Economics*. (Baltimore, MD: The Johns Hopkins University Press)
- Costanza, R. (1992). Toward an operational definition of ecosystem health. In Costanza, R., Norton, B.G. and Haskell, B.D. (eds) *Ecosystem Health: New Goals for Environmental Management*, pp. 239-56. (Washington, DC: Island Press)
- Coulombe, M.J. (1995). Sustaining the world's forests: the Santiago Agreement. *Journal of Forestry*, 93, 18-21
- Crumpacker, D.W.; Hodge, S.W., Feidley, D. and Gregg, W.P., Jr. (1988). A preliminary assessment of the status of major terrestrial and wetland ecosystems on Federal and Indian lands in the United States. *Conservation Biology*, 2, 103-15
- Daily, G.C. (1997). Preface. In Dailey, G.C. (ed.) *Nature's Services: Societal Dependence on Natural Ecosystems*, pp. xv-xvi. (Washington, DC: Island Press)
- Droege, S. (1990). The North American breeding bird survey. In Sauer, J.R. and Droege, S. (eds) *Survey Designs and Statistical Methods for the Estimation of Avian Population Trends*, pp. 1-4. US Fish and Wildlife Service Biological Report 90(1). (Washington, DC)
- Fahrig, L. (1998). When does fragmentation of breeding habitat affect population survival? *Ecological Modelling*, 105, 273-92
- Fahrig, L. and Paloheimo, J. (1988). Effect of spatial arrangement of habitat patches on local population size. *Ecology*, 69, 468-75
- Falk, D.A. and Holsinger, K.E. (1991). *Genetics and Conservation of Rare Plants*. (New York: Oxford University Press)
- Flather, C.H., Wilson, K.R., Dean, D.J. and McComb, W.C. (1997). Identifying gaps in conservation networks: of indicators and uncertainty in geographic-based analyses. *Ecological Applications*, 7, 531-42
- Flather, C.H., Knowles, M.S. and Kendall, I.A. (1998). Threatened and endangered species geography: characteristics of hot spots in the conterminous United States. *Bioscience*, 48, 365-76
- Flather, C.H., Brady, S.J. and Knowles, M.S. (1999). *Wildlife Resource Trends in the United States: a Technical Document Supporting the 2000 USDA Forest Service RPA Assessment*. US Department of Agriculture, Forest Service, Rocky Mountain Research Station, General Technical Report. RMRS-GTR 33. (Fort Collins, CO)
- Franklin, J.F. (1993). Preserving biodiversity: species, ecosystems, or landscapes? *Ecological Applications*, 3, 202-5
- Friedel, M.H. (1991). Range condition assessment and concept of thresholds: a viewpoint. *Journal of Range Management*, 44, 422-6
- Goodland, R. (1995). The concept of environmental sustainability. *Annual Review of Ecology and Systematics*, 26, 1-24
- Gustafson, E.J. (1998). Quantifying landscape spatial

- pattern: what is the state of the art? *Ecosystems*, 1, 143-56
- Herkert, J.R. (1994). The effects of habitat fragmentation on midwestern grassland bird communities. *Ecological Applications*, 4, 461-71
- Hobbs, R.J. and Humphries, S.E. (1995). An integrated approach to the ecology and management of plant invasions. *Conservation Biology*, 9, 761-70
- Hof, J. and Flather, C.H. (1996). Accounting for connectivity and spatial correlation in the optimal placement of wildlife habitat. *Ecological Modelling*, 88, 143-55
- Hunter, M.L. (1991). Coping with ignorance: the coarse-filter strategy for maintaining biodiversity. In Kohm, K.A. (ed.) *Balancing on the Brink of Extinction: the Endangered Species Act and Lessons for the Future*, pp. 266-81. (Washington, DC: Island Press)
- Hurlbert, S.H. (1971). The nonconcept of species diversity: a critique and alternative parameters. *Ecology*, 52, 577-86
- Huston, M.A. (1994). *Biological Diversity; the Coexistence of Species on Changing Landscapes*. (New York: Cambridge University Press)
- IUCN (1990). *1990 United Nations List of national Parks and Protected Areas*. (Gland, Switzerland: IUCN)
- IUCN (1994). *Guidelines for Protected Areas Management Categories*. (Cambridge, UK: IUCN)
- Jenkins, R.E. (1985). Information methods: why the heritage programs work. *Nature Conservancy News*, 35 (6), 21-3
