APPLICATION OF ECOLOGICAL INDICATORS*

Gerald J. Niemi¹ and Michael E. McDonald²

¹Natural Resources Research Institute and Department of Biology, University of Minnesota, Duluth, Minnesota 55811; email: gniemi@d.umn.edu
²U.S. Environmental Protection Agency, Environmental Monitoring and Assessment Program, Reston, Virginia 20191; email: McDonald.Michael@epa.gov

Key Words assessment, condition, monitoring, responses, stressors

Abstract Ecological indicators have widespread appeal to scientists, environmental managers, and the general public. Indicators have long been used to detect changes in nature, but the scientific maturation in indicator development primarily has occurred in the past 40 years. Currently, indicators are mainly used to assess the condition of the environment, as early-warning signals of ecological problems, and as barometers for trends in ecological resources. Use of ecological indicators requires clearly stated objectives; the recognition of spatial and temporal scales; assessments of statistical variability, precision, and accuracy; linkages with specific stressors; and coupling with economic and social indicators. Legislatively mandated use of ecological indicators occurs in many countries worldwide and is included in international accords. As scientific advancements and innovation in the development and use of ecological indicators continue through applications of molecular biology, computer technology such as geographic information systems, data management such as bioinformatics, and remote sensing, our ability to apply ecological indicators to detect signals of environmental change will be substantially enhanced.

INTRODUCTION

Humans trying to understand the current condition or predict the future condition of ecosystems have often resorted to simple, easily interpreted surrogates. Often these surrogates have been indicators that allow humans to isolate key aspects of the environment from an overwhelming array of signals [National Research Council (NRC) 2000]. Early humans used indicators like seasonal migratory movements of animals or flowering by spring flora to provide insight into changing environmental conditions. The first reference to environmental indicators is attributed to Plato, who cited the impacts of human activity on fruit tree harvest (Rapport 1992). Morrison (1986) reviewed the work of Clements (1920) and noted that the

*The U.S. Government has the right to retain a nonexclusive, royalty-free license in and to any copyright covering this paper.
The concept of indicators for plant and animal communities can be traced to the 1600s. Clements’s (1920) work set the scientific stage for using plants as indicators of physical processes, changes to soil conditions, and other factors. In the 1920s, indicators were also being successfully used to determine changing environmental conditions, such as water clarity (Rapport 1992) or air quality with “the canary in the mine” (Burrell & Siebert 1916), which we continue to use (Van Biema 1995).

One of the more elaborate early environmental indicators was the saprobian system (Kolkwitz & Marsson 1908), which used benthic and planktonic plants as indicator species for classifying stream decomposition zones.

The past 40 years have seen a rapid acceleration of scientific interest in the development and application of ecological indicators. This focus on indicators stems from the need to assess ecological condition in making regulatory, stewardship, sustainability, or biodiversity decisions. For example, the Clean Water Act of 1972 requires that each state produce a report every two years on the condition of all its waters to the U.S. Environmental Protection Agency (US EPA) for Congress. Decisions regarding sustainability and biodiversity involve both research and policy issues (e.g., Mann & Plummer 1999, Ostrom et al. 1999, Tilman 1999). In the United States, this research has been legislatively mandated to various federal agencies, in particular to the U.S. Department of Agriculture through the National Forest Management Act of 1976, to the U.S. Department of Interior (1980, Parsons 2004), and to the US EPA (2002b). These mandates have resulted from the increasing concern for the loss of species, deteriorating water quality and quantity, sustainability of resource use, climate change, and overall condition of the environment. This interest has generated many new books, articles, and reviews on ecological indicators (e.g., McKenzie et al. 1992; US EPA 2002b,c), as well as a new journal (Ecological Indicators in 2001).

The public has increasingly demanded a better accounting of the condition or health of the environment and whether it is improving or getting worse (Heinz Center 1999; www.heinzctr.org/ecosystems). Developing scientifically defensible indicators to establish environmental baselines and trends is a universal need at a variety of levels. For instance, federal governments in the United States and Canada (Environment Canada and US EPA 2003), Europe (www.eionet.eu.int), and Australia (www.csiro.au/csiro/envind/index.htm) have developed or are developing programs for routine reporting on ecological indicators. Recent international accords (e.g., RIO Accord) have demanded an accounting and reporting of indicators on the state of the environment. The Montréal Process (www.mpci.org) representing 12 countries was established in 1994 to develop and implement internationally agreed upon criteria and indicators for the conservation and sustainable management of temperate and boreal forests. In 2003, US EPA (2003a) released its first state of the environment report (www.epa.gov/indicators/roe/index.htm). As the world human population continues to increase exponentially (Cohen 2003), and with consequent environmental demands, the applications of indicators to determine status and trends in environmental condition will continue to grow.
DEFINITIONS

Early uses of indicators primarily reflected environmental conditions, and the terms environmental and ecological indicators have often been used interchangeably. Environmental indicators should reflect all the elements of the causal chain that links human activities to their ultimate environmental impacts and the societal responses to these impacts (Smeets & Weterings 1999). Ecological indicators are then a subset of environmental indicators that apply to ecological processes (NRC 2000). For policy makers, the amount of ecological data is often overwhelming. Environmental indicators are an attempt to reduce the information overload, isolate key aspects of the environmental condition, document large-scale patterns, and help determine appropriate actions (Niemeijer 2002). An example of a large-scale, policy-relevant environmental indicator is the environmental sustainability index (ESI). The ESI was developed to allow quantitative international comparisons of environmental conditions (World Economic Forum 2002). The ESI has five major categories: environmental systems, reducing environmental stresses, reducing human vulnerability, social and institutional capacity, and global stewardship. In 2001 the ESI included information on 68 indicators within these categories from 142 countries (World Economic Forum 2002).

