Essays

Indicators of Biodiversity for Ecologically Sustainable Forest Management

DAVID B. LINDENMAYER,* CHRIS R. MARGULES,† AND DANIEL B. BOTKIN‡

*Centre for Resource and Environmental Studies & Department of Geography, The Australian National University, Canberra, ACT 0200, Australia, email davidl@cres.anu.edu.au

†CSIRO Division of Wildlife and Ecology, GPO Box 284, Canberra, ACT 2601, Australia, email chris.margules@dwe.csiro.au

‡George Mason University, Fairfax, VA 22202, and The Center for the Study of the Environment, P.O. Box 6945, Santa Barbara, CA 93160, U.S.A., email dbotkin@silcom.com

Abstract: *The conservation of biological diversity has become one of the important goals of managing forests in an ecologically sustainable way. Ecologists and forest resource managers need measures to judge the success or failure of management regimes designed to sustain biological diversity. The relationships between potential indicator species and total biodiversity are not well established. Carefully designed studies are required to test relationships between the presence and abundance of potential indicator species and other taxa and the maintenance of critical ecosystem processes in forests. Other indicators of biological diversity in forests, in addition or as alternatives to indicator species, include what we call structure-based indicators. These are stand-level and landscape-level (spatial) features of forests such as stand structural complexity and plant species composition, connectivity, and heterogeneity. Although the adoption of practices to sustain (or recreate) key characteristics of forest ecosystems appear intuitively sensible and broadly consistent with current knowledge, information is lacking to determine whether such stand- and landscape-level features of forests will serve as successful indices of (and help conserve) biodiversity. Given our limited knowledge of both indicator species and structure-based indicators, we advocate the following four approaches to enhance biodiversity conservation in forests: (1) establish biodiversity priority areas (e.g., reserves) managed primarily for the conservation of biological diversity; (2) within production forests, apply structure-based indicators including structural complexity, connectivity, and heterogeneity; (3) using multiple conservation strategies at multiple spatial scales, spread out risk in wood production forests; and (4) adopt an adaptive management approach to test the validity of structure-based indices of biological diversity by treating management practices as experiments. These approaches would aim to provide new knowledge to managers and improve the effectiveness of current management strategies.*

Indicadores de Biodiversidad para el Manejo Ecológicamente Sostenible de Bosques

Resumen: *La conservación de la diversidad biológica se ha convertido en una de las metas importantes del manejo de bosques de manera ecológicamente sostenible. Los ecólogos y manejadores de recursos forestales necesitan medidas para juzgar el éxito o el fracaso de los regímenes designados para mantener la diversidad biológica. La relación entre las especies indicadoras potenciales y la biodiversidad total no ha sido bien establecida. Se requiere de estudios diseñados cuidadosamente para determinar las relaciones entre la presencia y abundancia de especies indicadoras potenciales y otros taxones y el mantenimiento de procesos críticos del ecosistema en los bosques. Otros indicadores de diversidad biológica en bosques, además de las especies indicadoras o como alternativas de las mismas, incluyen lo que llamamos "indicadores basados en la estructura". Estas son características a nivel de rodal y a nivel de paisaje (espacial) del bosque tales como la complejidad estructural del rodal y la composición de especies de plantas, la conectividad y la heterogeneidad. A pesar de que la adopción de prácticas para mantener (o reproducir) las características clave de ecosistemas forestales aparentan ser intuitivamente sensibles y ampliamente consistentes con el conocimiento actual, se*

Paper submitted November 12, 1998, revised manuscript accepted October 26, 1999.

carece de información para determinar si dichas características del bosque, a nivel de rodal o de paisaje, servirán como indicadores de la biodiversidad (y ayudarán a conservarla). Dado el limitado conocimiento sobre las especies indicadoras y los indicadores basados en estructura, proponemos las siguientes cuatro estrategias para incrementar la conservación de la biodiversidad de los bosques: (1) establecer áreas de prioridad para la biodiversidad (por ejemplo, reservas) manejadas principalmente para la conservación de la diversidad biológica; (2) dentro de bosques productivos, aplicar indicadores basados en estructura incluyendo la complejidad, la conectividad y la heterogeneidad; (3) dispersar el riesgo en bosques de producción maderera, utilizando estrategias múltiples de conservación a escalas espaciales múltiples; y (4) adoptar una estrategia de manejo adaptable para probar la validez de los índices de diversidad biológica basados en la estructura al tratar a las prácticas de manejo como experimentos. Estas estrategias intentan proveer información nueva a los manejadores y mejorar la efectividad de las actuales estrategias de manejo.

Introduction

It is now widely accepted that forests should be managed in an ecologically sustainable fashion (United Nations 1992; Kohm & Franklin 1997). For the purposes of this paper, we understand ecologically sustainable forestry to include forest ecosystems, wood production, and nontimber values. At the ecosystem level, this requires perpetuating ecosystem processes, including chemical cycling, within specified bounds. At the landscape level, this requires the maintenance of ecosystem integrity, which means that a landscape has a range and distribution of forest structures, species composition, and biological diversity consistent with set standards such as the historic range of variation.

The conservation of biological diversity is one of the goals of ecologically sustainable forestry, although the concept encompasses much more than biodiversity conservation alone. Biodiversity includes diversity at the genetic, species, landscape, and ecosystem levels (Noss & Cooperrider 1994). Given this complexity and the inadequate descriptions of local biodiversity currently available (e.g., Torsvik et al. 1990), it is difficult to judge whether forests are being managed in an ecologically sustainable way (Botkin & Talbot 1992). Moreover, it is impossible to measure and monitor the effects of various management practices on all species. An array of international and national initiatives (Arborvitae 1995) have sought to overcome this problem by identifying indicators — a subset of attributes that could serve as surrogates for total biodiversity and be used as indicators to monitor the success or failure of management practices to sustain biodiversity.

