ECOLOGICAL INDICATORS: PANACEA OR LIABILITY?

PETER B. LANDRES

USDA Forest Service, Forestry Sciences Laboratory, 800 East Beckwith, PO Box 8089, Missoula, Montana 59807, USA

74.1 INTRODUCTION

Environmental indicators have been used for nearly 100 years, providing "... information about the state of environmental quality not obtainable in other ways" (Inhaber, 1976, p. 105). Individual species are currently used as indicators in three ways: (1) like the miner's canary, to assess environmental contamination from toxic compounds (e.g., Wren, 1986; Levin et al., 1989); (2) to assess environmental conditions such as temperature, nutrient concentration, and pH on land (e.g., Zonneveld, 1983, 1988) and in water (e.g., Hellawell, 1986; Soule and Kleppel, 1988); and (3) to assess ecological attributes, primarily population trends of other species (e.g., Szaro and Balda, 1982; Starfield and Bleloch, 1983), and habitat quality or ecosystem health (e.g., Powell and Powell, 1986). Using indicator species in the first two ways is well established with a broad empirical database. In contrast, using ecological indicators to assess ecological attributes is a relatively new and rapidly increasing procedure, but its use is neither conceptually nor empirically well established (Jarvinen, 1985; Gotmark et al., 1986; Landres et al., 1988; Soule, 1988).

This paper critically examines the use of terrestrial ecological indicators to assess population trends of other species and habitat quality or ecosystem health (Fig. 74.1). This paper briefly reviews some traditional and current uses of ecological indicators in the United States, discusses potentially serious conceptual and practical problems in using vertebrate species as ecological indicators, presents a detailed analysis of an ecosystem-based approach to assessment using ecosystem indicators as an alternative to traditional indicators, and offers recommendations for mitigating some, but not all, of the problems in using ecological indicators.

1295

From:

McKenzie, D.H.; Hyatt, D.E.; McDonald, V.I., eds. Ecological Indicators. Vol. 2. Amsterdam: Elsevier Applied Scientific Publishers: 1295-1318. (/992)

Aldo Leopold Wilderness Research Institute: Publication # 246

CITATION: Landres, Peter B. 1992. Ecological indicators: panacea or liability? In: McKenzie, D.H.; Hyatt, D.E.; McDonald, V.I., eds. Ecological Indicators. Vol. 2. Amsterdam: Elsevier Applied Scientific Publishers: 1295-1318.



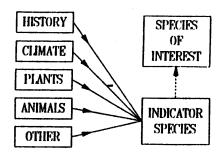


Fig. 74.1. Conceptual model showing measurement of environmental conditions directly influencing the indicator species, and inference or extrapolation of these conditions to the species of interest. Solid lines show direct influence and the dashed line shows inference.

74.2 CURRENT USES OF ECOLOGICAL INDICATORS

Many of the current uses of individual species as ecological indicators were initiated by the United States Fish and Wildlife Service and the United States Forest Service. The U.S. Fish and Wildlife Service developed Habitat Evaluation Procedures (HEP) (USDI, 1980a,b,c) "... to document the quality and quantity of available habitat for selected species of wildlife" (USDI, 1980b, p. 1-1) referred to as "evaluation species." Evaluation species are chosen by socioeconomic and ecological criteria. Habitat preferences of evaluation species are then extrapolated to other species in the wildlife community. HEP procedures were initially derived for assessing impacts of water developments on wildlife habitat (Daniel and Lamaire, 1974), were subsequently refined and tested, and are now widely used in aquatic and terrestrial habitats.

In the U.S. Forest Service, each National Forest must identify "Management Indicator Species" (MIS), as specified in the Code of Federal Regulations (1985) pursuant to the National Forest Management Act of 1976. MIS include recovery species which are identified by State or Federal governments as threatened, endangered, or rare; featured species which are of social or economic value; sensitive species which are identified by Regional Foresters as particularly sensitive to management activities; and ecological indicators which are used to monitor environmental factors, population trends of other species, or habitat conditions. Specific goals, objectives, and standards for MIS are in each National Forest Plan.

74.3 THE NEED FOR ECOLOGICAL INDICATORS

Ecological indicators are needed because "... of a very practical problem: too many needs, too few funds" (Jarvinen, 1985, p. 102). In general, using individual species as ecological indicators appears to overcome this problem. Indicators reduce costs by reducing the number of variables that need to be monitored and by providing spatial and temporal averaging of environmental conditions. For example, honey bees (Apis millifera) from a single hive forage over several square

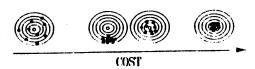


Fig. 74.2. "Target" diagrams illustrating how the accuracy 4 nearness to the "bulls eye" or center of the target) and precision (or scatter) of data influence the cost of a study. The target at the far left shows that neither precise nor accurate data are relatively inexpensive. Accurate but not very precise data (right center) are comparable to data that are precise but not accurate (left center). Data that are both precise and accurate (far right) are relatively expensive.

miles yielding a spatially averaged sample useful in assessing environmental contamination from a variety of air pollutants (Bromenshenk et al., 1985).

The increased use of ecological indicators results from two assumptions. First monitoring one or several indicator species is assumed to be a cost-effective alternative to studying many species, processes, and environmental conditions within an ecosystem. And second, monitoring one or several ecological indicators is assumed to be a sufficiently accurate and precise alternative to exhaustive assessment and monitoring. "Sufficiently accurate and precise" entails further subjective, statistical, and conceptual assumptions in determining whether an ecological indicator reliably represents populations of other species. These assumptions are examined below.

74.4 ARE ECOLOGICAL INDICATORS EFFECTIVE AND RELIABLE?

74.4.1 Cost-effectiveness

Costs may be reduced by using indicators that are abundant, conspicuous, and easily recognized (Szaro and Balda, 1982; Sidle and Suring, 1986). However, Verner (1986) dispelled the cost-effectiveness argument by showing that to reliably detect a 10% change between years (with 95% confidence) in population numbers of the pileated woodpecker (*Dryocopus pileatus*) sampled at random locations, total costs would exceed \$1 million per year. Verner's analysis reveals that even conspicuous and easily recognized species (such as the pileated woodpecker) can be very expensive to monitor. Detecting statistically significant change in most ecological parameters will likely be expensive.

In addition, there are no clear guidelines for choosing the number of indicators needed for assessment or monitoring efforts. HEP guidelines for determining the number of indicators are ambiguous at best (Landres et al., 1988). In the only study on the number of indicators used in HEP, Fry et al. (1986) recommended that the maximum possible number of species be used to increase assessment precision. If statistical accuracy and precision are maintained for all indicator species, monitoring efforts will be very expensive (Fig. 74.2). This expense requires subjective decisions to balance precision, accuracy, and cost, potentially abrogating the effectiveness and reliability of using indicator species.

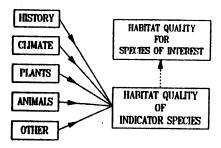


Fig. 74.3. Conceptual model showing measurement of environmental conditions directly influencing habitat quality of the indicator species, and inference or extrapolation of these conditions to the species of interest. Solid lines show direct influence and the dashed line shows inference.

74.4.2 Indicators of population trends

Both the U.S. Fish and Wildlife Service and U.S. Forest Service use indicator species to assess population trends of other species. HEP guidelines state that "... predicted impacts for these [evaluation] species can be extrapolated to a larger segment of the wildlife community..." (USDI, 1980b, p. 3-2). The Code of Federal Regulations (1985) mandates the U.S. Forest Service to use "... population changes [of management indicator species to]... indicate the effects of management activities on other species."