Ecological indicators embody various definitions of ecology, such as the “interactions that determine the distribution and abundance of organisms” (Krebs 1978), or more broadly the “structure and function of nature” (Odum 1963). Thus, they are often primarily biological and respond to chemical, physical, and other biological (e.g., introduced species) phenomena. We have chosen to combine the definitions of the US EPA (2002b) and the hierarchy of Noss (1990), and we define ecological indicators as: measurable characteristics of the structure (e.g., genetic, population, habitat, and landscape pattern), composition (e.g., genes, species, populations, communities, and landscape types), or function (e.g., genetic, demographic/life history, ecosystem, and landscape disturbance processes) of ecological systems.

Ecological indicators are derived from measurements of the current condition of ecological systems in the field and are either used directly or combined into one or more summary values (US EPA 2002b). These ecological indicators can be aggregated into ecological attributes with reporting categories, such as biotic condition, chemical and physical characteristics, ecological processes, and disturbance (Harwell et al. 1999, US EPA 2002b). Ecosystem disturbance can be natural (e.g., fire, wind, and drought) and part of the functional attributes of ecosystems (Noss 1990), or it can be anthropogenic. Ecological indicators have been applied in many ways in the context of both natural disturbances and anthropogenic stress. However, the primary role of ecological indicators is to measure the response of the ecosystem to anthropogenic disturbances, but not necessarily to identify specific anthropogenic stress(es) causing impairment (US EPA 2002b). These indicators have been referred to as “state indicators” in the State of the Lakes Ecosystem Conference (SOLEC), which is a joint effort of Canada and the United States to develop indicators for the Great Lakes (Environment Canada and US EPA 2003).
SOLEC defines state indicators as response variables (e.g., fish, bird, amphibian populations) and pressure indicators as the stressors (e.g., phosphorus concentrations, atmospheric deposition of toxic chemicals, or water level fluctuations).

In this review we focus on ecological indicators, but clearly they can be integrated with the broader issues of ecosystem health (Rapport et al. 1998) and ultimately with economic indicators (Milon & Shogren 1995) to be even more useful for making policy decisions. There is a continuing debate on how to accomplish this integration. A common goal of linking economic and environmental indicators is often based on the concept of sustainability. For example, Ekins et al. (2003) provided a framework for linking economic, social, and environmental sustainability. Their approach identified how economic and social options were constrained if critical environmental functions were sustained. Lawn (2003) explored the theoretical foundation of several indexes of sustainability, including the Index of Sustainable Economic Welfare and the Genuine Progress Indicator. He found that these indexes were theoretically sound, but more robust valuation methods were necessary. Although progress is being made, there are no indicators that link economic, social, or environmental trends in a way that is meaningful to the public.

**USE OF ECOLOGICAL INDICATORS**

Ecological indicators are primarily used either to assess the condition of the environment (e.g., as an early-warning system) or to diagnose the cause of environmental change (Dale & Beyeler 2001). The widespread decline of the peregrine falcon (*Falco peregrinus*) in the 1950s is an excellent example of both uses. The catastrophic decline of the species served as an early-warning signal of problems in the environment, and research on the cause of the decline led to the diagnosis of widespread contamination by chlorinated hydrocarbons such as DDT (Ratcliffe 1980). The widespread decline of amphibians has also been viewed as an early-warning signal of problems in the environment, yet further research has failed to identify a specific cause for the decline. Amphibian declines are likely due to a variety of factors, including habitat change, global climate change, chemical contamination, disease and pathogens, invasive species, and commercial exploitation (Blaustein & Wake 1995, Semlitsch 2003).

The information gathered by ecological indicators can also be used to forecast future changes in the environment, to identify actions for remediation, or, if monitored over time, to identify changes or trends in indicators (Figure 1). As the complexity of the system being monitored increases (e.g., greater spatial scales and levels of biological organization) or as the temporal scale increases, the cost of gathering, analyzing, and reporting on indicators increases. Complexity also arises from the need to quantify linkages between specific stressors and ecological indicators (Table 1). In the few cases in which such relationships have been determined, these ecological indicators are often considered diagnostic; however, these linkages have seldom been made (Suter et al. 2002). A major challenge
Figure 1  Illustration of the suite of ecological indicators (left) for which a suite of assessment capabilities (right) are desired. Constraints on the development of ecological indicators at all levels for all assessment endpoints are due to a lack of scientific understanding and the predominance of policies requiring low cost monitoring. Goals in applications generally include a compromise between cost-effectiveness and the ability to defend the ecological indicator scientifically at the spatial and temporal scale appropriate to answer the desired management objectives.

continues to be the difficulty of discerning specific stressor-response relationships in a multiple stressor environment and the difficulty of separating anthropogenic from natural sources of variation (Niemi et al. 2004).

Ecological indicators are usually developed by scientists and focused on aspects of ecosystems they believe are important for the assessment of condition. However, environmental managers and policy makers require indicators that are understood by the public (Schiller et al. 2001). Ideally, policy-relevant indicators would allow: (a) assessment of both existing and emerging problems; (b) diagnosis of the anthropogenic stressors leading to impairments; (c) establishment of trends in condition for measuring environmental policy and program performance; and (d) ease of communication to the public. Besides capturing the complexities of an ecosystem and being easy to communicate, an indicator should also be easily and routinely measurable (Dale & Beyeler 2001). Moreover, the cost of monitoring and subsequent analyses is also a consideration for state and federal agencies. Classifications of indicators that include scientific performance, policy relevance, and public acceptance have been proposed (Noss 1990, Cairns et al. 1993). However, the final choice of indicators should depend on the questions being asked and the quality of the science supporting the indicator.