The lists of criteria for biodiversity conservation and indicators of biodiversity as part of ecologically sustainable forestry are extensive (e.g., Canadian Council of Forest Ministers 1997) and have been embraced by many national and international organizations (e.g., Convention for Sustainable Development Intergovernmental Panel on Forests; see Arborvitae 1995). It is difficult, however, to determine how the criteria and indicators of biodiversity might be identified, measured, interpreted or monitored. In part, this is because ecological knowledge lags behind policy initiatives. For example, a basic requirement for the use of many of the proposed biodiversity indicators is knowledge of what species are in a forest, where they are, and how they might respond to disturbance. Yet the prospect of complete species inventories, which include location as well as identity, is dim (Margules et al. 1995), as is an understanding of population dynamics sufficient to predict levels of abundance and population demographic structures necessary for the assessment of long-term viability. There are no easy answers to these problems, but they need to be tackled now if conservation biology is to make a contribution to forest policy, planning, and management before the opportunity to do so is gone.

Concepts associated with indicators and indicator species are not well understood, yet there is strong pressure on forest managers to embrace indicators in the conservation of biological diversity (e.g., Commonwealth of Australia 1998). Selection of the wrong or inappropriate indicators could give a false impression of scientific understanding, managerial knowledge, and ecological sustainability. This could have negative effects on biological diversity in forest ecosystems.

We reviewed some of the approaches to indicators of biodiversity. Although biodiversity includes genetic, species, landscape, and ecosystem diversity, we focused on species. Within this more restricted arena, indicators of biodiversity can be divided into two broad groups: (1) biological or taxon-based indicators, particularly indicator species and guilds, and (2) what we call structure-based indicators—stand -and landscape-level (spatial) features such as stand structural complexity, plant species composition and connectivity and heterogeneity. We discuss the limitations of these broad groups of indicators and consider what can be done to promote the conservation of biodiversity in forests despite existing limitations.

Taxon-Based Biodiversity Indicators

Indicator Species

The search for indicators of biodiversity has tended to focus on biological entities, such as gene frequencies, populations, species, species assemblages, and communities, that might function as surrogates or proxies for other forms of biodiversity and/or reflect changes in ecosystem patterns or processes (Burgman & Lindenmayer 1998). Although indicators are required at a wide range of organizational levels, most efforts to date have focused on particular species or members of species assemblages (e.g., guilds). Landres et al. (1988: p.317) defined an indicator species as "an organism whose characteristics (e.g. presence or absence, population density, dispersion, reproductive success) are used as an index of attributes too difficult, inconvenient, or expensive to measure for other species or environmental conditions of interest."

The term *indicator species* can mean many different things (Spellerberg 1994), including (1) a species whose presence indicates the presence of a set of other species and whose absence indicates the lack of that entire set of species; (2) a keystone species (sensu Terborgh 1986), which is a species whose addition to or loss from an ecosystem leads to major changes in abundance or occurrence of at least one other species (e.g., Mills et al. 1993); (3) a species whose presence indicates human-created abiotic conditions such as air or water pollution (often called a pollution indicator species; Spellerberg 1994); (4) a dominant species that provides much of the biomass or number of individuals in an area; (5) a species that indicates particular environmental conditions such as certain soil or rock types (Klinka et al. 1989); (6) a species thought to be sensitive to and therefore to serve as an early warning indicator of environmental changes such as global warming (Parsons 1991) or modified fire regimes (Wolseley & Aguirre-Hudson 1991) (sometimes called a bio-indicator species); and (7) a management indicator species, which is a species that reflects the effects of a disturbance regime or the efficacy of efforts to mitigate disturbance effects (Milledge et al. 1991). Types 1, 2, and 4 have been proposed as indicators of biological diversity and types 3, 5, 6, and 7 as indicators of abiotic conditions and/or changes in ecological processes.

The Southern Cassowary (*Casuarius casuarius*) is an example of type 2. Found in the rainforests of Queensland, northern Australia, it is the only disperser of more than 100 plant species that have large fruits (Crome 1976). Thus, the loss of the Southern Cassowary could result in the loss of a large set of other species dependent on it for seed dispersal.

Type 3 species are typically used to monitor pollution. In fact, the indicator species concept has probably been best developed in the field of pollution monitoring (e.g., Spellerberg 1994). For example, the absence of lichens that grow on tree trunks in places where they would ordinarily occur indicates the existence of specific air pollutants (Loppi et al. 1998).

Some plants (type 5 indicators) are virtually restricted to soils derived from serpentine bedrock, a rock low in some essential chemical elements and overabundant in others (Lyons et al. 1974). For these "almost endemic" species, the major portion of their distribution is on serpentine soil, and they are found elsewhere only rarely. The presence of one of these plants almost certainly indicate that the soil is derived from serpentine rock (R. Haller, personal communication).

Kirtland's Warbler (*Dendroica kirtlandii*) is an example of type 6. It has been proposed as a potential biological indicator of global warming because it nests only in jack pine (*Pinus banksiana*) trees at the southern edge of their range, where they grow on a soil type suitable for this bird (Botkin et al. 1991).

Examples of type 7 include recovery indicator species such as ants, which are considered useful in assessing the effectiveness of mine site rehabilitation (e.g., Andersen 1993).

Problems with Species as Indicators

Although the concept of indicator species has considerable intuitive appeal, there are many instances where its application would be unsuccessful. The American chestnut (*Castanea dentata*) is an example of the failure of a species as a type 4 indicator. The American chestnut was once one of the dominant trees of the mid-Atlantic forests of the United States. Although a fungal blight essentially eliminated the species as a canopy tree by the 1930s (Anagnostakis 1972), no other species are known to have become extinct or suffered declines that would leave them threatened as a direct result of the demise of the chestnut. For example, the gray squirrel (*Sciurus carolinensis*), which fed heavily on chestnuts, remains abundant today (Botkin & Keller 1995). Similarly, frogs have been suggested as type 6 indicator species because their decline was thought to indicate global climate change. The decline, however, seems to be a result of many factors that vary with locality (e.g., Pechmann et al. 1991; Laurance 1996). Thus, it remains unclear what environmental or other changes are indicated by declines in frog populations.