Extrapolating the population response from one species to another is conceptually problematic (Landres, 1983; Verner, 1984), and empirical studies confirm these problems (Mannan et al., 1984; Szaro, 1986). Each animal species has a unique set of breeding characteristics, foraging behaviors, diet, and habitat requirements. These differences among species make extrapolation from one species to another difficult or impossible. Population density in some species may be limited or regulated by habitat, and in others by predation, disease, extreme weather conditions, or unknown factors on migration routes or wintering grounds. Given such variation among species, it is very unlikely that population trends between any pair of species would change in parallel fashion. Neither conceptual nor empirical studies support extrapolating the population trend of an indicator species to other species. This approach to ecological monitoring should be rejected unless justified by long-term research on the specific species.

74.4.3 Indicators of habitat quality

Both the U.S. Fish and Wildlife Service (USDI, 1980h) and the U.S. Forest Service (Nelson and Salwasser, 1982; Capp et al., 1984; Hoover and Willis, 1984; Code of Federal Regulations, 1985) use indicator species to assess habitat quality for other species. Using indicator species in this way assumes that population density of the indicator is a reliable index of habitat quality for that species, and that habitat quality for any species in that ecosystem may be inferred from what is deemed to be adequate habitat quality for the indicator (Fig. 74.3). For example, in one National Forest it was suggested that management of 414 species of forest verte, brates could be achieved by managing for elk and three species of accipiter hawks (Mealey and Horn, 1981), and several current Forest Plans show a similar use of indicator species. Conceptual problems of this use of ecological indicators are discussed below.



Fig. 74.4. Confounding of criteria used in selecting indicator species. Solid lines show selection of indicator species directly from socio-economic and political criteria. The dashed line shows inference or assumption of fulfilling the ecological criterion after indicator species have been chosen by other criteria.

74.4.3.1 Population density as an index of habitat quality

There are several problems with this assumption. Density is a tenuous index of habitat quality if winter habitat, dominance status, reproductive success, predator populations, and seasonal fluctuations in resources and abiotic conditions are not considered (Van Horne, 1983; Maurer, 1986). Difficulties in estimating density may also yield inaccurate results and conclusions, particularly over the short-run. Sampling problems are especially severe in species with low population densities, despite such species often being considered good indicators for other reasons. Finally, stochastic variation in population attributes unrelated to environmental change would reduce the reliability of the species as an ecological indicator.

74.4.3.2 Geographic extrapolation

There are several problems when an indicator chosen in one area is assumed to be appropriate for use in another area. Although geographically separated habitats may appear similar, subtle differences in habitat attributes and environmental conditions may influence an indicator's density or role in the community. In addition, genetic differences among distinct populations of an indicator species, combined with different species composition of the associated wildlife community, will likely influence how the indicator responds to environmental change. Wildlife, habitat-relationship models strive to quantify interactions among these variables, but much improvement is still needed in these models (see Verner et al., 1986). Because every population of a species is embedded in a unique environmental matrix, it is not appropriate to assume that an indicator chosen in one area is necessarily valid in another area.

74.4.3.3 Confounded selection criteria

Selection criteria used to choose indicator species are often confounded or arbitrary (Landres et al., 1988). That is, species chosen to fill the needs of one criterion are then used to satisfy a different criterion (Fig. 74.4). For example, HEP guidelines state that "species of high public interest should be included . . . because in many cases such species do serve as ecological indicators" (USDI, 1980h, p. 3-3). And in some National Forests, elk (Cervus elaphus), a species with high socioeconomic value, is proposed as an indicator of habitat quality for other species. The criterion used to select evaluation species and MIS in large part determines the success or failure of meeting stated project goals. Allen et al. (1984) strongly argue that the criterion used for observing a system determines the ability to make

accurate and meaningful conclusions about that system. Confounded selection criteria, such as using elk for an ecological indicator when it was chosen primarily under socioeconomic criteria, destroys the credibility of an indicator species.

74.4.3.4 Species-specific resources

Managing an area for an indicator species might maintain those environmental conditions needed by that species, while ignoring ecological resources and processes needed by other species (Kushlan, 1979). Indeed, the more that is known about an indicator species, the more exact management actions can be, and the less likely these actions will suffice for other species (Ruggiero et al., 1988). The result is that one gets what one manages for, and maybe little else.

Several scholars (e.g., Wilcox, 1984; Soule, 1986) and Federal agencies suggest using high-trophic level mammalian and avian carnivores as indicators of habitat quality, based on the assumption that the large area requirements of such "umbrella species" likely includes the spectrum of resources needed by other organisms dependent on that habitat. Such charismatic megavertebrates also garner public attention and increased funding.

In contrast to the above view, umbrella species may not be reliable ecological indicators for several reasons. Species with large area requirements likely shift their use of resources within their home range, integrating adverse and beneficial environmental changes, indicating little beyond their own resource requirements. In the short-term, Federally listed threatened and endangered species such as the grizzly bear (Ursus horriblis) and northern spotted owl (Strix occidentalis caurina) provide an expedient umbrella because large areas of land are immediately set aside for these species. In the long-term however, it is not known whether managing for one or several umbrella species will maintain all of the resources needed by all of the species in the habitat. If the goal is to maintain all of the species in that habitat, it is ecologically more appropriate to manage for the habitat or ecosystem per se, providing a course filter ensuring maintenance of the full range of species, ecological resources, and processes, rather than relying on umbrella species which may provide only a fine filter allowing the eventual loss of other species.

74.4.3.5 Defining habitat quality

Without a precise definition for the phrase habitat quality it is uncertain what the ecological indicator is assessing. Habitat quality likely includes such factors as species composition and structure of the vegetation, wildlife taxa and their reproductive rates, interactions among the biota, as well as abiotic and stochastic factors. Given such complexity, it is very unlikely that a single species could serve as an index of the structure and functioning of an entire community or ecosystem (Ward, 1978; Cairns, 1986), just as a single index or number will never be an adequate estimator of complex behavior (Allen et al., 1984; Westman, 1985). Schroeder (1987) suggested that a lack of quantitative studies clearly linking indicators with specific community attributes precludes using them at the habitat or community level. Olendorff et al., (1980) reached a similar conclusion regarding raptorial birds as indicator species of habitat quality. Without long-term research

it is difficult or impossible to judge the efficacy of an indicator species as an index of habitat quality for other species.

74.5 ECOSYSTEM INDICATORS

The above uses of ecological indicators result, in part, from the traditional use of a species-based approach to management and assessment, which is now being questioned (Hutto et al., 1987; Scott et al., 1988). In contrast, an ecosystem-based approach relying on indicators of ecosystem structure and function offer several benefits over the traditional focus on individual species, including:

- Maintaining the spectrum of biotic and abiotic resources and processes that provide the framework and conditions for evolution. From a biocentric view, evolution allows species to adapt to environmental changes, both natural and human-caused. From an anthropocentric view, evolution provides the species and genetic resources vital for agriculture, medicine, and economic development.
- 2. Preventing species from becoming threatened and endangered, averting the need for a brinkmanship approach to saving species and costly recovery programs.
- 3. Maintaining ecosystem services (Ehrlich and Mooney, 1983) that directly and inexpensively benefit humans. Such services include erosion and flood control, plant nutrients released from decomposition, pollination of food crops, biodegradation of pollutants, and many others.
- 4. Lower management costs. It is probably easier, more efficient, and costeffective to protect and manage an area of land or water with an intact,
 functioning ecosystem than to manage and monitor every component of an
 ecosystem individually.
- 5. Reducing costly (in terms of dollars and effects) management mistakes. Despite many successes, natural resource management policy and action frequently produces costly failures, especially in light of new information and the clear vision of hindsight. An ecosystem approach to managing and assessing natural resources is a conservative approach, ensuring maintenance of all ecosystem components and processes. This idea was eloquently expressed by Leopold (1953): "If the biota, in the course of aeons, has built something we like but do not understand, then who but a fool would discard seemingly useless parts? To keep every cog and wheel is the first precaution of intelligent tinkering."