Frost et al. (1992) suggest that ecological indicators should trade off two potentially contradictory endpoints. They should be sensitive enough to react in a detectable way when a system is affected by anthropogenic stress, and they should also remain reasonably predictable in unperturbed ecosystems. McGeoch (1998)
TABLE 1  Examples of ecological responses to natural and anthropogenic stress

<table>
<thead>
<tr>
<th>Stress</th>
<th>Ecological response</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Natural disturbance</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Forest fire</td>
<td>Landscape pattern</td>
<td>Turner et al. 1994</td>
</tr>
<tr>
<td>Drought</td>
<td>Bird populations</td>
<td>Blake et al. 1994</td>
</tr>
<tr>
<td>Herbivory</td>
<td>Vegetation and litter</td>
<td>McInnes et al. 1992</td>
</tr>
<tr>
<td>Wind</td>
<td>Forest stands</td>
<td>Foster 1988</td>
</tr>
<tr>
<td>Anthropogenic stress</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Acid rain</td>
<td>Feather moss</td>
<td>Hutchinson &amp; Scott 1988</td>
</tr>
<tr>
<td>Eutrophication</td>
<td>Aquatic macrophytes</td>
<td>Kangas et al. 1982</td>
</tr>
<tr>
<td>Introduced species</td>
<td>Bird populations</td>
<td>Savidge 1984</td>
</tr>
<tr>
<td>Sedimentation</td>
<td>Shrubs</td>
<td>Johnston 2003</td>
</tr>
<tr>
<td>Logging</td>
<td>Landscape pattern</td>
<td>Franklin &amp; Forman 1987</td>
</tr>
<tr>
<td>Heavy metals</td>
<td>Mosquito gene frequencies</td>
<td>Guttman 1994</td>
</tr>
<tr>
<td>Urbanization</td>
<td>Bird guilds</td>
<td>O’Connell et al. 2000</td>
</tr>
<tr>
<td>Air pollution</td>
<td>Plant species</td>
<td>Stolte &amp; Mangis 1992</td>
</tr>
<tr>
<td>Air quality</td>
<td>Lichens</td>
<td>Kinnunen et al. 2003</td>
</tr>
</tbody>
</table>

provided an extensive list of suggested criteria to consider in the selection of bioindicators that included cost, species abundance, baseline data on species biology, and sensitivity to stress. Indicator selection will always be a compromise among many factors and must be optimized for the intended purpose.

There has been a strong recent interest in reporting on the ecological condition of the environment (Heinz Center 2002, US EPA 2003a) for the purposes of planning, management, and public reporting (US EPA 2003a). To accomplish these goals, the ecological indicators must be able to detect anthropogenic change against a background of natural variability. At issue is that ecological indicators at the population or community levels are not tightly coupled to the primary biological effects of stressors, which results in a slower response time, high natural variability, and low sensitivity (Jenkins & Sanders 1992). Confounding this further, communities and populations are responding to many other factors, some of which are not necessarily stressor related. In some cases it may be our attempts at aggregating the data that affect change detection. Frost et al. (1992) found that the level of taxonomic aggregation of the zooplankton populations affected the detection of change in an acid sensitive lake. Natural variability decreased with increasing taxonomic aggregation, but sensitivity had a less straightforward response. At intermediate levels of taxonomic aggregation, zooplankton populations exhibited the highest sensitivity (Frost et al. 1992). Thus, some intermediate level of taxonomic aggregation may be required to optimize the trade-off between sensitivity and variability in producing a useful ecological indicator.

At the organism level, important physiological processes can change in response to anthropogenic stress (e.g., growth, fecundity, developmental rates). However,
the initial biological response often occurs at the cellular or subcellular level. This fact has advanced the use of biomarkers to detect physiologic condition and exposure to stressors (Jenkins & Sanders 1992). These biochemical and cellular indicators tend to be more sensitive to contaminants and more responsive than higher level indicators. Metallothionein induction is an example. Metallothioneins are low molecular weight, metal binding proteins that are involved in homeostasis regulation and compartmentalization of essential metals (e.g., Brouwer et al. 1989). In the presence of excess metals, induction of metallothioneins is enhanced for detoxification (Hamer 1986). The drawback to this strong indicator of anthropogenic insult is in its interpretation in the broader ecological context. For instance, it is unclear whether the biomarker is related to the condition or population of the species.

The questions, goals, and objectives of a monitoring program determine which ecological indicators are used (Dixon et al. 1998). Ecological indicators have been applied from the level of the gene (e.g., Rublee et al. 2001) to the landscape (e.g., Lausch & Herzog 2002) (Table 2). Researchers need to recognize which part of the ecological indicator spectrum is relevant to the objectives of their investigation. For example, is the indicator an early-warning system that may be related to a specific stress? Is the indicator a measurement of the condition of the ecological system? Is it important to know the cause of any change in the indicator? Clearly stated goals and objectives are essential (Yoccoz et al. 2001).

Most ecological monitoring programs are based on an aggregation of selected sites (Olsen et al. 1999), and researchers often infer regional trends from the accumulation of these site-specific trends (Urquhart et al. 1998). Many of these studies are useful for establishing temporal variability and mechanistic relationships, but larger regional trends cannot be compiled from these site-specific data unless the sites were selected in a representative and unbiased manner within the region of interest (Urquhart et al. 1998). Thus, researchers must integrate the selection of ecological indicators for examining large-scale spatial trends in an ecosystem within an appropriate statistical design (McDonald et al. 2004).