There also appears to be problems with the concept of management indicator species (type 7). Milledge et al. (1991) argued that the maintenance of suitable habitat for a management indicator species would conserve other taxa with similar requirements. Any species, however, that is the specific target for conservation by particular management actions can no longer be an independent yardstick of those actions and, in turn, be regarded as a suitable indicator species for other taxa (Landres et al. 1988). In Australian wood production forests, two species of arboreal marsupials, the greater glider (*Petauroides volans*) and the yellow-bellied glider (*Petaurus australis*), have been proposed as potentially useful management indicator species (Davey 1989;

Milledge et al. 1991). Lindenmayer and Cunningham (1997) tested this idea in the forests of central Victoria, southeastern Australia. They found no support for the hypothesis that the presence of greater glider, yellow-bellied glider, or any other species of arboreal marsupial was a good surrogate for the presence or abundance of the other taxa in the assemblage, in part because (1) few sites support many different species of arboreal marsupials and (2) there is resource partitioning among the different members of the arboreal marsupial assemblage. There are differences among species in diet, body size, habitat requirements, nest tree use, mating system, and other life-history characteristics (Lindenmayer 1997). One of the key habitat requirements for virtually all species of arboreal marsupials is hollow trees, which are used as nest and den sites. The abundance of these trees is a factor limiting populations over large areas of forest. Rather than a management indicator species, the prevalence of hollow trees might serve as a useful indicator. But many other forest taxa are not dependent on hollow trees, and such an indicator would have limited or no relevance to them (Burgman & Lindenmayer 1998). Indeed, in another study, the structural complexity of different vegetation types in Western Australia proved to be a poor indicator of species richness in several invertebrates and lizards (Abensperg-Traun et al. 1997).

Even in the case of pollution indicator species (type 3 above), for which the indicator species concept has been best developed, the behavior of some indicator species may prove to be contrary to what was first expected. Hence, there are problems stemming simply from choosing the wrong indicator species. The case of the bivalve mollusc (*Velesunio ambiguus*) in Australian river systems is a classic example. Early research suggested that the species was an indicator of the presence of heavy metals (Walker 1981). Subsequent work found that the uptake of heavy metals by *V. ambiguus* did not reflect the extent of pollution in the surrounding riverine system, making the mollusc an unreliable and thus unsuitable indicator species (Millington & Walker 1983).

There are other potential problems with the concept of indicator species. One is the lack of taxonomic work within the most diverse groups (e.g., invertebrates). The indicator species approach is hamstrung and monitoring programs are jeopardized (Cranston 1990) because different invertebrate taxa can have markedly different responses to disturbance (Davies & Margules 1998). In addition, the population dynamics of many species of invertebrates is episodic, but such marked changes in abundance are rarely synchronous across taxa, limiting the value of the status of any given taxon as a surrogate for the dynamics of another. A problem also arises from the choice of the appropriate scale over which one taxon could indicate the status of supposedly associated taxa (Weaver 1994). Finally, there are problems associated with the lack of sensitivity of indicators. Indicators with a high threshold response may result in some environmental problems being well advanced (and difficult to reverse) before they are detected. A good example of this is pitch pine (*Pinus rigida*). A second-growth natural forest was subjected to ionizing radiation from cesium-137 for 15 years at the U.S. Brookhaven National Laboratory, and pitch pine was much more sensitive to cesium-137 than the other dominant tree species. Radiation levels of 10 roentgens per day killed 100% of the pitch pine but had no effects on other species of trees such as scarlet oak (*Quercus coccinea*) (Woodwell & Rebuck 1967). Much higher levels were required to affect scarlet oak, making it a poor indicator species for ionizing radiation.

Problems with Guilds

Several authors have suggested that the response of one member of a guild or other form of assemblage might predict the responses of other members of that guild or assemblage (e.g., Johnson 1981). Members of a guild, however, may not respond in the same way to a given disturbance (Morrison et al. 1992). Thiollay (1992) found that of five sympatric, closely related, and morphologically similar rainforest bird species, the population of one declined markedly, another substantially increased, and three were moderately influenced following selective logging. Lindenmayer et al. (1999*a*) have shown that different species of arboreal marsupials respond differently to disturbances such as landscape change and habitat fragmentation and that it was not possible to predict population responses from one species to another, even for species that are closely related. Thus, the patterns of response to change exhibited by different species within the same guild may not be readily predictable, even among groups of closely related taxa.

There are other good reasons to believe that not all members of a guild will respond in the same way to the same phenomena. First, the same group of taxa can be partitioned into different guilds for different purposes, and in some cases guilds so constructed may have only limited ecological meaning (Mac Nally 1994). Second, the competitive exclusion principle suggests that each member of a guild must have somewhat different environmental requirements and therefore all the members of the guild cannot be indicators of exactly the same conditions. Finally, if a guild represents species with similar niches, but if the niches differ quantitatively, then conditions that favor one member of the guild may not favor another.

Species Lists as Indicators

Given the problems with the use of species and guilds as indicators, one might attempt to seek a measure of the complete species list or an estimator of that list. A direct measure of this list, however, is not practicable except in certain ecosystems of extreme habitats, such as those in thermal hot springs, where there are few species. Slobodkin et al. (1980) discussed the advantages and problems of a species list as an indicator of ecosystem status. They proposed a foundation for an ecological theory in which the complete species list is the ultimate defining feature of an ecosystem. Slobodkin et al. (1980) discussed how a limited, observed list (a subset of the complete species list) could serve as a practical estimator of the complete list. Simply stated, the knowledge that one species is present tells us that many other species cannot be present; for example, the presence of moose (*Alces alces*) tells us that other species such as whales, mahogany trees, and most of the grasses of the tall grass prairie, are not present. It also tells us that many taxa are likely to be present, including parasites and symbionts of moose. Therefore, each new species observed refines the list. As the observed list lengthens, an asymptotic curve to total species diversity can be estimated. Although we cannot expect to enumerate the complete species list, we might be able to develop an "indicator species list" that could be used in practice. This approach has potential, but remains undeveloped in practice, and we do not have such estimators at this time.