If the ecosystem is the most appropriate level for management and assessment efforts, and "many properties of ecosystems cannot be studied at smaller than ecosystem scales . . . in any meaningful way" (Schindler, 1990), then research and monitoring must be geared specifically towards this level. The need for an ecosystem-based approach is clear (Agee and Johnson, 1988; Hunt, 1989); the important question is "How?" The answer requires defining what an ecosystem is, and

discussing how the concepts of ecosystem "health" and "stress" directly affects the benefits and limitations of using ecosystem indicators.

74.5.1 Defining ecosystem health and stress

An ecosystem is the biotic and abiotic components of an environment that interacts to produce a flow of energy and cycling of nutrients. Although this definition is commonly accepted and used in textbooks, an ecosystem is exceedingly difficult to practically define for several reasons. The boundary of an ecosystem is dynamic and permeable: every ecosystem is embedded in a mosaic or matrix of other ecosystems, with matter and energy flowing across their boundaries (Wiens et al., 1985), significantly affecting ecosystem structure (Rickless et al., 1984). Spatial variation in environmental conditions, historical influences, and disturbance means that the components of a given ecosystem will likely be different from one area to another. Also, species respond individually to resource needs and opportunities, further increasing spatial variation (Westman, 1990). Finally, ecosystems change over short and long time scales with succession and climate shifts. All this variation implies that ecosystems are arbitrarily defined, both in space and time, and that only clearly defined management and assessment goals allow a working classification of ecosystem boundaries and discerning the effects of perturbations on ecosystems.

Current research aims to understand the effects of pollutants and other stresses on ecosystems (e.g., Levin et al., 1989). In the United States, Woodwell (1962, 1967) was the first to study these effects, examining the impact of radiation on terrestrial ecosystems. Similarly, Barrett (1968), Malone (1969), and Shure (1971) investigated the impact of insecticides. Woodwell (1970) applied the concept of organismal stress to analyze the effects of perturbations on ecosystems, and Barrett et al., (1976) introduced "stress ecology" as the systematic study of these effects. Barrett and Rosenberg (1981) and Rapport et al., (1985) significantly clarified and expanded the application of organismal stress to ecosystems. In the literature, the word stress is used both as a perturbation and as a response (e.g., stressed ecosystem). In this paper, stress is used to denote an external factor, force, or stimulus (e.g., toxic chemicals or habitat fragmentation) applied to an ecosystem.

Ecosystems that are unaffected by stresses are essential as controls to compare and understand the effects of perturbation. Leopold (1949) drew a direct comparison between pristine ecosystems and the concept of health, writing that "a science of land health needs, first of all, a base datum of normality, a picture of how healthy land maintains itself as an organism" and that the "... most perfect norm is wilderness." Schaeffer et al., (1988, p. 448) define ecosystem health as "... the absence of [ecosystem] disease," defining ecosystem disease as "... damage to, or impairment of, ecosystem components. Disease in ecosystems, as in humans, has short-term and long-term, major and minor effects. A disease is of concern if homeostatic repair mechanisms are insufficient so that illness progresses to disease where the failure of the ecosystem to function within acceptable (healthy) limits occurs." Rapport et al., (1985) develop this idea into an "ecosystem-level distress syndrome" exhibiting a "linked set of symptoms."

Despite interest and some success in applying concepts of human health and stress to ecosystems (e.g., Rapport et al., 1981, 1985), these may be specious analogies for two reasons. First, ecosystem components vary both spatially and temporally, in contrast to the body of an organism. While the addition of a different organ or the lack of certain organs would be devastating to a body, such circumstances are within the bounds of normal variation for most ecosystems. Second, unlike a body, disturbance is an essential part of many ecosystems, necessary for maintaining heterogeneity and the survival of certain (e.g., fireadapted) species. Both aspects, variation and disturbance, are crucial in defining ecosystems and identifying change in response to stress. Like the attempt to define an ecological community as a super-organism (McIntosh, 1985), defining ecosystem health or stress on a human model may be ill-conceived, diverting attention and effort from more effective and productive analyses. An alternative to using ecosystem health in identifying stress is presented below.

74.5.2 Identifying ecosystem health and stress

Ecosystem health may be identified without resorting to tenuous analogies of human health or stress syndromes. It is more direct and effective to use a set of reference areas or sites to define the standard of "health" or the nominal values for the ecosystem of interest. Similarly, those same components and observations used to characterize each ecosystem could then be used as indicators of change in different areas of the same ecosystem type. Observations of these indicators in the area of interest would be compared with nominal values of these same attributes from the reference areas, taking into account known variation, disturbance history, and the age or maturity of the ecosystem. Similarly, Odum and Cooley (1980) suggested developing an ecosystem profile in a disturbed area based on several indicators; this profile was then compared with the profile from an undisturbed area.

A set of reference areas is needed for each ecosystem type to quantify variation in the components used to characterize that ecosystem. Reference areas should be as pristine as possible (Schindler, 1987), although it is doubtful that any uncontaminated or unperturbed ecosystems exist today on Earth. There are two problems with using reference areas to define a standard of comparison for normal variation (Christensen, 1988). First, arbitrary decisions must be made in choosing specific sites as reference areas. Decisions defining what exactly is the same ecosystem will be difficult because there is so much variability within an ecosystem type caused by factors such as soil type, topographic position, disturbance history, chance events, or the mix of surrounding ecosystems. Indeed, suitable reference areas may not exist. Second, as ecosystems change over time, for example with succession, climate changes, and changing patterns of land use, the standard of comparison also changes. Both problems basically address the difficulty of defining spatial and temporal boundaries of an ecosystem as discussed above. Management and assessment goals will be vital for resolving these decisions on a case-by-case basis.

Either positive or negative change from the nominal values of the reference areas

signals impact on the ecosystem and the magnitude of change signals the extent of impact (Rapport et al., 1985). Depending on management and assessment goals, some changes from the nominal values may be acceptable, requiring that criteria for assessing "significant" change be established before monitoring. For example, if one species of bacterium or bird is lost or replaced by another, a significant change has probably not occurred. Defined limits of allowable or acceptable change let natural resource managers know when concern or action is warranted.

74.5.3 Defining ecosystem indicators

An ecosystem indicator is any variable or component of an ecosystem that is used to infer other attributes of that ecosystem, providing a synthetic or summary view of the ecosystem or its components. Typically, a single ecosystem indicator would be used to infer several attributes. For any effective ecosystem-based management and assessment plan, ecosystem indicators are probably necessary to reduce the number of variables to a tractable level. Ecosystems are composed of hundreds or thousands of species, and their myriad interactions sustain complex ecological processes that are just beginning to be understood. This complexity makes it extremely difficult to understand how ecosystems work, to effectively manage them, and to accurately assess change.

The goal of ecosystem indicators is to provide a shorthand method that precisely and accurately reflects the structure and function of an ecosystem, and identifies undesirable changes that have occurred or are likely to occur. The need for precision and accuracy is paramount because ecosystem indicators will undoubtedly be used by policy makers and interpreted by courts in judicial actions. Especially valuable are early warning and diagnostic indicators (Kelly and Harwell, 1989). Early warning indicators respond rapidly to stress and need not be stress-specific because their purpose is to signal that attention and research are necessary. Diagnostic indicators are sensitive and reliable to specific stresses, helpful in identifying the cause of stress. Because each ecosystem is unique, it is imperative to select indicators that fulfill the early warning and diagnostic criteria on a case-by-case basis; even similar ecosystems in different geographical areas may require different indicators.