**INDICATOR SPECIES**

Most applications of ecological indicators have focused at the species level owing to concerns arising from endangered species and species conservation issues (Fleishman et al. 2001). For instance, Noss (1990) stated that “the use of indicator species to monitor or assess environmental conditions is a firmly established tradition in ecology, environmental toxicology, pollution control, agriculture, forestry, and wildlife and range management.” The measurement of an indicator species assumes that a single species represents many species with similar ecological requirements (Landres et al. 1988). Typically, ecological indicator species tend to be from the macroflora and macrofauna, especially aquatic macroinvertebrates, fish, birds, and vascular plants. The primary reasons for their use are: (a) relative
TABLE 2  Examples of indicators that have been applied within different ecological levels of organization (modified from Noss 1990 and US EPA 2003)

<table>
<thead>
<tr>
<th>Type</th>
<th>Example</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Compositional</td>
<td>Genes</td>
<td>Species differentiation</td>
</tr>
<tr>
<td></td>
<td>Cell and subcellular Tissue Species</td>
<td>Immune response</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Metal concentration</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Butterflies</td>
</tr>
<tr>
<td></td>
<td>Populations</td>
<td>Birds</td>
</tr>
<tr>
<td></td>
<td>Communities</td>
<td>Floristic quality</td>
</tr>
<tr>
<td></td>
<td>Ecosystems</td>
<td>Lakes</td>
</tr>
<tr>
<td></td>
<td>Landscape types</td>
<td>Land use/cover</td>
</tr>
<tr>
<td>Functional</td>
<td>Genetic processes</td>
<td>Mutation rates</td>
</tr>
<tr>
<td></td>
<td>Behavior</td>
<td>Feeding rate</td>
</tr>
<tr>
<td></td>
<td>Life history</td>
<td>Species traits</td>
</tr>
<tr>
<td></td>
<td>Demographic processes</td>
<td>Productivity</td>
</tr>
<tr>
<td></td>
<td>Ecosystem processes</td>
<td>Growth</td>
</tr>
<tr>
<td></td>
<td>Landscape processes</td>
<td>Diatoms</td>
</tr>
<tr>
<td>Structural</td>
<td>Genetic structure</td>
<td>Zooplankton genotypic differentiation</td>
</tr>
<tr>
<td></td>
<td>Population structure</td>
<td>Bird guilds</td>
</tr>
<tr>
<td></td>
<td>Habitat physiognomy</td>
<td>Forest structure</td>
</tr>
<tr>
<td></td>
<td>Landscape patterns</td>
<td>Fragmentation</td>
</tr>
<tr>
<td>Integrative</td>
<td>Index of biotic integrity</td>
<td>Fish</td>
</tr>
<tr>
<td></td>
<td>AMOEBA</td>
<td>Multiple taxa</td>
</tr>
<tr>
<td></td>
<td>Multivariate</td>
<td>Biomarkers</td>
</tr>
<tr>
<td></td>
<td>Species assemblages</td>
<td>Beetles</td>
</tr>
<tr>
<td></td>
<td>Index of environmental integrity</td>
<td>Multiple indices</td>
</tr>
</tbody>
</table>

ease of identification, (b) interest to the public, (c) relative ease of measurement, (d) relatively large number of species with known responses to disturbance, and (e) relatively low cost.

We use indicator species as a general term to refer to approaches that use one or a few species to “indicate” condition or a response to stress that may apply to other species with similar ecological requirements. Lawton & Gaston (2001) suggest that indicator species are used in three distinct ways: (a) to reflect the biotic or abiotic state of the environment; (b) to reveal evidence for the impacts of environmental change; or (c) to indicate the diversity of other species, taxa, or communities within an area. The first two reflect the common uses of indicators as measures of condition and the diagnosis of potential cause(s) of environmental
change. The third expands the concept of indicators to incorporate the idea of a single species serving as a surrogate for many other species. This idea has been largely untested and has been the focus of much debate and criticism in applications (see below). Because of the criticism, many new approaches and terms have been developed to refine the indicator species concept. These include focal species, umbrella species, flagship species, or guilds as indicators (Verner 1984, Landres et al. 1988, Lambeck 1997, Simberloff 1998, Noss 1999).

The term focal species has been used in many ways in the literature. For example, Cox et al. (1994) identified 44 focal species to serve as umbrella or indicator species of biological diversity in Florida. Lambeck (1997) identified focal species as a subset of the total pool of species in a landscape. Carroll et al. (2001) used carnivores as focal species in regional conservation planning because their distributional patterns reflected regional-scale population processes. There is not a consistent definition of a focal species, except when they are selected by various means as the “focus” of study. Focal species tend to differ from indicator species in that they do not necessarily serve to measure ecological condition nor do they convey a stress-response relationship. The focal species concept has generally been used in conservation planning, landscape ecology, and protection of biological diversity.

Fleischman et al. (2001) define umbrella species as those “whose conservation confers a protective umbrella to numerous co-occurring species.” They also point out that “blurred discriminations between umbrella and indicator species have led to misunderstandings over how umbrella species should be selected.” Flagship species are those that have large public appeal, such as charismatic megafauna like bears and tigers. The guild concept has been explored as an alternative to indicator species both in wildlife management and in determining regional condition (e.g., Verner 1984, O’Connell et al. 2000). Guilds were originally defined by Root (1967) as a “group of species that exploit the same class of environmental resources in a similar way”; Verner (1984) concluded that the guild concept held promise but required more testing. O’Connell et al. (2000) distinguished 16 behavioral and physiological response guilds of birds and were able to combine their bird community data into a bird community index (BCI). They related the BCI to landscape condition and change from forested to nonforested areas.