In summary, the concept of indicator species remains an appealing and potentially important one because of the impossibility of monitoring everything. If indicator species could be identified, they would be a powerful management tool, but taxon-based indicators are not adequate at present. Indeed, although many taxa have been proposed as indicator species, the specific entities or conditions that they are supposed to indicate are often not stated explicitly. In other cases, those entities or conditions are nebulous or are difficult to define rigorously (e.g., ecosystem health). Moreover, the causal linkages between an indicator and other entities (e.g., species or ecosystem processes) are not well demonstrated (Simberloff 1998). Considerable work is needed before reliable indicator species can be identified and included in ecologically sustainable management programs. Carefully designed experiments are required to test relationships between the presence and abundance of potential indicator species and other taxa and the maintenance of critical forest ecosystem processes such as nutrient cycling.

Structure-Based Biodiversity Indicators

While studies of indicator species proceed, forests continue to be logged, certification of management practices for ecological sustainability will be required under international trade agreements (Wallis et al. 1997), and other types of biodiversity indicators will be needed. A potentially powerful and complementary approach is to focus on management practices per se using what we call structure-based indicators that include (1) stand complexity and plant species composition in logged stands, (2) connectivity, and (3) heterogeneity.

Stand Complexity

In many types of forest, timber harvesting operations result in marked, medium-length changes in stand structure and floristic composition (Halpern & Spies 1995). It is possible that the effects of such activities could be mitigated and many species conserved in wood production forests if the natural complexity of stand structure is sustained in the form of features such as large, old trees, logs, and the range of overstory and understory species (Kohm & Franklin 1997). For example, a number of Australian studies have highlighted the potential value of retained trees in promoting the recolonization of logged and regenerated forests by vertebrates (Gibbons & Lindenmayer 1996). Similar results have been obtained in the United States, although not all taxa will respond to such strategies (Hansen et al. 1995).

The structural and floristic features of uncut stands provide an indication of the attributes that need to be retained and perpetuated in logged forests (McComb et al. 1993). Stand complexity would seem most effective for biological diversity if the structural features left after human disturbance closely match those resulting from natural disturbance (Hunter 1994). Franklin et al. (1997) and Lindenmayer and Franklin (1997) describe how silvicultural systems could be modified to allow the types of structural and floristic features of naturally disturbed forest to be perpetuated in logged forests.

Connectivity

Connectivity among forest stands allows for the exchange of seeds, pollen, and individual animals and it can be important for many processes including, among others, the persistence or re-colonization of cutover areas and the exchange of genes among populations (Noss 1991). Natural forests typically consist of a system of stands in different successional stages among which species can migrate. Connectivity in wood production forests is important because timber harvesting has the potential to eliminate species from logged areas and to fragment and isolate populations remaining in uncut areas.

Connectivity may be facilitated by establishing corridors, and these may be useful not only for animals but also plants (Bennett 1998). What constitutes a suitable corridor varies among species (Beier & Noss 1998). In the case of animals, corridor suitability is a function of an array of factors, including mode of dispersal, social behavior, diet, status of the surrounding (logged) matrix, and corridor location and dimensions (e.g., width, length, and habitat suitability) (reviewed by Lindenmayer 1998). Corridors may not be effective for all taxa, such as those for which corridor location is not congruent with movement pathways (Gustafson & Gardner 1996) or those that disperse randomly (Eastern Screech-Owl [*Otus asio*]; Belthoff & Ritchison 1989). Although corridors such as those located in gullies act as dispersal routes for some terrestrial animals (Hewittson 1997), corridors may be required in other parts of a landscape for species inhabiting forests outside the riparian zone (Claridge & Lindenmayer 1994). Thus, the concept of connectivity embodies more than corridors because it relates, in part, to the extent of the hostility or permeability of logged areas for movement (Wiens 1997). Hence, connectivity also may involve the retention of some components of the original vegetation on logged areas within managed forest landscapes (Franklin 1993). For example, the approach to the conservation of the Northern Spotted Owl (*Strix occidentalis caurina*) has been underpinned by connectivity via stand (green tree) retention regimes on cutover areas throughout logged landscapes.

Heterogeneity

The size and spatial arrangement of habitat patches appear to be important for some taxa (reviewed by Hanski 1994), so another objective of forest management should be sustaining spatial complexity or heterogeneity over a range of spatial scales (Franklin & Forman 1987). Habitats within forests include biological features such as the range of forest age classes, the size of patches in each class, and variation in overstory and understory structure and floristics. These, in turn, are related to environmental changes in terrain, aspect, elevation, and soil type (Austin et al. 1990). Human and natural disturbances such as logging and fire alter spatial heterogeneity (Franklin & Forman 1987).

Strategies to perpetuate heterogeneity in wood production forests may include using patch sizes and shapes that fall within the range of those created by natural disturbance regimes (e.g., fire or windstorms) as a template for guiding the spatial location of harvested sites (e.g., Mladenhoff et al. 1993). This would create congruence between natural and human disturbance patterns over a range of spatial scales (Haila et al. 1994). This approach is underpinned by the general (although largely untested) concept that human disturbance regimes such as logging will have less impact on biodiversity if they are congruent with ecological processes (Hunter 1994) and within the bounds of natural disturbance regimes (Attiwill 1994).

Studies are required to contrast heterogeneity and landscape composition between cut and uncut landscapes and the response of organisms to such differences. The results of some empirical investigations to date have been equivocal (e.g., McGarigal & McComb 1995). This is possibly because the metrics employed to characterize heterogeneity (e.g., Haines-Young & Chopping 1996) are not always particularly meaningful for assessing species response (Cale & Hobbs 1994), and other measures that relate better to coincidences of disturbance patterns and animal movement (e.g., home range patterns) may be better predictors (Carey et al. 1992). Nevertheless, further empirical investigations are critical because heterogeneity appears to be important for many taxa (Bennett 1998).