Which components of an ecosystem would be reliable indicators of change? There is considerable debate about whether structural components (e.g., species composition) or functional processes (e.g., primary production) are most appropriate for assessing change (Kelly, 1989). In addition, structural and functional components are linked together in different ways in different ecosystems, each with very different consequences for selecting appropriate ecosystem indicators. Caims and Pratt (1986) suggest three possible linkages: (1) Structural and functional components are so closely linked that a change in one causes a change in the other, either component can be monitored and an accurate response in the other inferred, (2) A change in structure does not cause a change in function because several species are functionally redundant, i.e., perform the same function. In this case, individual species may be lost without affecting ecosystem function, inferences cannot be made between the two, and function is the less sensitive indicator of stress. (3) A

change in function occurs without a change in structure. For example, a perturbation may affect a species' metabolic activity without killing it, thereby altering an ecosystem function. As in the previous case, inferences cannot be made between the two components, but now structure is the less sensitive indicator. These three different linkages between structure and function demonstrate that it is impossible to select an indicator without detailed information on the specific ecosystem of interest.

For theoretical and pragmatic reasons, both structural and functional observations are needed to characterize an ecosystem. These facts were recognized early on by Odum (1962) and summarized by Schindler (1987, p. 11): "After 18 years of manipulating whole [lake] ecosystems, I find that changes in ecosystem function, such as production, decomposition, or nutrient cycling, cannot be properly interpreted without analogous information on the organization and structure of the biotic communities which perform the function." Theoretically, ecosystems are so complex that no single observation or index could adequately summarize this complexity (see Indicators of Habitat Quality above). Also, different aspects or levels of interest in the ecosystem require different types of observations and criteria for assessing change (Allen et al., 1984; Kelly, 1989). Pragmatically, increasing the number of observations and indicators increases the likelihood of detecting change, because stresses or impacts typically cause a series of linked changes that ripple throughout different components of the ecosystem.

74.5.4 Selecting ecosystem indicators

Ecosystem indicators must precisely and accurately reflect the ecosystem as well as management and assessment goals. Ecosystem indicators may be based on the following simple conceptual framework that is suggested as necessary and sufficient to characterize all ecosystems for management and assessment purposes:

Ecosystem structure. Ecosystem structure is the species composition, dispersion pattern, and organization of plant and animal species into higher ordered levels, such as trophic levels, food webs, or guilds. Dispersion pattern refers to the spatial distribution of species and biomass, both vertically and horizontally. Although structure usually refers to a "moment in time" picture of an ecosystem, temporal structure, or the change of structural parameters through time, is important for the long-term view of ecosystems.

2. Ecosystem function. Ecosystem function is the set of processes that result from interactions among the biotic and abiotic components of the ecosystem. Three classes of processes are important from both scientific and management views. First, processes that affect the rate and total quantity of energy flow, such as primary and secondary production, and production/ respiration or production/biomass ratios. Second, processes that affect the rate and total quantity of nutrient cycling, such as decomposition, nutrient turnover, and nutrient mobilization/immobilization. And third, processes that influence ecosystem services important to humans.

3. Ecosystem variation. Variety is the essence of an ecosystem, as many factors

influence ecosystem structure and function. Spatial, temporal, and seasonal variation determine what we perceive as an ecosystem. For example, spatial variation occurs with topographic position on north- versus south-facing slopes, which influences insolation and temperature, available water, soil development, decomposition, primary production, and species composition of the community. Long-term temporal variation occurs with succession and climate changes, while short-term variation occurs seasonally and with natural and anthropogenic disturbance.

4. Disturbance regime. Watt (1947) first recognized the central importance of disturbance, but only recently (Whittaker and Levin, 1977; Pickett and White, 1985) has the general importance of disturbance been recognized as a primary factor contributing to the landscape pattern we see today. Important variables in describing disturbance (Christensen, 1988) include: patch size, or the areal extent of a disturbance; frequency, or the number of disturbances per time; return time, or the average time between disturbances at a particular site; intensity, or the physical force of a disturbance; severity, or the effects on a given organism; and predictability, or the regularity of the above variables.

Of these four general ecosystem components, structural and functional components are used as ecosystem indicators, while variation and disturbance regime define the limits of "normal" or "acceptable" change of ecosystem structure and function.

Choosing the specific structural and functional attributes that are appropriate for ecosystem indicators is a highly subjective process. Management and assessment goals are vital in choosing ecosystem indicators; specific goals require specific indicators. Specific goals also allow managers to discern when change in structure or function may be acceptable. The uniqueness of every ecosystem means there will be no predetermined or inviolate rules to determine which structural and functional attributes need to be monitored. Goals, biases, local experience, funding, available data, and intuition will all influence selecting ecosystem indicators.

74.5.5 Indicators of ecosystem structure

Indicators of ecosystem structure typically rely on the species that comprise the ecosystem. In some cases, individual species will show the effects of ecosystem stress before functional indicators for the simple reason that species may be affected directly and immediately. Identification of the cause of ecosystem stress may also be possible if the biology of the species is sufficiently known. There are many problems in using individual species as ecosystem indicators, as has been already discussed (see Indicators of Habitat Quality above). Even so, in some ecosystems and areas, individual species may serve as structural indicators, (e.g., functionally dominant or keystone species discussed below).

Generally, because of the hundreds or thousands of species in most ecosystems, species need to be combined into groups or sets, and attributes of these groups assessed as structural indicators. Deciding which sets of species to monitor depends on ecological values and management goals, which in turn depend on societal values and priorities. Conceptually, ecosystems are composed of just three major

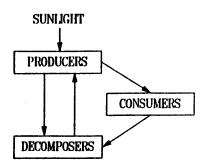


Fig. 74.5. The three primary groups of organisms in most ecosystems. Arrows show the flow of energy from the sun to producers, consumers, and decomposers. The arrow going from decomposers to producers shows the mineralization of organic matter by decomposers and subsequent use of nutrients by plants.

groups of species: producers, consumers, and decomposers (Fig. 74.5). Although in some cases consumers provide important regulatory functions such as pollination services, they typically contribute little to energy flow and nutrient cycling. Therefore, quantifying attributes of just the producers and decomposers may be sufficient to broadly characterize ecosystem structure from an ecological perspective.

Within each major group (however defined), species could be further divided into guilds based on their use of similar resources. The resulting guild structure, similar to a food web, shows which resources are being used, how they are being used, and who is using them (Landres, 1983), providing a tractable handle on ecosystem structure. Alternatively, if there are specific management goals, a guild structure based on management guilds (Verner, 1984) focuses on specific resources and their use.

Once groups of species are defined, the next step is selecting attributes of these groups that serve as meaningful ecosystem indicators. The following attributes likely apply in many ecosystems, but their suitability must be decided on a case-by-case basis. In particular, several of the following attributes are interdependent, potentially confounding any analysis, but each conveys different information and may be important in certain situations.

- 1. Species composition. Species composition is important because individual species may show the effects of ecosystem stress directly through physiological impairment (e.g., decreased metabolic activity or tumors), and death or avoidance of the area. Plants (because they can't escape stress) and animal species with short generation times, high metabolic rates, or those involved in obligatory mutualisms, are likely to be especially sensitive, immediately showing the effects of ecosystem stress. Quantifying species composition also demonstrates if retrogressive succession is occurring in response to ecosystem stress (Rapport et al., 1985).
- 2. Species reproduction. In several cases, decreased reproduction was the first observable response to ecosystem stress. For example, reproductive failure in brown pelicans (Pelicans occidentals) was seen before any observable change in the adults (Blus et al., 1974).
- 3. Species richness. Species richness may decrease in response to ecosystem stress as sensitive species are eliminated (Fig. 74.6(a)). The result is a

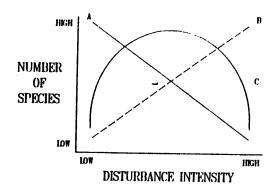


Fig. 74.6. Influence of disturbance on the number of species in a community. See text for explanation of the three possible effects of disturbance.

simplification of community structure as tolerant species increase in dominance. Alternatively, species richness may increase as ecosystem stresses fragment a habitat, increasing environmental heterogeneity in the short run, reducing dominance by a single species (Fig. 74.6(b)). The intermediate-disturbance hypothesis (Connell, 1978) suggests that species richness increases with moderate stress levels, but at greater levels richness decreases because few species can cope with the stress (Fig. 74.6(c)). In all of these possible scenarios, whether species richness increases or decreases is of less concern than the fact that there is a change, because any change in dominance relations signals a potential impact.