Lambeck (1997) expanded on the concepts of umbrella and focal species to incorporate more specific responses to landscape and management regimes. His analysis focused on identifying focal species with the most demanding survival requirements for several parameters threatened by anthropogenic stressors. Noss (1999) further extended and combined these concepts for indicator, focal, and umbrella species in a forest management context. In his approach, indicator species were represented by a suite of focal species, each of which was defined by different attributes that had to be present in the landscape to retain the biota. Landscape attributes included: (a) area-limited species, (b) dispersal-limited species, (c) resource-limited species, (d) process-limited species, (e) keystone species, (f) narrow endemic species, and (g) special cases such as flagship species that
are of public concern in the region. Noss (1999) suggested that at least for the first four categories umbrella species could be defined that are the most sensitive to the landscape attribute.

Birds have been the primary focus for most terrestrial applications of indicator species, but insects hold great promise because of their species richness, biomass, and role in ecosystem functioning. McGeoch (1998) recognized the potential applications of insects as indicator species and defined their use as environmental, ecological, or biodiversity indicators. Researchers have attempted to examine vertebrates as possible umbrella species for insects, especially for butterflies. For example, Rubinoff (2001) analyzed the use of a bird species, the California gnatcatcher (*Polioptila californica*), as a potential umbrella species for three species of butterflies. However, the gnatcatcher was a poor indicator primarily because of its ubiquity in the landscape studied. Insects and other microfauna offer excellent potential as indicator species. They are of limited use in terrestrial systems because of the cost of sampling and processing and because there is limited acceptance by resource managers, politicians, and the general public.

Researchers have developed other indexes to provide more holistic approaches to ecological condition. These indexes range from simple diversity indexes, such as the Shannon and Wiener Index (Shannon & Weaver 1949), to multimetric indexes (e.g., Karr 1981, Kerans & Karr 1994, Karr 2000, Simon 2003). Multimetric ecological indicators are sets of mathematically aggregated or weighted indicators (US EPA 2000a, Kurtz et al. 2001) that combine attributes of entire biotic communities into a useful measure of condition (US EPA 2002a). The US EPA has recently used an index for biotic integrity (IBI) for estuarine invertebrates as one of the indicators in the assessment of the condition of the nation’s estuaries (US EPA 2004). Because of the increasing use of multimetric and other indicators, researchers have developed specific guidelines for evaluating their performance (US EPA 2000a).

Another aspect of ecological indicators is whether to use them as relative or absolute measures. As a relative measure, the initial measurement becomes the baseline for comparison of future measures. Most monitoring agencies prefer or require a more quantitative benchmark for measuring and regulating changes in ecosystems. These benchmark or reference conditions can be defined as the conditions of ecological resources under minimal contemporary human disturbance (McDonald et al. 2004). As these conditions are often not available for direct measurement, models and historic information are often invoked as best approximations. However, the selection of reference conditions remains problematic (NRC 1990).

In summary, focal species represent those selected as a focus for a specific investigation. There is no consistent definition of focal species, but the concept has been expanded for use in conservation and management. Focal species have been used to identify potential indicator species when there is a desire to describe ecological condition or measure the response to a disturbance. Either a focal species or an indicator species may serve as an umbrella species if the goals
are to monitor or manage one species as a surrogate for other species or to identify conservation areas for preservation. Focal, indicator, or umbrella species could be flagship species if they have a high profile or interest to the public. Moreover, any of them could be keystone species (sensu Paine 1969a,b) if they are particularly important in establishing or maintaining key ecological processes or structure for other species within an ecosystem (Simberloff 1998). Before any investigation, researchers must clearly define these terms and rigorously test whether the species can fulfill its purpose as an indicator, umbrella, or keystone species.

COMPLEXITIES IN APPLICATIONS OF ECOLOGICAL INDICATORS

Monitoring for ecosystem or resource management often requires data about a specific site or sites, whereas public policy decisions typically require information across broader geographical regions (Olsen et al. 1999). Many of the existing ecological monitoring programs are periodically or continually used at certain sites, which may lead to a better understanding of the temporal variability at the site but may not be representative of a larger area (Urquhart et al. 1999). Thus, ecological indicators are needed to assess status and trends in ecological systems and to diagnose cause(s) of declining condition across a range of spatial and temporal scales (Kratz et al. 1995, NRC 2000, Dale & Beyeler 2001, Niemi et al. 2004).

Each ecological indicator responds over different spatial and temporal scales; thus, the context of these scales must be explicitly stated for each ecological indicator. Furthermore, understanding the response variability in ecological indicators is essential for their effective use (US EPA 2002c). Without such an understanding, it is impossible to differentiate measurement error from changing condition, or an anthropogenic signal from background variation. Work has begun on understanding how natural and anthropogenic variability of indicators can affect status and trend detection, but it is closely tied to different statistical design considerations (Larsen et al. 1995). Specific monitoring designs and indicators can be implemented to detect changes across temporal and spatial scales (US EPA 1997, 2002d).

In general, as one moves up levels of organization from cellular phenomena to landscape processes, the spatial and temporal scales of application increase immensely. Similarly, as larger spatial and temporal scales are considered, the linkage to specific stressors can be either obscured or refined depending on the stressor. For example, one of the largest and most successful monitoring programs is the U.S. Geological Survey Breeding Bird Survey (BBS), which has gathered data over a 38-year period (1966 to present) (Sauer et al. 2003). The BBS is intended to indicate breeding bird species trends over relatively large regional and national spatial scales. Thus, researchers must exercise caution in interpreting results for specific regions or combining results from different regions (James et al. 1996).