Promoting heterogeneity in wood production forests needs careful consideration. Increasing heterogeneity may have negative effects on some species, including those requiring large, intact areas of particular age classes such as old growth (Okland 1996).

Limitations of Structure-Based Biodiversity Indicators

Structure-based indicators attempt to ensure that management perpetuates inherent taxonomic, structural, and landscape complexities characteristic of forest ecosystems and in so doing contributes to the conservation of biodiversity (Kohm & Franklin 1997). Although these structure-based indicators are intuitively sensible and reflect current knowledge of forest biodiversity, their long-term effectiveness remains unknown (McComb et al. 1993). For example, there are few data on the number and spatial configuration of retained trees needed to promote the re-invasion of logged sites by forest biota (Gibbons & Lindenmayer 1996). Therefore, empirical tests of the value of structure-based indicators are required.

Strategies for Immediate Implementation

The lack of information on taxon- and structure-based indicators leads us to conclude that there are four actions that should be adopted now, with or without adequate information, to enhance the likelihood that forest biodiversity will be protected. (1) Establish an adequate amount of representative biodiversity priority areas (e.g., reserves) managed primarily for the conservation of biological diversity (McNeely 1994). (2) Within production forests, apply structure-based indicators that include structural complexity, connectivity, and heterogeneity. (3) Employ a risk-spreading approach in wood production forests using multiple conservation strategies at multiple spatial scales. (4) Adopt an adaptive management approach to test the validity of structure-based indices of biological diversity by treating management practices as experiments.

Biodiversity Priority Areas

The goal of a network of biodiversity priority areas should be to represent adequately the biodiversity of a region. Existing protected-area networks contain a biased sample of biodiversity typical of locations in environments less suited to natural resource exploitation (e.g., Pressey 1994). Explicit, efficient, and flexible methods such as reserve selection algorithms (Margules et al. 1995) and gap analysis (e.g., Noss & Cooperrider 1994) can be employed to help resolve some of these problems.

The presence of a species within a biodiversity priority area should not imply a lack of need for active management regimes inside that area (e.g., Kuchling et al. 1992), such as the restoration of burning regimes that may be required by taxa dependent on particular seral stages or vegetation mosaics (e.g., Burbidge et al. 1988). And, the identification of biodiversity priority areas does not mean that off-reserve management is not needed, because reserves will never sample all biodiversity, may not provide sufficient suitable habitat for some taxa (Grumbine 1990), and may not be large enough to sustain some of the species they do contain without sympathetic management of surrounding areas (Swenson et al. 1986). Thus, the adoption of the structure-based principles outlined in the previous section will be important for the conservation of biodiversity in wood production areas.

Risk Spreading and Variety of Conservation Strategies at Different Spatial Scales

Because different taxa have different resource, spatial, and other requirements, indicator species often fail as useful measures of biological diversity, and a single conservation strategy (e.g., tree retention on logged sites), although appropriate for a particular species, may not ensure the persistence of all other taxa, even closely related ones. Thus, implementing an array of management strategies, including setting aside biodiversity priority areas or reserves, establishing wildlife corridors, and maintaining elements of original stand structure on cutover sites, may help meet the diverse requirements of different taxa. For example, empirical studies suggest that although the provision of wildlife corridors and retained trees on logged sites will make a major contribution to the conservation of populations of the mountain brushtail possum (*Trichosurus caninus*) in Australian mountain ash forests (Lindenmayer et al. 1993), uncut biodiversity priority areas containing large, continuous stands dominated by old-growth trees are important for the conservation of the yellow-bellied glider in this same forest type (Lindenmayer et al. 1999*b*).

Another important advantage of a multifaceted approach to management is that if any one strategy is found to be ineffective (e.g., the establishment of wildlife corridors), others (e.g., tree retention throughout logged areas) will be in place that might better protect those elements of forest biodiversity under threat. This is a form of "risk spreading" in forest management. For example, in the forests of Victoria in southeastern Australia, reserves, corridors, and stand retention strategies each have some potential limitations for the conservation of the endangered Leadbeater's possum (*Gymnobelideus leadbeateri*), and a combination of all three strategies will be needed to ensure its persistence (Lindenmayer & Franklin 1997).

Finally, a given management strategy may generate benefits for another strategy implemented at a different spatial scale. For example, increased levels of stand retention on logged sites may limit rates of windthrow and vegetation loss in adjacent wildlife corridors, in particular the attrition of trees with hollows that provide den sites for many cavity-dependent taxa (Lindenmayer et al. 1997). The integrity of wildlife corridors will, in turn, help maintain their effectiveness as linear strips of habitat for wildlife and may promote their use as movement conduits for dispersing animals.

Instigating Management-by-Experiment-and-Monitoring Studies

An adaptive management approach (Holling 1978) integrating research, monitoring, and management should be adopted to test the validity of principles such as stand complexity, connectivity, and heterogeneity as structure-based indices of biological diversity. The best approach is to treat logging as an experiment and implement monitoring systems and feedback mechanisms to management (McComb et al. 1993). This would provide new knowledge to managers and improve the effectiveness of management strategies.

At least five steps underpin effective adaptive logging "experiments." (1) Employ a carefully designed monitoring system, including baseline measurements prior to any new action, to track the response of the forest ecosystem. Indeed, a forest cannot be considered constructively managed if it is not monitored. (2) Use a variety of logging practices within wood production areas. For example, some areas could be clearcut, some selectively harvested, and others could be left with varying levels of stand retention. Control areas with no timber harvesting are necessary to interpret results (e.g., Margules et al. 1994). (3) Record and store data on the intensity of disturbance and the extent of vegetation retention on logged sites. (4) Change practices based on the results of the experiments. (5) Continue monitoring and data interpretation as part of any change in management actions, including the development of indicators of the status of biodiversity.