Direct change and indirect or cascading change (Lovejoy et al., 1986) in species composition and richness will also affect the trophic structure or food web.

Odum (1985, p. 421) suggested that "the impact of stress on the food web is not clear-cut," and offered some evidence that shorter food chains result from lake eutrophication. In contrast, Schindler (1990) found shorter food chains in acidified lakes, but not in eutrophied lakes.

- 4. Species functional dominance. In several ecosystems keystone species provide pivotal functional roles that maintain both ecosystem structure and function. In his classic experiment, Paine (1966) showed how a seastar (Pisaster) maintained rocky intertidal species richness. Similarly, Estes and VanBlaricom (1988) showed the wide-ranging effects of the sea otter (Enhydra lutris). Where a functionally dominant species is known to occur, monitoring all aspects of its natural history is imperative and costly.
- 5. Species size distribution. In some cases, ecosystem stresses cause a decrease in the average size distribution of the dominant plant and animal species, changing the vertical structure of the ecosystem. This was clearly shown in the vegetation of an experimentally irradiated temperate forest (Woodwell, 1967, 1970) and a boreal forest affected by sulfur dioxide emissions

(Freedman and Hutchinson, 1980). Rapport et al., (1985) describe similar effects of several environmental stresses on fish populations. Woodwell (1967) and Rapport et al., (1985), respectively, suggest two reasons for this size decrease: first, smaller species may have more energy available for maintenance and repair than larger species, and the reproductive tissue of smaller plant species is closer to the ground and therefore more protected from injury than the meristimatic tissue of taller species.

6. Guild structure. Quantifying guild structure (e.g., the number, kinds, and biomass of various guilds), may provide a convenient grasp of certain components of ecosystem structure. For example, decomposition is an essential process that requires various guilds of detritivores and decomposers. From an ecosystem perspective, these guilds of bacteria, invertebrates, and microarthropods are essential for processing different classes of detritus, while species composition per se of these guilds is probably of less importance.

74.5.6 Indicators of ecosystem function

Functional indicators convey information about ecological processes that are vital to the long-term maintenance of the ecosystem and the continuing evolution of species (Ricklefs et al., 1984). Although species composition changes with normal variation within an ecosystem-type, the set of ecological processes or functions that provide energy flow, essential, nutrients and other resources do not vary in the same way. From this view, ecosystems are defined by their processes and not by species composition.

The importance of ecological and ecosystem-level processes is not disputed, but they generally are not considered useful indicators of stress because they respond slower and recover quicker than structural indicators, shown conceptually by Odum (1985) and empirically in aquatic ecosystems by Schindler (1990). For example, ecological processes result from species' interactions, so functional impairment occurs only after component species are affected. Also, functional redundancy of species increases the length of time before functional impairment occurs, and may speed recovery of a perturbed function, because if one species is affected another is still available to perform the function. In addition, species replacement may simply maintain the process at its former level. All these factors that slow the response of ecological processes to change led Odum (1985, p. 421) to observe that when these processes do change, "... there is real cause for alarm, for it may signal a breakdown in [ecosystem] homeostasis."

Despite this sceptical view on the usefulness of ecological processes, they may be sensitive early warning indicators of stress, especially in terrestrial ecosystems. For example, in three separate studies, O'Neil et al., (1977, p. 271) found that "in each case, disturbance could be detected in nutrient cycling, but no significant change was evident in the population/community [structural] parameters." Similarly, Kelly (1989) showed that primary production and decomposition were the most responsive indicators of exposure to toxic fluids from oil drilling in seagrass (Thalassia) ecosystems. Several ecological processes can be sampled rela-

tively quickly and easily (e.g., primary production, detrital mass, and nutrient concentration in the soil solution and in detrital and soil leachate).

Since ecosystems are traditionally defined on the basis of energy flow and nutrient cycling, and both are essential for the maintenance of an ecosystem and its species, these parameters are the logical basis for functional indicators. In addition, ecosystem services important to humans need to be monitored on a case-by-case basis. As with indicators of ecosystem structure, the following attributes likely apply in many ecosystems, but their suitability must be decided in each situation.

1. Primary production. Primary production is an essential ecosystem function, as plants, phytoplankton, algae, and some bacteria are the only organisms on Earth capable of fixing solar radiation into carbohydrates that are the basis for most food chains. Either an increase or decrease in primary production beyond normal variation signals potential ecosystem dysfunc-

tion, with wide-ranging consequences.

2. Production/respiration, production/biomass ratios. Ecosystem stress likely requires organisms to spend more of their energy on maintenance and repair and less on biomass, pushing the production/respiration (P/R) ratio away from a value of 1 commonly seen in unperturbed ecosystems and also increases the production/biomass (P/B) ratio (Odum, 1985). Schindler (1990) found that in both acidified and eutrophied lakes P/R ratios increased from baseline values, especially in certain groups of producers, but that P/B ratios did not change. Rapport et al. (1985) argue for P/B ratios as an indicator of stress on theoretical grounds, but finally reject its use because of a lack of empirical support. Both ratios warrant further research to confirm their usefulness as indicators of ecosystem stress.

3. Decomposition rate. Decomposition is an essential process in all terrestrial ecosystems, breaking down detritus and mineralizing nutrients required by plants and other producers. The rate of decomposition determines the rate at which nutrients are made available to producers, strongly influencing primary production. Despite its theoretical importance, the large number of decomposer species in most ecosystems likely results in extensive functional redundancy, reducing the effectiveness of using decomposition rate as an indicator of ecosystem stress. Quantifying decomposer community structure, especially the presence of keystone decomposer species, may be an

effective way of assessing this important ecosystem process.

4. Nutrient cycling. Nutrient cycling is also an essential process in ecosystems, providing nutrients necessary for plants and other producers. O'Neil et al., (1977) first called attention to nutrient cycling as an indicator of ecosystem stress, stating that "by focusing on [nutrient cycling] it may now be possible to identify monitoring points that reflect changes in the total ecosystem.

... Because of the large number of interacting components, detrimental increases in nutrient loss might be detected irrespective of which specific

organisms or processes were being affected." (p. 270).

Several aspects of nutrient cycling have been proposed as indicators of ecosystem stress. Odum (1985) suggested using nutrient turnover, horizontal transport, vertical cycling, and nutrient loss. Schindler (1990) found changes in each of these parameters from baseline conditions, although results were inconsistent between acidified and eutrophied lakes. Shugart et al., (1976) recommend monitoring the concentration of nutrients in the soil solution. O'Neil et al., (1977) and Vitousek et al., (1981) showed increased leaching of soil nutrients in perturbed systems. The adenylate energy charge, a composite biochemical index of metabolic activity of individuals and microbial communities involved in decomposition and nutrient cycling (Ivanovici and Wiebe, 1981) may be another indicator.