- Jenkins, R.E. (1988). Information management for the conservation of biodiversity. In Wilson, E.O. (ed.) *Biodiversity*, pp. 231-9. (Washington, DC: National Academy of Sciences)
- Joyce, L.A., Mitchell, J.E. and Loftin, S. (2000). Applicability of Montreal Process Criterion 3 - maintenance of ecosystem health - to rangeland sustainability. *The International Journal of Sustainable Development and World Ecology*, 7, 107-27
- Karr, J.R. (1990). Biological integrity and the goal of environmental legislation: lessons for conservation biology. *Conservation Biology*, 4, 244-50
- Karr, J.R. and Dudley, D.R. (1981). Ecological perspectives on water quality goals. *Environmental Management*, 5, 55-68
- Kempton, R.A. (1979). Structure of species abundance and measurement of diversity. *Biometrics*, 35, 307-22
- Lacy, R.C. (1987). Loss of genetic diversity from managed populations: interacting effects of drift, mutation, immigration, selection and population subdivision. *Conservation Biology*, 1, 143-58
- Langner, L.L. and Flather, C.H. (1994). *Biological Diversity: Status and Trends in the United States*. US Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, General Technical Report. RM-244. (Fort Collins, CO)
- Leach, M.K. and Givnish, T.J. (1996). Ecological determinants of species loss in remnant prairies. *Science*, 273, 1555-8
- Losos, E. (1993). The future of the US Endangered Species Act. *Trends in Ecology and Evolution*, 8, 332-6
- Loveland, T.R. and Shaw, D. (1996). Multiresolution land characterization: building collaborative partnerships. In Tear, T. and Scott, M. (eds) *Gap Analysis, a Landscape Approach to Biodiversity Planning*, pp. 17-25. (Bethesda, MD: American Society of Photogrammetry and Remote Sensing)
- Lubchenco, J., Olson, A.M., Brubaker, L.B., Carpenter, S.R., Holland, M.M., Hubbell, S.P., Levin, S.A., MacMahon, J.A., Matson, P.A., Melillo, J.M., Mooney, H.A., Peterson, C.H., Pulliam, H.R., Real, L.A., Regal, P.J. and Risser, P.G. (1991). The sustainable biosphere initiative: an ecological research agenda. *Ecology*, 72, 371-412
- Lunetta, R.S. and Sturdevant, J.A. (1993). The North American Landscape Characterization Landsat Pathfinder Project. In Pettinger, L.R. (ed.) *Pecora 12 Symposium, Land Information from Space-Based Systems, Proceedings*, pp. 363-71 (Bethesda, MD: American Society of Photogrammetry and Remote Sensing)
- MacArthur, R.H. (1972). *Geographical Ecology: Patterns in the Distribution of Species*. (New York: Harper and Row)
- Magurran, A.E. (1988). *Ecological Diversity and its Measurement*. (Princeton, NJ: Princeton University Press)
- Mares, M.A. (1992). Neotropical mammals and the myth of Amazonian biodiversity. *Science*, 225, 976-9
- Maurer, B.A. (1994). *Geographical Population Analysis: Tools for the Analysis of Biodiversity*. (Boston, MA: Blackwell Scientific Publications)
- McNeely, J.A. (1994a). Lessons from the past: forests and biodiversity. *Biodiversity and Conservation*, 3, 390-405
- McNeely, J.A. (1994b). Protected areas for the 21st century: working to provide benefits to society. *Biodiversity and Conservation*, 3, 390-405
- Meyer, J.L. and Helfman, G.S. (1993). The ecological basis of sustainability. *Ecological Applications*, 3, 569-71
- Mitchell, J.E. and Joyce, L.A. (2000). Applicability of the Montreal Process to rangelands: introduction. *The International Journal of Sustainable Development and World Ecology*, 7, 77-80

- Mitchell, W.B., Gupitill, S.C., Anderson, K.E., Fagus, R.G. and Hallam C.A. (1977). *GIRAS: a Geographic Information Retrieval and Analysis System for Handling Land Use and Land Cover Data*. US Department of the Interior, Geological Survey, Geological Survey Professional Paper 1059
- Morrison, M.L., Marcot, B.G. and Mannan, R.W. (1992). *Wildlife-Habitat Relationships: Concepts and Applications*. (Madison, WI: The University of Wisconsin Press)
- Myers, N. (1979). *The Sinking Ark*. (Oxford, UK Pergamon Press)
- Myers, N. (1997). Consumption: challenge to sustainable development. *Science*, 276, 53-5