Disturbance experiments must be well designed to ensure that the monitoring data generated can be subjected to rigorous statistical analyses and can identify important trends such as population declines. The design of a monitoring program should include treatment replicates to account for spatial heterogeneity and random variation and to provide error estimates, pretreatment monitoring to establish "natural" trends and pretreatment differences between plots, environmental stratification to detect any interactions between treatments and environmental variables, a period of time sufficient to establish treatment effects and distinguish them from climatic fluctuations or other episodic or stochastic events, and replication at more than one location to avoid location-specific phenomena or geographic bias (Margules et al. 1994).

With careful monitoring and experimental design, it may not be necessary to wait a full logging rotation or more to start management-by-experiment-and-monitoring studies. Information on forest disturbance can be gathered relatively quickly from comparison among different treatments and from retrospective studies of sites logged in the past.

Adaptive management by monitoring and experiment is already underway at the stand level in several temperate wood production forests (e.g., western Canada; Phillips 1996). It is also important to apply adaptive management at the landscape level; some adaptive management experiments have commenced (e.g., Schmiegelow & Hannon 1993), many more are needed (Simberloff 1998).

Summary

Measures of the success of biodiversity conservation are weak, making it difficult to determine if forests are being managed in an ecologically sustainable way. Much of the search for measures of success have focused on taxon-based indicator species. Even when a restricted definition of biodiversity is employed (e.g., a species-level focus is used, and genetic, landscape, and ecosystem diversity is ignored), robust linkages between an indicator species and other entities or conditions are not well established. Thus, there is an urgent need to test relationships between the presence and abundance of potential indicator species and other taxa or the maintenance of critical ecosystem processes (e.g., nutrient cycling).

Given limited knowledge of taxon-based indicator species, we suggest that structure-based indicators be used at the present time as potential indicators of biodiversity in forests. These are stand- and landscape-level (spatial) features of forests such as stand structural complexity and plant species composition, connectivity, and heterogeneity. We advocate the adoption of an adaptive management approach to test the validity of these structure-based indices of biological diversity by treating management practices as experiments. This approach would aim to provide new knowledge to managers and improve the effectiveness of management strategies. Indeed, a commitment to adaptive management experiments could be seen in itself as an indicator of a commitment to learning and adopting new knowledge so that managers implement the best current knowledge at any given time.

Acknowledgments

We thank the Australian Research Council (D.B.L.) and Environment Australia (C.R.M.) for supporting earlier work on biodiversity indicators. M. Burgman, J. Franklin, H. Recher, S. Dovers, D. Saunders, and R. Cunningham have made major contributions to collaborative studies and discussions on topics related to those we have outlined. Comments from K. McGarigal, B. McComb, and several anonymous referees greatly improved earlier versions of this paper. We are indebted to G. Meffe for his encouragement of this work.

Literature Cited

Abensperg-Traun, M., G. Arnold, D. Steven, G. Smith, L. Atkins, J. Viveen, and M. Gutter. 1997. Biodiversity indicators in contrasting vegetation types: a case study from Western Australia. Memoirs of the Museum of Victoria **56:**637–641.

Anagnostakis, S. A. 1972. Biological control of chestnut blight. Science **215:**446–471

Andersen, A. N. 1993. Ants as indicators of restoration success at a uranium mine in tropical Australia. Restoration Ecology **3:**156–167.

Arborvitae. 1995. Arborvitae. Forest conservation newsletter World Conservation Union/World Wildlife Fund, Gland, Switzerland. September 1995:5.

Attiwill, P. M. 1994. Ecological disturbance and the conservative management of eucalypt forests in Australia. Forest Ecology and Management **63:**301–346.

Austin, M. P., A. O. Nicholls, and C. R. Margules. 1990. Measurement of the realized qualitative niche: environmental niches of five *Eucalyptus* species. Ecological Monographs **60:**161–177.

Belthoff, J. R., and G. Ritchison. 1989. Natal dispersal of Eastern Screech-Owls. Condor **91:**254–265.

Beier, P., and R. Noss. 1998. Do habitat corridors provide connectivity. Conservation Biology **12:**1241–1252.

Bennett, A. F. 1998. Linkages in the landscape. The role of corridors and connectivity in wildlife conservation. World Conservation Union, Gland, Switzerland.

Botkin, D. B., and E. A. Keller, 1995. Environmental science: earth as a living planet. Wiley, New York.

Botkin, D. B., and L. M. Talbot. 1992. Biological diversity and forests. Pages 47–74 in N. Sharma editor. Contemporary issues in forest management: policy implications. The World Bank, Washington, D. C.

Botkin, D. B., D. A. Woodby, and R. A. Nisbet. 1991. Kirtland's Warbler habitats: a possible early indicator of climatic warming. Biological Conservation **56:**63–78.

Burbidge, A. A., K. A. Johnson, P. Fuller, and R. I. Southgate. 1988. Aboriginal knowledge of the mammals of the central deserts of Australia. Australian Wildlife Research **15:**9–39.

Burgman, M. A., and D. B. Lindenmayer. 1998. Conservation biology for the Australian environment. Surrey Beatty and Sons, Chipping Norton, New South Wales, Australia.

Cale, P. G., and R. J. Hobbs. 1994. Landscape heterogeneity indices: problems of scale and applicability, with particular reference to animal habitat description. Pacific Conservation Biology **1:**183–193.

Canadian Council of Forest Ministers. 1997. Criteria and indicators of sustainable forest management in Canada. Technical report. Ottawa, Canada.

Carey, A. B., S. P. Horton, and B. L. Biswell. 1992. Northern Spotted Owls: influence of prey base and landscape character. Ecological Monographs **62:**223–250.

Commonwealth of Australia. 1998. A framework of regional (subnational) level criteria and indicators of sustainable forest management in Australia. Commonwealth of Australia, Canberra, Australian Capital Territory.

Claridge, A. W., and D. B. Lindenmayer. 1994. The need for a more sophisticated approach toward wildlife corridor design in the multiple-use forests of southeastern Australia:the case for mammals. Pacific Conservation Biology **1:**301–307.

Cranston, P. S. 1990. Biomonitoring and invertebrate taxonomy. Environmental Monitoring and Assessment **14:**265–273.