74.5.7 Limitations of using ecosystem indicators

Despite the potential benefits of an ecosystem-based approach to management and assessment and the use of ecosystem indicators, several obstacles remain:

- Ecosystem indicators do not provide a complete description of the environment. All indicators (including both ecosystem indicators and individual indicator species) are chosen by certain criteria, ultimately reflecting societal values and priorities. All indicators, therefore, merely reflect those conditions or aspects of the environment a society deems worthy of monitoring.
- 2. There are no policies or other mandates in the United States to establish an ecosystem-based approach to management and assessment. Although several authors (e.g., Keiter, 1988; Hunt, 1989; Grumbine, 1990) have discussed the need and benefits of such a mandate, it would take considerable time before such a policy is made into law and then implemented via regulations.
- 3. Very little is known about ecosystems, therefore, "adaptive management" (Holling, 1978; Walters, 1986) must be employed, treating monitoring plans with ecosystem indicators as an experiment in which hypothesis testing and resulting feedback change the original plan. For example, the particular structural and functional attributes used for monitoring need to be viewed as hypotheses on assessing ecosystem change. This is similar to the "muddling-through" approach to wildlife management (Bailey, 1982; McNab, 1983).
- 4. The dynamic and permeable nature of ecosystem boundaries causes three problems. First, political/administrative boundaries and jurisdictions usually do not conform to ecological boundaries (Newmark, 1985), resulting in the loss of species and unknown effects on ecological processes. Second, large areas of land are essential for maintaining natural flows of energy and matter, yet there are no large areas left, which requires using public and private "semi-natural" lands explicitly for the maintenance of species and ecological processes (Salwasser, 1987; Westman, 1990). Third, boundary dynamics among adjacent ecosystems may be vital for maintaining an area of interest, requiring interagency cooperation for the maintenance of regional landscapes. Such cooperation has been difficult in the past (Sax and

Keiter, 1987), but recent developments between the U.S. Forest Service and U.S. Park Service in the Yellowstone region show that interagency cooperation is possible.

- 5. If reference areas are used to determine standards for comparison, many representative "pristine" samples of every ecosystem type need to be preserved. Because of the variation in ecosystem components, determining statistical significance at even the 80% probability level will require many reference areas, and such a number of pristine ecosystems do not exist nor will it be practical to sample them all.
- 6. Long-term research is needed to assess ecosystem variation and the effects of disturbance (Franklin *et al.*, 1990), but such research is currently being conducted in only a small number of ecosystems. For most ecosystems the magnitude or effects of variation and disturbance are not known.
- 7. The more ecologically appropriate a management plan is, the less manageable it is. There are a plethora of factors affecting any single ecological observation. If any of these factors change, the observation may change as a result. It will be difficult at best for managers to deal with such chaos in meeting targeted goals.

Only by fully recognizing and working with these limitations will ecosystem indicators be effective and reliable estimators of change, and be useful in the management of natural resources.

74.6 ECOLOGICAL INDICATORS: PANACEA OR LIABILITY?

The current use of ecological indicators to assess population trends and habitat quality for other species of interest is financially not practical, conceptually inappropriate, and empirically unsupported, potentially leading to inaccurate long-term management and assessment decisions. Although funding is rarely adequate, inexpensive shortcuts usually result in flawed science, poor management, and increased long-term costs.

At present, there are few alternatives to using status quo ecological indicators for monitoring and assessment. The choices seem to be (1) continuing current uses of indicator species, (2) long-term research on an indicator species' ability to show population trends and habitat quality for other species adversely affected by environmental stresses and management actions, or (3) adapting a habitat or ecosystem-based approach in which the structure and functioning of the system is more important than the presence of individual species. The author suggests that the first choice above, not be used until ecological indicators are proven effective and reliable. The second choice above is probably too costly and we do not sufficiently understand habitats or ecosystems to know every species likely to be affected. The third choice, developing indicators of ecosystem structure and function, is probably the most practical and cost-effective over the long-term, but has not yet proven effective and reliable.

74.7 RECOMMENDATIONS FOR USING ECOLOGICAL INDICATORS

Despite the above criticisms, using indicator species to assess population trends and habitat quality will continue because the tradition of using them is firmly established, they are believed to be cost-effective, and current regulations mandate their use. Until alternative monitoring and assessment tools are developed, the following recommendations should make the use of ecological indicators more rigorous, effective, and reliable.

- Clearly state management and assessment goals, including criteria used to determine when those goals have been achieved.
- 2. Use indicator species only when appropriate and necessary. In general, there are no clear guidelines to determine when an indicator is needed. For "species management" or management of species mandated under socioeconomic and political criteria, indicator species are not appropriate because direct measurement of requisite resources and species' populations is required for monitoring and assessment. Likewise, for "resource management" or management of specific resources or habitats, direct measurement is usually feasible, cost-effective, and averts the need for inference from an indicator. Ecological indicators should be used only when direct measurement is impossible (Beanlands and Duinker, 1983).
- Choose ecological indicators by criteria that are unambiguously and explicitly defined, and are in accord with assessment goals. Researchers and managers must clearly state the reasons for choosing selection criteria and underlying assumptions for their choice.
- 4. Include all species (or other indicators) that fulfill the selection criteria. Typically, socioeconomic, political, and ecological criteria will be needed to meet assessment goals, requiring different indicators. Within these three broad criteria, specific criteria are needed to prioritize the selection of specific indicators.
- 5. Know the biology and ecology of the indicator species. Because assessments and resulting recommendations depend on species-specific data, all assumptions about life history, food requirements, and habitat requirements need to be verified.
- 6. Develop a conceptual and statistical model for every use of an ecological indicator, treating the indicator as a formal statistical estimator (e.g., as in a path regression analysis). This allows the accuracy and precision of an ecological indicator to be determined quantitatively.
- 7. Identify and define all sources of subjectivity in selecting, monitoring, and interpreting ecological indicators. Every assessment and technical decision entails value judgments. If treated formally, these could be discussed and the merits of each determined (Susskind and Dunlap, 1981).
- Submit monitoring and assessment design, methods of data collection, and proposed statistical analyses to external peer review. Interpretations, conclusions, and recommendations of management plans could also be

reviewed. While cumbersome, peer review would also increase assessment quality and effectiveness (Beanlands and Duinker, 1983; Palmer, 1987).

ACKNOWLEDGEMENTS

My sincere thanks to the careful eye and sharp wit of Mary Arthur, Rob Brooks, Alan Carpenter, Mary Jo Croonquist, Tim Hogan, Madeline Mazurski, and an anonymous reviewer who helped clarify the concepts and my abstruse writing in previous drafts of this manuscript.

REFERENCES

- Agee, J. K. and D. R. Johnson. (1988). A direction for ecosystem management. In *Ecosystem management for parks and wilderness*, ed. J. K. Agee and D. R. Johnson, 226-32. Washington, University of Washington Press.
- Allen, T. F. H., R. V. O'Neil and T. W. Hockstra. (1984). Interlevel relations in ecological research and management: some working principles from hierarchy theory. USDA Forest Service General Technical Report RM-110. Rocky Mountain Forest and Range Experiment Station, Colorado.
- Bailey, J. A. (1982). Implications of 'muddling through' for wildlife management. Wildlife Society Bulletin, 10, 363-9.
- Barrett, G. W. (1968). The effects of an acute insecticide stress on a semi-enclosed grassland ecosystem. *Ecology*, 49, 1019-35.
- Barrett, G. W. and R. Rosenberg. (1981). Stress effects on natural ecosystems. New York, John Wiley and Sons.
- Barrett, G. W., G. M. Van Dyne and E. P. Odum. (1976). Stress ecology. BioScience, 26, 192-4.
- Beanlands, G. E. and P. N. Duinker. (1983). An ecological framework for environmental impact assessment in Canada. Institute for Resource and Environmental Studies, Dalhousie University, Canada.
- Blus, L. J., B. S. Neely, A. A. Belisle and R. M. Prouty. (1974). Organochlorine residues in brown pelican eggs: relation to reproductive success. *Environmental Pollution*, 7, 81-91.
- Bromenshenk, J. J., S. R. Carlson, J. C. Simpson and J. M. Thomas. (1985). Pollution monitoring of Puget Sound with honeybees. *Science*, 227, 632-4.
- Cairns, J., Jr. (1986). The myth of the most sensitive species. BioScience, 36, 670-2.
- Cairns, J., Jr. and J. R. Pratt. (1986). On the relation between structural and functional analyses of ecosystems. *Environmental Toxicology and Chemistry*, 5, 785-6.
- Capp, J. C., W. W. Sandfoot and J. F. Lipscomb. (1984). Managing forested lands for wildlife: Roaring Creek Management Area, Roosevelt National Park. In *Managing forested lands for wildlife*, ed. R. L. Hoover and D. L. Willis, 323-46. Colorado Division of Wildlife and U.S.D.A. Forest Service, Rocky Mountain Region, CO.
- Christensen, N. L. (1988). Succession and natural disturbance: paradigms, problems, and preservation of natural ecosystems. In Ecosystem management for parks and wilderness, ed. J. K. Agee and D. R. Johnson, 62-86. Washington, University of Washington Press. Code of Federal Regulations (1985). 36 CFR Chapter II 219.19:64.
- Connell, J. (1978). Diversity in tropical rainforests and coral reefs. Science, 199, 1302-10. Daniel, C. and R. Lamaire. (1974). Evaluating effects of water resource developments on
- wildlife habitat. Wildlife Society Bulletin, 2, 114-18.