- National Research Council. (1992). *Conserving Biodiversity: A Research Agenda for Development Agencies*. (Washington, DC: National Academy Press)
- National Research Council. (1994). *Rangeland Health: New Methods to Classify, Inventory, and Monitor Rangelands*. (Washington, DC: National Academy Press)
- Nichols, J.D., Boulinier, T., Hines, J.E., Pollock, K.H. and Sauer, J.R. (1998). Inference methods for spatial variation in species richness and community composition when not all species are detected. *Conservation Biology*, 12, 1390-8
- Noss, R.F. (1987). From plant communities to landscapes in conservation inventories: a look at The Nature Conservancy (USA). *Biological Conservation*, 41, 11-37
- Noss, R.F., LaRoe, E.T. and Scott, J.M. (1995). *Endangered Ecosystems of the United States: a Preliminary Assessment of Loss and Degradation*. US Department of the Interior, National Biological Service, Biological Report 28. (Washington, DC)
- Nusser, S.M. and Goebel, J.J. (1997). The national resources inventory: a long-term multi-resource monitoring programme. *Environmental and Ecological Statistics*, 4, 181-204
- Opdam, P. (1991). Metapopulation theory and habitat fragmentation: a review of holarctic breeding bird studies. *Landscape Ecology*, 5, 93-106
- Orians, G.H. (1993). Endangered at what level? *Ecological Applications*, 3, 206-8
- Peters, R.L. (1992). Conservation of biological diversity in the face of climate change. In Peters, R.L. and Lovejoy, T.E. (eds) *Global Warming and Biological Diversity*, pp. 15-30. (New Haven: Yale University Press)
- Pimentel, D., Wilson, C., McCullum, C., Huang, R., Dwen, P., Flack, J., Tran, Q., Saltman, T. and Cliff, B. (1997). Economic and environmental benefits of biodiversity. *BioScience*, 47, 747-57
- Pimm, S.L., Russell, G.J., Gittleman, J.L. and Brooks, T.M. (1995). The future of biodiversity. *Science*, 269, 347-50
- Pimm, S.L. and Lawton, J.H. (1998). Planning for biodiversity. *Science*, 279, 2068-9
- Pressey, R.L., Humphries, C.J., Margules, C.R., Vane-Wright, R.I. and Williams, P.H. (1993). Beyond opportunism: key principles for systematic reserve selection. *Trends in Ecology and Evolution*, 8, 124-8
- Pressey, R.L. (1994). Ad hoc reservations: forward or backward steps in developing representative reserve systems? *Conservation Biology*, 8, 662-8
- Primack, R.B. (1993). *Essentials of Conservation Biology*. (Sunderland, MA: Sinauer Associates)
- Rapport, D.J., Regier, H.A. and Hutchinson, T.C. (1985). Ecosystem behavior under stress. *American Naturalist*, 125, 617-40
- Raven, P.H. and Wilson, E.O. (1992). A fifty-year plan for biodiversity surveys. *Science*, 258, 1099-100
- Reid, W.V., McNeely, J.A., Tunstall, D.B., Bryant, D.A. and Winograd, M. (1993). *Biodiversity Indicators for Policy-Makers*. (Washington, DC: World Resources Institute)
- Risser, P.G. (1988). Diversity in and among grasslands. In Wilson, E.O. (ed.) *Biodiversity*, pp. 176-80. (Washington, DC: National Academy of Sciences)
- Robinson, S.K. (1998). Another threat posed by forest fragmentation: reduced food supply. *The Auk*, 115, 1-3
- Ryan, M.G., Joyce, L.A., Andrews, T. and Jones, K. (1994). *Research Natural Areas in Colorado, Nebraska, North Dakota, South Dakota, and parts of Wyoming*. US Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, General Technical Report. RM-251. (Fort Collins, CO)
- Sala, O.E. and Paruelo, J.M. (1997). Ecosystem services in grasslands. In Daily, G.C. (ed.) *Nature's Services: Societal Dependence on Natural Ecosystems*, pp. 237-52. (Washington, DC: Island Press)
- Samson, F. and Knopf, F. (1994). Prairie conservation in North America. *BioScience*, 44, 418-21
- Saunders, D.A., Hobbs, R.J. and Margules, C.R. (1991). Biological consequences of ecosystem fragmentation: a review. *Conservation Biology*, 5, 18-32
- Schonewald-Cox, C.M., Chambers, S.M., MacBryde, B. and Thomas, L. (eds) (1983). *Genetics and Conservation*. (Menlo Park, CA: The Benjamin/Cummings Publishing Company)