Crome, F. H. 1976. Some observations on the biology of the Cassowary in northern Queensland. Emu **76:**8–14.

Davey, S. M. 1989. Thoughts towards a forest wildlife management strategy. Australian Forestry **52:**56–67.

Davies, K. F., and C. R. Margules. 1998. Effects of habitat fragmentation on carabid beetles: experimental evidence. Journal of Animal Ecology **67:**460–471.

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

Franklin, J. F., and R. T. Forman. 1987. Creating landscape patterns by forest cutting: ecological consequences and principles. Landscape Ecology **1:**5–18.

Franklin, J. F., D. E. Berg, D. A. Thornburgh, and J. C. Tappeiner. 1997. Alternative silvicultural approaches to timber harvest: variable retention harvest systems. Pages 111–139 in K. A. Kohm and J. F. Franklin, editors. Creating a forestry for the 21st century. Island Press, Covelo, California.

Gibbons, P., and D. B. Lindenmayer. 1996. A review of issues associated with the retention of trees with hollows in wood production forests of New South Wales. Forest Ecology and Management **83:** 245–279.

Grumbine, R. E. 1990. Viable populations, reserve design, and federal lands management: a critique. Conservation Biology **4**:127–134.

Gustafson, E. J., and R. H. Gardner, 1996. The effect of landscape heterogeneity on the probability of patch colonisation. Ecology **77:** 94–107.

Haila, Y., I. K. Hanski, J. Niemela, P. Puntilla, S. Raivio, and H. Tukia. 1994. Forestry and the boreal fauna: matching management with natural forest dynamics. Annales Zoologici Fennici **31:**187–202.

Haines-Young, R., and M. Chopping. 1996. Quantifying landscape structure: a review of landscape indices and their application to forested environments. Progress in Physical Geography **20:**418–445.

Halpern, C. B., and T. A. Spies. 1995. Plant species diversity in natural and managed forests of the Pacific Northwest. Ecological Applications **5:**913–934.

Hansen, W., C. McComb, R. Vega, M. G. Raphael, and M. Hunter. 1995. Bird habitat relationships in natural and managed forests in the west Cascades of Oregon. Ecological Applications **5:**555–569.

Hanski, I. 1994. Patch occupancy dynamics in fragmented landscapes. Trends in Evolution and Ecology **9:**131–134.

Hewittson, H. 1997. The genetic consequences of habitat fragmentation on the bush rat (*Rattus fuscipes*) in a pine plantation near Tumut, NSW. Honours thesis. Division of Botany and Zoology, The Australian National University, Canberra, Australian Capital Territory.

Holling, C. S., editor. 1978. Adaptive environmental assessment and management. International series on applied systems analysis 3. International Institute for Applied Systems Analysis and Wiley, Toronto.

Hunter, M. L. 1994. Fundamentals of conservation biology. Blackwell, Cambridge, Massachusetts.

Johnson, R. A. 1981. Application of the guild concept to environmental impact analysis of terrestrial vegetation. Journal of Environmental Management **13:**205–222.

Klinka, K., V. J. Krajina, A. Ceska, and A. M. Scagel. 1989. Indicator plants of coastal British Columbia. University of British Columbia Press, Vancouver, Canada.

Kohm, K., and J. F. Franklin. 1997. Forestry in the 21st century. Island Press, Covelo, California.

Kuchling, G., J. P. Dejose, A. A. Burbidge, and S. D. Bradshaw. 1992. Beyond captive breeding: the western swamp tortoise *Pseudemydura umbrina* recovery programme. International Zoo Year Book **31:**37–41.

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

Laurance, W. F. 1996. Catastrophic declines of Australian rainforest frogs: is unusual weather responsible ? Biological Conservation **77:** 203–212.

Lindenmayer, D. B. 1997. Differences in the biology and ecology of arboreal marsupials in southeastern Australian forests and some implication for conservation. Journal of Mammalogy **78:**1117–1127.

Lindenmayer, D. B. 1998. The design of wildlife corridors in wood production forests. Occasional paper series. Forest issues paper 4. New South Wales National Parks and Wildlife Service, Sydney.

Lindenmayer, D. B., and R. B. Cunningham. 1997. Patterns of co-occurrence among arboreal marsupials in the forests of central Victoria, south-eastern Australia. Australian Journal of Ecology **22:**340–346.

Lindenmayer, D. B., and J. F. Franklin. 1997. Forest structure and sustainable temperate forestry: a case study from Australia. Conservation Biology **11:**1053–1068.

Lindenmayer, D. B., R. B. Cunningham, and C. F. Donnelly. 1993. The conservation of arboreal marsupials in the montane ash forests of the Central Highlands of Victoria, south-east Australia. IV. The distribution and abundance of arboreal marsupials in retained linear strips (wildlife corridors) in timber production forests. Biological Conservation **66:**207–221.

Lindenmayer, D. B., R. B. Cunningham, and C. F. Donnelly. 1997. Tree decline and collapse in Australian forests: implications for arboreal marsupials. Ecological Applications **7:**625–641.

Lindenmayer, D. B., M. A. McCarthy, and M. L. Pope. 1999*a*. A test of Hanski's simple model for metapopulation model. Oikos **84:**99–109.

Lindenmayer, D. B., R. B. Cunningham, and M. A. McCarthy. 1999b. Landscape analysis of the occurrence of arboreal marsupials in the montane ash forests of the Central Highlands of Victoria, south-eastern Australia. Biological Conservation **89:**83–92.

Loppi, S., E. Putorti, C. Signorini, S. Fommei, S. A. Pirintsos, and V. de Dominicis. 1998. A retrospective study using epiphytic lichens as biomonitors of air quality: 1980 and 1996 (Tuscany, central Italy). Acta Oecologica **19:**405–408.

Lyons, M. T., R. R. Brooks, and D. C. Craig. 1974. The influence of soil composition of the Coolac Serpentinite belt in New South Wales. Journal and Proceedings, Royal Society of New South Wales **107:** 67–75.