 Ehrlich, P. R. and H. A. Mooney. (1983). Extinction, substitution, and ecosystem services.

 BioScience, 33, 248-54.

- Estes, J. A. and G. R. VanBlaricom. (1988). Concluding remarks. In *The community ecology of sea otters*, ed. J. A. Estes and G. R. VanBlaricom, 210-37. New York, Springer-Verlag.
- Franklin, J. F., C. S. Bledsoe and J. T. Callahan. (1990). Contributions of the Long-Term Ecological Research Program. *BioScience*, 40, 509-23.
- Freedman, B. and T. C. Hutchinson. (1980). Effects of smelter pollutants on forest leaf litter decomposition near a nickle-copper smelter at Sudbury, Ontario. Canadian Journal of Botany, 58, 1722-36.
- Fry, M. E., R. J. Risser, H. A. Stubbs and J. P. Leighton. (1986). Species selection for habitat-evaluation procedures. In *Wildlife 2000: modeling habitat relationships of terrestrial vertebrates*, ed. J. Verner, M. L. Morrison and C. J. Ralph, 105-08. Wisconsin, University of Wisconsin Press.
- Gotmark, F., M. Ahlund and M. O. G. Eriksson. (1986). Are indices reliable for assessing conservation value of natural areas? An avian case study. *Biological Conservation*, 38, 55-73.
- Grumbine, E. R. (1990). Viable populations, reserve size, and federal lands management. *Conservation Biology*, 4, 127-34.
- Hellawell, J. M. (1986). Biological indicators of freshwater pollution and environmental management. London, Elsevier Applied Science Publishers.
- Holling, C. S. (1978). Adaptive environmental assessment and management. New York, John Wiley and Sons.
- Hoover, R. L. and D. L. Willis. (1984). Managing forested lands for wildlife. Colorado Division of Wildlife and U.S.D.A. Forest Service, Rocky Mountain Region, Colorado.
- Hunt, C.E. (1989). Creating an endangered ecosystems act. Endangered Species Update, 6, 1-5.
- Hutto, R. L., S. Reel and P. B. Landres. (1987). A critical evaluation of the species approach to biological conservation. *Endangered Species Update*, 4, 1-4.
- Inhaber, H. (1976). Environmental indices. New York, John Wiley and Sons.
- Ivanovici, A. M. and W. J. Wiebe. (1981). Towards a working "definition" of "stress": a review and critique. In *Stress effects on natural ecosystems*, ed. G. W. Barrett and R. Rosenberg, 13-28. New York, John Wiley and Sons.
- Jarvinen, O. (1985). Conservation indices in land use planning: dim prospects for a panacea. *Ornis Fennica*, 62, 101-06.
- Keiter, R. B. (1988). Natural ecosystem management in park and wilderness areas: looking at the law. In *Ecosystem management for parks and wilderness*, ed. J. K. Agec and D. R. Johnson, 15-40. Washington, University of Washington Press.
- Kelly, J. R. (1989). Ecotoxicology beyond sensitivity: a case study involving "unreasonable-ness" of environmental change. In *Ecotoxicology: problems and approaches*, ed. S. A. Levin, M. A. Harwell, J. R. Kelly and K. D. Kimball, 473-96. New York, Springer-Verlag.
- Kelly, J. R. and M. A. Harwell. (1989). Indicators of ecosystem response and recovery. In Ecotoxicology: problems and approaches, ed. S. A. Levin, M. A. Harwell, J. R. Kelly and K. D. Kimball, 9-35. New York, Springer-Verlag.
- Kushlan, J. A. (1979). Design and management of continental wildlife reserves: lessons from the Everglades. Biological Conservation, 15, 281-90.
- Landres, P. B. (1983). Use of the guild concept in environmental impact assessment. Environmental Management, 7, 393-8.
- Landres, P. B., J. Verner and J. W. Thomas. (1988). Ecological uses of vertebrate indicator species: a critique. *Conservation Biology*, 2, 316-28.
- Leopold, A. (1949). A Sand County almanac. New York, Oxford University Press.
- Leopold L. B. (1953). Round River: from the journals of Aldo Leopold. New York, Oxford University Press.
- Levin, S. A., M. A. Harwell, J. R. Kelly and K. D. Kimball. (1989). In *Ecotoxicology:* problems and approaches. New York, Springer-Verlag.
- Lovejoy, T. E., R. O. Bierregaard, A. B. Rylands, J. R. Malcolm, C. E. Quintela, L. H.

- Harper, K. S. Brown, A. H. Powell, G. V. N. Powell, H. O. R. Schubart and M. B. Davis. (1986). Edge and other effects of isolation on Amazon forest fragments. In *Conservation Biology: the science of scarcity and diversity*, ed. M. E. Soule, 257-85. Massachusetts, Sinauer Associates.
- Malone, C. R. (1969). Effects of diazion contamination on an old-field ecosystem. *American Midland Naturalist*, 82, 1-27.
- Mannan, R. W., M. L. Morrison and E. C. Meslow. (1984). The use of guilds in forest bird management. Wildlife Society Bulletin, 12, 426-30.
- Maurer, B. A. (1986). Predicting habitat quality for grassland birds using density-habitat correlation. *Journal of Wildlife Management*, 50, 556-66.
- McIntosh, R. P. (1985). The background of ecology: concept and theory. Cambridge, Cambridge University Press.
- McNab, J. (1983). Wildlife management as scientific experimentation. Wildlife Society Bulletin, 11, 397-401.
- Mealey, S. P. and J. R. Horn. (1981). Integrating wildlife habitat objectives into the forest plan. Transactions of the North American Wildlife and Natural Resources Conference, 46, 488-500.
- Nelson, R. D. and H. Salwasser. (1982). The Forest Service Wildlife and Fish Habitat Relationship Program. Transactions of the North American Wildlife and Natural Resources Conference, 47, 174-83.
- Newmark, W. D. (1985). Legal and biotic boundaries of western North American national parks: a problem of congruence. *Biological Conservation*, 33, 197–208.
- Odum, E. P. (1962). Relationships between structure and function in the ecosystem. Japanese Journal of Ecology, 12, 108-18.
- Odum, E. P. (1985). Trends expected in stressed ecosystems. BioScience, 35, 419-22.
- Odum, E. P. and J. L. Cooley. (1980). Ecosystem profile analysis and performance curves as tools for assessing environmental impact. In *Biological evaluation of environmental impacts*. 94-102. Washington, DC, U.S. Fish and Wildlife Service.
- Olendorff, R. R., R. S. Motroni and M. W. Call. (1980). Raptor management the state of the art in 1980. In *Management of western forests and grasslands for nongame birds*, 468-523, USDA Forest Service General Technical Report INT-86.
- O'Neil, R. V., B. S. Ausmus, D. R. Jackson, R. I. Van Hook, P. Van Voris, C. Washburne and A. P. Watson. (1977). Monitoring terrestrial ecosystems by analysis of nutrient export. *Water, Air, and Soil Pollution*, 8, 271-7.
- Paine, R. T. (1966). Food web complexity and species diversity. *American Naturalist*, 100, 65-75.
- Palmer, M. E. (1987). A critical look at rare plant monitoring in the United States. Biological Conservation, 39, 113-27.
- Pickett, S. T. A. and P. S. White. (ed.) (1985). Ecology of natural disturbance and patch dynamics. New York, Academic Press.
- Powell, G. V. N. and A. H. Powell. (1986). Reproduction by great white herons Ardea herodias in Florida Bay as an indicator of habitat quality. Biological Conservation, 36,101-13.
- Rapport, D. J., H. A. Regier and C. Thorpe. (1981). Diagnosis, prognosis, and treatment of ecosystems under stress. In Stress effects on natural ecosystems, ed. G. W. Barrett and R. Rosenberg, 269-80. New York, John Wiley and Sons.
- Rapport, D. J., H. A. Regier and T. C. Hutchinson. (1985). Ecosystem behavior under stress. American Naturalist, 125, 617-40.
- Ricklefs, R. E., Z. Naveh and R. E. Turner. (1984). Conservation of ecological processes. *International Union for Conservation of Nature and Natural Resources, Commission on Ecology Papers* Number 8 (also in The Environmentalist Vol. 4, Supplement No. 8).
- Ruggiero, L. F., R. S. Holthausen, B. G. Marcot, K. B. Aubry, J. W. Thomas and E. C. Meslow. (1988). Ecological dependency: the concept and its implications for research and