In contrast, nesting tree swallows (Tachycineta bicolor) are an effective wildlife
indicator species of sediment chemical contaminant problems. Because nestlings are fed flying adult insects, which typically have aquatic early life histories, the uptake of chemicals by nestlings can be related to sediment chemical levels near the nesting site (Nichols et al. 1995, Jones 2003). Changes in bird trends from the BBS over large areas are powerful because of the large number of sample routes and the a priori experimental design, but the causes of changes in species trends are speculative. In contrast, contaminant uptake in nestling tree swallows and potential risk to wildlife can clearly be connected to food supplies derived from sediment. Many of the same problems exist for multimetric indexes commonly used to assess condition of surface waters across large regions. These indexes can distinguish degraded sites from sites with little or no human impact, but they do not diagnose the causes of impairment by themselves (US EPA 2003b).

ADVANCEMENTS IN ECOLOGICAL INDICATORS OF BIOLOGICAL COMMUNITIES

Historically, ecological indicators were primarily based on parameters associated with individual species (e.g., presence) or simple community metrics (e.g., species richness or diversity). However, many of these indicators did not fully represent the entire biological community of organisms present. Hence, Karr (1981) introduced the IBI using stream fish communities. This index was a numerical summation of subsets of the fish community from one area compared with a suitable reference area. These reference areas ideally represented areas that were natural or undisturbed from the same geographic area and with the same general ecological condition. Karr (1981) calculated the IBI using fish community data for a specific area and subdivided these data into 12 metrics, including the number of individuals and species found in the sample, the relative abundance of guilds (e.g., carnivores), specific species in the sample, and other categories (e.g., sunfish species). The IBI was expressed as deviations from the suitable reference area such that larger values represented communities similar to the reference area, whereas lower values represented areas that deviate from the reference, potentially because of stress. The IBI has received considerable attention and application over the past 20 years, including applications to fish (Fausch et al. 1984, Angermeier & Karr 1986, Karr et al. 1986, Simon & Emery 1995), macroinvertebrates (Kerans & Karr 1994, Klemm et al. 2003), plant communities (Simon et al. 2001, DeKeyser et al. 2003), aquatic communities (Simon et al. 2000), and birds (O’Connell et al. 2000).

Many other multimetric indexes have evolved over the past 20 years, such as the Hilsenhoff biotic index (Hilsenhoff 1982) and biological response signatures (Simon 2003). In contrast to multimetric indexes, multivariate indexes (Reynoldson et al. 1997, Karr 2000) are statistical analyses of the biological community using a host of multivariate techniques, such as principal components analysis (O’Connor et al. 2000), canonical correspondence analysis (Kingston et al. 2000).
1992), and combinations of multivariate analyses (Dufrêne & Legendre 1997). For example, O’Connor et al. (2000) integrated information from five different taxonomic groups (diatoms, benthos, zooplankton, fish, and birds) to provide an index of the ecological condition of lakes. Their approach was effective in relating the gross condition of the lakes across taxa, but it was also effective in identifying a differential response by fish to nearshore conditions. Dufrêne & Legendre (1997) used a combination of multivariate analyses of carabid beetle community data to determine indicator species and species assemblages for groups of sites. Their approach also includes a randomization procedure to test the significance of the indicator values.

Many analytical approaches of biological community data are currently being developed, tested, and used for ecological indicators. For instance, Andreasen et al. (2001) and Paul (2003) have recently introduced indexes of ecological and environmental integrity, respectively. These indexes combine information from several levels (e.g., biological communities, habitat, expert opinion) into an overall measure of integrity. The exploration and debate of these approaches will likely continue in the future.

CRITICISMS OF INDICATORS

Virtually all attempts to use ecological indicators have been heavily criticized, and many criticisms are well deserved. For instance, many existing monitoring programs of indicators suffer from two deficiencies: lack of well-articulated objectives and neglect of different sources of error (Yoccoz et al. 2001). Indicator species have been especially criticized in the context of forest management-related issues (Landres et al. 1988, Landres 1992, Niemi et al. 1997, Rolstad et al. 2002, Failing & Gregory 2003). Many of these criticisms have focused on the lack of:

(a) identification of the appropriate context (spatial and temporal) for the indicator,
(b) a conceptual framework for what the indicator is indicating,
(c) integration of science and values, and
(d) validation of the indicator.

Many of these criticisms have led to more focused efforts on individual species and to the development of additional concepts such as focal species or umbrella species (Lambeck 1997, Fleischman et al. 2001). Roberge & Angelstam (2004) recently reviewed the umbrella species concept and concluded that multispecies strategies were more compelling. Lawler et al. (2003) evaluated several indicator groups (e.g., birds, fish, mammals, and mussels) to test whether one group could provide habitat protection for other taxa in a large area of the Mid-Atlantic region of the United States. No single taxonomic indicator group could provide adequate protection for another group, especially for at-risk species within each of the groups. The failure was likely attributable to the narrow geographic ranges and restricted habitat distribution of rare species. Hence, information on rare species and those that are at risk was essential, yet gathering data on rare species is generally difficult, time-consuming, and expensive. In contrast to the indicator species
approach, Manley et al. (2004) evaluated an innovative, multispecies monitoring approach that included all terrestrial vertebrate species over a large ecoregional scale (7 million ha). The design of this comprehensive approach reduced the emphasis on indicator species because the spatial coverage allowed many species to be adequately monitored. A fundamental problem with these approaches continues to be the inability to link species presence or relative abundance with relevant aspects of habitat quality (Van Horne 1983), such as productivity.

Many of these same criticisms apply to indexes (Suter 1993). Indexes have been viewed as oversimplifications and generalizations of biological processes, in which important data can be lost (May 1985). There are also concerns about how these indexes are calibrated (Seegert 2001) and whether or how they are evaluated across gradients (US EPA 2000a). Despite such criticisms, these indexes can play an important management role by helping characterize ecological condition (Rakocinski et al. 1997).