- Scott, J.M., Davis, F., Csuti, B., Noss, R., Butterfield, B., Groves, C., Anderson, S., Caicco, S., D'Erchia, F., Edwards, T.C., Jr., Ulliman, J. and Wright, R.G. (1993). Gap analysis: a geographic approach to protection of biological diversity. *Wildlife Monographs*, 123, 1-41
- Shafer, C.L. (1990). *Nature reserves: island theory and conservation practice*. (Washington, DC: Smithsonian Institution Press)
- Smith, M.H. and Rhodes, O.E. (1992). Genetics and

- biodiversity in wildlife management. *Transactions of the North American Wildlife and Natural Resources Conference*, 57, 243-51
- Solbrig, O.T. (ed.) (1991). *From Genes to Ecosystems: a Research Agenda for Biodiversity*. (Paris, France: International Union of Biological Sciences)
- Soule, M.E. and Mills, L.S. (1998). No need to isolate genetics. *Science*, 282, 1658-9
- Steinauer, E.M. and Collins, S.L. (1996). Prairie ecology -the tallgrass prairie. In Samson, F.B. and Knopf, F.L. (eds) *Prairie Conservation: Preserving North America's Most Endangered Ecosystem*, pp. 39-52. (Washington, DC: Island Press)
- The Keystone Center (1991). *Biological Diversity on Federal Lands: Report of a Keystone Policy Dialogue*. (Keystone, CO: The Keystone Center)
- Thompson, W.L., White, G.C. and Gowan, C. (1998). *Monitoring Vertebrate Populations*. (New York: Academic Press)
- Tilman, D. (1997). Biodiversity and ecosystem functioning. In Dailey, G.C. (ed.) *Nature's Services: Societal Dependence on Natural Ecosystems*, pp. 93-112. (Washington, DC: Island Press)
- Tilman, D. and Downing, J.A. (1996). Biodiversity and stability in grasslands. *Nature*, 367, 363-5
- Tilman, D., May, R.M., Lehman, C.L. and Nowak, M.A. (1994). Habitat destruction and the extinction debt. *Nature*, 371, 65-6
- Turner, M.G. and Gardner, R.H. (1991). Quantitative methods in landscape ecology: an introduction. In Turner, M.G. and Gardner, R.H. (eds.) *Quantitative Methods in Landscape Ecology*, pp. 3-14. (New York: Springer-Verlag)
- US Department of the Interior, Geological Survey. (1987). Land Use and Land Cover Digital Data from 1:250,000- and 1:100,000-Scale Maps: Data Users Guide. US Geological Survey, National Mapping Program. (Reston, VA)
- Usher, M.B., Kruger, F.J., Macdonald, I.A.W., Loope, L.L. and Brockie, R.E. (1988). The ecology of biological invasions into nature reserves: an introduction. *Biological Conservation*, 44, 1-8
- van Jaarsveld, A.S., Freitag, S., Chown, S.L., Muller, C., Kock, S., Hull, H., Bellamy, C., Kruger, M., Endrody-Younga, S., Mansell, M.W. and Scholtz, C.H. (1998). Biodiversity assessment and conservation strategies. *Science*, 279, 2106-8
- West, N.E. (1993). Biodiversity of rangelands. *Journal of Range Management*, 46, 2--1 3
- West, N.E. (1999). Managing for biodiversity of rangelands. In Collins, W.W. and Qualset, C.O. (eds) *Biodiversity in Agrosystems*, pp. 101-26. (Boca Raton, FL: CRC Press)
- Westemeier, R.L., Brawn, J.D., Simpson, S.A., Esker, T.L., Jansen, R.W., Walk, J.W., Kershner, E.L., Bouzat, J.L. and Paige, K.N. (1998). Tracking the long-term decline and recovery of an isolated population. *Science*, 282, 1695-8
- Western, D. (1989). Conservation without parks: wildlife in the rural landscape. In Western, D. and Pearl, M.C. (eds) *Conservation for the Twenty-First Century*, pp. 158-65. (New York: Oxford University Press)
- Westman, W.E. (1990). Managing for biodiversity. *Bioscience*, 40, 26-33
- Westoby, M., Walker, B. and Noy-Meir, I. (1989). Opportunistic management for rangelands not at equilibrium. *Journal of Range Management*, 42, 266-74
- Wilcove, D.S., McLellan, C.H. and Dobson, A.P. (1986). Habitat fragmentation in the temperate zone. In Soule, M.E. (ed.) *Conservation Biology*, pp. 237-56. (Sunderland, MA: Sinauer Associates)
- World Resources Institute. (1992). *World Resources 1992-1993*. (New York: Oxford University Press)
- Wright, S. (1977). *Evolution and the Genetics of Populations*. (Chicago, IL: University of Chicago Press)