management. Transactions of the North American Wildlife and Natural Resources Conference, 53, 115-26.

Salwasser, H. (1987). Editorial. Conservation Biology, 1, 275-8.

Sax, J. L. and R. B. Keiter. (1987). Glacier National park and its neighbors: a study of federal interagency relations. Ecology Law Quarterly, 14, 207-63.

Schaeffer, D. J., E. É. Herricks and H. W. Kerster. (1988). Ecosystem health: I. Measuring ecosystem health. Environmental Management, 12, 445-55.

Schindler, D. W. (1987). Detecting ecosystem responses to stress. Canadian Journal of Fisheries and Aquatic Sciences, 33 (Supplement 1), 6-25.

Schindler, D. W. (1990). Experimental perturbations of whole lakes as tests of hypotheses concerning ecosystem structure and function. Oikos, 57, 25-41.

Schroeder, R. L. (1987). Community models for wildlife impact assessment: a review of concepts and approaches. USDI Fish and Wildlife Service, Biological Report 87(2).

Scott, J. M., B. Csuti, K. Smith, J. E. Estes and St. Caicco. (1988). Beyond endangered species: an integrated conservation strategy for the preservation of biological diversity. Endangered Species Update, 5, 43-8.

Shugart, H. H., D. E. Reichle, N. T. Edwards and J. R. Kercher. (1976). A model of calcium-cycling in an east Tennessee Liridendron forest: model structure, parameters and frequency response analysis. Ecology, 57, 99-109.

Shure, D. J. (1971). Insecticide effects on early succession in an old-field ecosystem. Ecology, 52, 271-9.

Sidle, W. B. and L. H. Suring. (1986). Management indicator species for the National Forest lands in Alaska. U.S.D.A. Forest Service, Alaska Region, Technical Publication R10-TP-Alaska.

Soule, M. E. (1986). Introduction. Viable populations, ed. M. E. Soule, 1-10. Cambridge, Cambridge University Press.

Soule, D. F. (1988). Marine organisms as indicators: reality or wishful thinking? Marine organisms as indicators, ed. D. F. Soule and G. S. Kleppel, 1-11. New York, Springer-

Soule, D. F. and G. S. Klepper. (1988). Marine Organisms as Indicators, New York, Springer-Verlag.

Starfield, A. M. and A. L. Bleloch. (1983). An initial assessment of possible lion population indicators. South African Journal of Wildlife Research, 13, 9-11.

Susskind, L. E. and L. Dunlap. (1981). The importance of nonobjective judgments in environmental impact assessments. Environmental Impact Assessment Review, 2, 335-66.

Szaro, R. C. (1986). Guild management: an evaluation of avian guilds as a predictive tool. Environmental Management, 10, 681-8.

Szaro, R. C. and R. P. Balda. (1982). Selection and monitoring of avian indicator species: an example from a ponderosa pine forest in the Southwest. U.S.D.A. Forest Service General Technical Report RM-89.

USDI (1980a). Habitat as a basis for environmental assessment. Ecological Services Manual Number 101. Division of Ecological Services, U.S.D.I. Fish and Wildlife Service, Washington, DC.

USDI (1980b). Habitat evaluation procedures (HEP). Ecological Services Manual Number 102. Division of Ecological Services, U.S.D.I. Fish and Wildlife Service, Washington, DC.

USDI (1980c). Standards for the development of habitat suitability index models. Ecological Services Manual Number 103. Division of Ecological Services, U.S.D.I. Fish and Wildlife Services, Washington. DC.

Van Horne, B. (1983). Density as a misleading indicator of habitat quality. Journal of Wildlife Management, 47, 893-901.

Verner, J. (1984). The guild concept applied to management of bird populations. Environmental Management, 8, 1-14.

Verner, J. (1986). Future trends in management of nongame wildlife: a researcher's view-

- point. In Management of nongame wildlife in the Midwest: a developing art, ed. J. B. Hale, L. B. Best and R. L. Clawson. 149-71. Michigan. Proceedings of the 47th Midwest Fish and Wildlife Conference.
- Verner, J., M. L. Morrison and C. J. Ralph. (ed.) (1986). Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. Wisconsin, University of Wisconsin Press.
- Vitousek, P. M., W. A. Reiners, J. M. Melillo, C. C. Grier and J. R. Gosz. (1981). Nitrogen cycling and loss following forest perturbation: the components of response. In *Stress effects on natural ecosystems*, ed. G. W. Barrett and R. Rosenberg, 115-27. New York, John Wiley and Sons.
- Walters, C. J. (1986). Adaptive management of renewable resources. New York, Macmillan Publishing Company.
- Ward, D. V. (1978). Biological environmental impact studies: theory and methods. New York, Academic Press.
- Watt, A. S. (1947). Pattern and process in the plant community. *Journal of Ecology*, 35, 1-22.
- Westman, W. E. (1985). Ecology, impact assessment and environmental planning. New York, John Wiley and Sons.
- Westman, W. E. (1990). Managing for biodiversity. BioScience, 40, 26-33.
- Whittaker, R. H. and S. A. Levin. (1977). The role of mosaic phenomena in natural communities. *Theoretical Population Biology*, 12, 117-39.
- Wiens, J. A., C. S. Crawford and J. R. Gosz. (1985). Boundary dynamics: a conceptual framework for studying landscape ecosystems. *Oikos*, 45, 421-7.
- Wilcox, B. A. (1984). In situ conservation of genetic resources: determinants of minimum area requirements. In National parks, conservation, and development: the role of protected areas in sustaining society, ed. J. A. McNeely and K. R. Miller, 639-47. Washington, DC, Smithsonian Institution Press.
- Woodwell, G. M. (1962). Effects of ionizing radiation on terrestrial ecosystems. *Science*, 138, 572-7.
- Woodwell, G. M. (1967). Toxic substances and ecological cycles. *Scientific American*, 216, 24-31.
- Woodwell, G. M. (1970). Effects of pollution on the structure and physiology of ecosystems. *Science*, 168, 429-33.
- Wren, C. D. (1986). Mammals as biological monitors of environmental metal levels. Environmental Monitoring and Assessment, 6, 127-44.
- Zonneveld, I. S. (1983). Principles of bio-indication. Environmental Monitoring and Assessment, 3, 207-17.
- Zonneveld, I. S. (1988). Environmental indication. In Vegetation mapping, ed. A. W. Kuchler and I. S. Zonneveld, 491-8. The Netherlands, Kluwer Academic Publishers.