Ecological indicators span broad levels of biological, spatial, and temporal organization within ecosystems. When establishing a monitoring program and selecting indicators, it is imperative that researchers articulate a clear statement of goals. Once the goals are unambiguously stated, the scientific soundness and objectivity of the indicator become a central issue (Niemeijer 2002). Researchers must recognize these complexities and limitations in the application and use of ecological indicators (Dale & Beyeler 2001). However, having effective indicators is only one component of the problem. Sound program design and effective data management, analysis, synthesis, and interpretation are also needed to implement monitoring and assessment programs successfully (NRC 1990). In the past five years, many publications have provided excellent guidance on how ecological indicators can be improved, including documents by the NRC (2000) and US EPA (2000a, 2002b).

FUTURE OF ECOLOGICAL INDICATORS
AND CONCLUSIONS

Advances in science and technology at all levels of biological organization will greatly improve our ability to apply ecological indicators in the future. Recently developed techniques in molecular biology such as biomarkers have proven useful in rapid identification of problems in ecological systems caused by pollution stress (e.g., Cormier & Racine 1992, Huggett et al. 1992). For example, Arcand-Hoy & Metcalfe (1999) found that both fluorescent aromatic compounds in bile and hepatic ethoxyresorufin-O-deethylase in fish could be used to detect exposure to polynuclear aromatic hydrocarbons in the lower Great Lakes. Evendon & Depledge (1997) identified the potential usefulness of genetically susceptible populations to environmental contaminants. Paerl et al. (2003) have recently used diagnostic photopigments of various phytoplankton groups as ecological indicators to detect changes in nutrients, noxious algal blooms, and overall water quality. Investigators
are optimistic about applying molecular techniques to address specific ecological problems and to act as early-warning signals of potential problems. However, research is necessary to illustrate how these techniques can be scaled up to address environmental problems over large regions. There is tremendous potential for application of these new techniques to provide real-time, remotely sensed condition assessments of environmental problems (Kerr & Ostrovsky 2003).

Global positioning systems (GPS), geographic information systems (GIS), remote-sensing technology, and computer hardware and software hold great potential for advancing the science of ecological indicators. GPS allows precise location of repeated field measurements, thus reducing errors associated with spatial variation. GIS provides unprecedented abilities to organize, analyze, synthesize, and display information gathered in the field over both space and time. Remote-sensing technology has also advanced substantially in resolution from 30 m to <4 m resolution (e.g., Kerr & Ostrovsky 2003, Clark et al. 2004). Database storage and software to manipulate these data have increased exponentially in the past ten years and have resulted in the new field of bioinformatics. These techniques in combination with data gathered in the field or combined with existing databases have proven effective in a myriad of applications, such as change detection in forest systems (Wolter & White 2002), mapping biodiversity patterns (Stockwell & Peterson 2003), and forecasting animal distributions and abundance over large regions (Venier et al. 2004).

Researchers have addressed many of the criticisms and failures that have plagued the applications of ecological indicators, resulting in substantial improvements in assessing condition in many areas (e.g., US EPA 1998, 2000b, 2003c). Guidelines for ecological indicator development need to be heeded (Kurtz et al. 2001). Depending on the indicator’s use and the spatial scales of application, experimental design considerations are crucial for appropriate inferences once the data are gathered (Urquhart et al. 1998, Olsen et al. 1999, Danz et al. 2004).

Of increasing interest is the integration of environmental indicators with other well-known economic and social indicators like the gross national product or the consumer price index (Milon & Shogren 1995, NRC 1997). The International Society for Ecological Economics, which recently began publishing the journal Ecological Economics, was formed partially to integrate this thinking into a “transdiscipline” aimed at developing a sustainable world (www.ecologicalconomics.org/about/index.htm). Moreover, a variety of authors have emphasized the need to consider human health and link it to environmental health (Pimentel et al. 2000, Karr 2002), as well as to establish an economic valuation system for ecological resources (Costanza 1997, Daily 1997) or for ecological sustainability (Armsworth & Roughgarden 2003). The motivation for this integration stems largely from managers’ need to better quantify ecological changes resulting from such issues as global climate change; species extinction rates; contaminated air, water, and soil; declining fish populations; human conflicts over resources such as water; and the emergence of new diseases (e.g., Pimentel et al. 2000, Brown 2003, Karr 2002) in relevant human social and economic terms. Clearly, the general public currently
NIEMI □ MCDONALD

has a paucity of information on which to judge the ecological condition of the environment or how the condition might relate to human health or to the economy. Yet, with such information, individuals make daily and long-term decisions on the basis of health indicators (e.g., blood pressure), economic indicators (e.g., NASDAQ, Dow Jones Industrial Average), and environmental indicators (e.g., weather forecasts). Despite three decades of discussion of the integration of economic and ecological indicators, there are limited applications of integrated analysis (Milon & Shogren 1995). US EPA’s (2003a) state of the environment report in 2003 is one of the first steps in informing the public of the ecological condition of the nation’s resources. Future reports on integrated and understandable measures will be welcome additions as indicators of environmental sustainability, but their acceptance and impacts on policy and public opinion will have to be determined.

Strong public interest and legislative mandates exist at local, state, federal, and international levels to understand the condition, trends, and cause for change in our ecosystems. A large array of ecological indicators are available for application to environmental problems; moreover, the number of tools and techniques that are available is rapidly increasing. Therein lies the challenge for the future: to select appropriate monitoring designs and ecological indicators that will provide convincing scientific underpinnings for management and policy decisions on real-world problems.