Mac Nally, R. 1994. Habitat-specific guild structure of forest birds in south-eastern Australia: a regional scale perspective. Journal of Animal Ecology **63:**988–1001.

Margules, C. R., G. A. Milkovits, and G. T. Smith. 1994. Contrasting effects of habitat fragmentation on the scorpion *Cercophonius squama* and an amphipod. Ecology **75:**2033–2042.

Margules, C. R., T. D. Redhead, M. F. Hutchinson, and D. P. Faith. 1995. BioRap. Guidelines for using the BioRap methodology and tools. Commonwealth Scientific, Industrial, and Research Organization, Canberra, Australian Capital Territory.

McComb, W. C., T. A. Spies, and W. H. Emmingham, 1993. Douglas-fir forests. Managing for timber and mature-forest habitat. Journal of Forestry **December:**31–42.

McGarigal, K., and W. C. McComb. 1995. Relationships between landscape structure and breeding birds in the Oregon Coast Range. Ecological Monographs **65:**235–260.

McNeely, J. A. 1994. Protected areas for the 21st century: working to provide benefits to society. Biodiversity and Conservation **3:**390–405.

Milledge, D. R., C. L. Palmer, and J. L. Nelson. 1991. "Barometers of change": the distribution of large owls and gliders in Mountain Ash forests of the Victorian central highlands and their potential as management indicators. Pages 55–65 in D. Lunney, editor. Conservation of Australia's forest fauna. Royal Zoological Society of New South Wales, Sydney.

Millington, P. J., and K. F. Walker. 1983. Australian freshwater mussel *Velesunio ambiguus* (Phillipi) as a biological indicator for zinc, iron and manganese. Australian Journal of Marine and Freshwater Research **34:**873–892.

Mills, L. S., M. E. Soulé, and D. F. Doak. 1993. The key-stone species concept in ecology and conservation. BioScience **43:**219–224.

Mladenhoff, D. J., J. White, J. Pastor, and T. R. Crow. 1993. Comparing spatial pattern in unaltered old-growth and disturbed forest landscapes. Ecological Applications **3:**294–306.

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

Noss, R. F. 1991. Landscape connectivity: different functions at different scales. Pages 27–39 in W. E. Hudson, editor. Landscape linkages and biodiversity. Island Press, Covelo, California.

Noss, R. F., and A. Y. Cooperrider. 1994. Saving nature's legacy: protecting and restoring biodiversity. Island Press, Covelo, California.

Okland, B. 1996. Unlogged forests: important sites for preserving the diversity of mycetophilids (Diptera: Sciaroidea). Biological Conservation **76:**297–310.

Parsons, P. 1991. Biodiversity conservation under global climatic change: the insect *Drosophila* as a biological indicator? Global Ecology and Biogeography Letters **1:**77–83.

Pechmann, J. H., D. I. Scott, R. D. Semlitch, J. P. Caldwell, L. J. Vitt, and J. W. Gibbons. 1991. Declining amphibian populations: the problem of separating human impacts from natural fluctuations. Science **253:**892–895.

Phillips, E. J. 1996. Comparing silvicultural systems in a coastal montane forest: productivity and cost of harvesting operations. Special report SR-109. Forest Engineering Research Institute of Canada, Victoria, British Columbia.

Pressey, R. L. 1994. Ad hoc reservations: forward or backward steps in developing representative reserve systems? Conservation Biology **8**:662–668.

Schmiegelow, F. K., and S. J. Hannon. 1993. Adaptive management, adaptive science and the effects of forest fragmentation on boreal birds in northern Alberta. Transactions of the North American Wildlife and Natural Resources Conference **58:**584–598.

Simberloff, D. A. 1998. Flagships, umbrellas, and keystones: is single-species management passe in the landscape era. Biological Conservation **83:**247–257.

Slobodkin, L. B., D. B. Botkin, B. Maguire Jr., B. Moore III, and H. J. Morowitz. 1980. On the epistemology of ecosystem analysis. Pages 497–507 in V. S. Kennedy, editor. Estuarine perspectives. Academic Press, New York.

Spellerberg, I. F. 1994. Monitoring ecological change. 2nd edition. Cambridge University Press, Cambridge, United Kingdom.

Swenson, J. E., K. L. Alt, and R. L. Eng. 1986. Ecology of bald eagles in the Greater Yellowstone ecosystem. Wildlife Monographs **95:**1–46.

Terborgh, J. 1986. Keystone plant resources in the tropical forest. Pages 330–344 in M. E. Soulé, editor. Conservation Biology: the science of scarcity and diversity. Sinauer Associates, Sunderland, Massachusetts.

Thiollay, J. 1992. The influence of selective logging on bird species diversity in a Guianan rain forest. Conservation Biology **6:**47–63.

Torsvik, V., J. Goksoyr, and F. Daae. 1990. High diversity in DNA of soil bacteria. Applied and Environmental Microbiology **56:**782–787.

United Nations. 1992. Agenda 21: the United Nations programme of action from Rio. United Nations, New York.

Walker, K. F. 1981. Ecology of freshwater mussels in the River Murray. Australian Water Resources Council technical paper 63. Australian Government Publishing Service, Canberra, Australian Capital Territory.

Wallis, A., D. Stokes, G. Wescott, and T. McGee. 1997. Certification and labelling as a new tool for sustainable forest management. Australian Journal of Environmental Management **4:**224–238.

Weaver, J. C. 1994. Indicator species and scale of observation. Conservation Biology **9:**939–942.

Wiens, J. 1997. Wildlife in patchy environments: metapopulations, mosaics and management. Pages 53–84 in D. R. McCullogh, editor. Metapopulations and wildlife conservation. Island Press, Covelo, California.

Wolseley, P. A., and B. Aguirre-Hudson. 1991. Lichens as indicators of environmental change in the tropical forests of Thailand. Global Ecology and Biogeography Letters **1:**170–175.

Woodwell, G. M., and A. L. Rebuck. 1967. Effects of chronic gamma radiation on the structure and diversity of an oak-pine forest. Ecological Monographs **37:**53–69.