ACKNOWLEDGMENTS

Although the research described in this article has been funded wholly or in part by the United States Environmental Protection Agency’s Science to Achieve Results (STAR) program through cooperative agreement R828675-00 to the University of Minnesota, it has not been subjected to the agency’s required peer and policy review and therefore does not necessarily reflect the views of the agency, and no official endorsement should be inferred. We thank James Cox, Robert Howe, and Lucinda Johnson for comments on an earlier version of this manuscript. This is publication number 359 of the Center for Water and the Environment, Natural Resources Research Institute, University of Minnesota, Duluth.

The Annual Review of Ecology, Evolution, and Systematics is online at http://ecolsys.annualreviews.org

LITERATURE CITED

Angermeier PL, Karr JR. 1986. Applying an


Dufrène M, Legendre P. 1997. Species assemblages and indicator species: the need
for a flexible asymmetrical approach. Ecol. Monogr. 67:345–66
Ostrom E, Burger J, Field CB, Norgard RB, Policansky D. 1999. Revisiting the
Paul GF. 2003. Developing and applying an index of environmental integrity for the US Mid-Atlantic region. J. Environ. Manage. 67:175–85


Underwood RJ, Roth RR. 2002. Demographic variables are poor indicators of wood thrush productivity. *Condor* 104: 92–102


US EPA. 2002c. Biological indicator variability and stream program integration: a Maryland
Verner J. 1984. The guild concept applied to management of bird populations. Environ. Manage. 8:1–14
**CONTENTS**

**Vertebrate Dispersal of Seed Plants Through Time, Bruce H. Tiffney**

**Are Diseases Increasing in the Ocean? Kevin D. Lafferty, James W. Porter, and Susan E. Ford**

**Bird Song: The Interface of Evolution and Mechanism, Jeffrey Podos, Sarah K. Huber, and Benjamin Taft**

**Application of Ecological Indicators, Gerald J. Niemi and Michael E. McDonald**

**Ecological Impacts of Deer Overabundance, Steeve D. Côté, Thomas P. Rooney, Jean-Pierre Tremblay, Christian Dussault, and Donald M. Waller**

**Ecological Effects of Transgenic Crops and the Escape of Transgenes into Wild Populations, Diana Pilson and Holly R. Prendeville**

**Mutualisms and Aquatic Community Structure: The Enemy of My Enemy Is My Friend, Mark E. Hay, John D. Parker, Deron E. Burkepile, Christopher C. Caudill, Alan E. Wilson, Zachary P. Hallinan, and Alexander D. Chequer**

**Operational Criteria for Delimiting Species, Jack W. Sites, Jr., and Jonathan C. Marshall**

**The New View of Animal Phylogeny, Kenneth M. Halanych**

**Landscapes and Riverscapes: The Influence of Land Use on Stream Ecosystems, J. David Allan**


**Avian Extinctions from Tropical and Subtropical Forests, Navjot S. Sodhi, L.H. Liow, and F.A. Bazzaz**

**Evolutionary Biology of Animal Cognition, Reuven Dukas**

**Pollination Syndromes and Floral Specialization, Charles B. Fenster, W. Scott Armbruster, Paul Wilson, Michele R. Dudash, and James D. Thomson**
CONTENTS

ON THE ECOLOGICAL ROLES OF SALAMANDERS, Robert D. Davic and Hartwell H. Welsh, Jr. 405

ECOLOGICAL AND EVOLUTIONARY CONSEQUENCES OF MULTISPECIES PLANT-ANIMAL INTERACTIONS, Sharon Y. Strauss and Rebecca E. Irwin 435

SPATIAL SYNCHRONY IN POPULATION DYNAMICS, Andrew Liebhold, Walter D. Koenig, and Ottar N. Bjørnstad 467

ECOLOGICAL RESPONSES TO HABITAT EDGES: MECHANISMS, MODELS, AND VARIABILITY EXPLAINED, Leslie Ries, Robert J. Fletcher, Jr., James Battin, and Thomas D. Sisk 491

EVOLUTIONARY TRAJECTORIES AND BIOGEOCHEMICAL IMPACTS OF MARINE EUKARYOTIC PHYTOPLANKTON, Miriam E. Katz, Zoe V. Finkel, Daniel Grzebyk, Andrew H. Knoll, and Paul G. Falkowski 523

REGIME SHIFTS, RESILIENCE, AND BIODIVERSITY IN ECOSYSTEM MANAGEMENT, Carl Folke, Steve Carpenter, Brian Walker, Marten Scheffer, Thomas Elmqvist, Lance Gunderson, and C.S. Holling 557

ECOLOGY OF WOODLAND HERBS IN TEMPERATE DECIDUOUS FORESTS, Dennis F. Whigham 583

THE SOUTHWEST AUSTRALIAN FLORISTIC REGION: EVOLUTION AND CONSERVATION OF A GLOBAL HOT SPOT OF BIODIVERSITY, Stephen D. Hopper and Paul Gioia 623

PREDATOR-INDUCED PHENOTYPIC PLASTICITY IN ORGANISMS WITH COMPLEX LIFE HISTORIES, Michael F. Benard 651

THE EVOLUTIONARY ECOLOGY OF NOVEL PLANT-PATHOGEN INTERACTIONS, Ingrid M. Parker and Gregory S. Gilbert 675

INDEXES

Subject Index 701
Cumulative Index of Contributing Authors, Volumes 31–35 721
Cumulative Index of Chapter Titles, Volumes 31–35 724

ERRATA

An online log of corrections to Annual Review of Ecology, Evolution, and Systematics chapters may be found at http://ecolsys.annualreviews.org/errata.shtml