

A Realistic Assessment of the Indicator Potential of Butterflies and Other Charismatic Taxonomic Groups

ERICA FLEISHMAN* AND DENNIS D. MURPHY†

*National Center for Ecological Analysis and Synthesis, 735 State Street, Suite 300, Santa Barbara, CA 93101, U.S.A., email fleishman@nceas.ucsb.edu

†Department of Biology, University of Nevada, Reno, NV 89557, U.S.A.

Abstract: *Charismatic groups of animals and plants often are proposed as sentinels of environmental status and trends. Nevertheless, many claims that a certain taxonomic group can provide more-general information on environmental quality are not evaluated critically. To address several of the many definitions of indicator species, we used butterflies to explore in some detail the attributes that affect implementation of indicators generically. There probably are few individual species, or sets of species, that can serve as scientifically valid, cost-effective measures of the status or trend of an environmental phenomenon that is difficult to measure directly. Nevertheless, there are species with distributions, abundances, or demographic characteristics that are responsive to known environmental changes. In this context, single or multiple species can serve as indicators when targets are defined explicitly, ecological relationships between the target and the putative indicators are well understood, and data are sufficient to differentiate between deterministic and stochastic responses. Although these situations exist, they are less common than might be apparent from an extensive and often confounded literature on indicators. Instead, the public appeal of charismatic groups may be driving much of their acclaim as indicators. The same taxon may not be appropriate for marketing a general conservation mission and for drawing strong inference about specific environmental changes. To provide insights into the progress of conservation efforts, it is essential to identify scientific and practical criteria for selection and application of indicators and then to examine whether a given taxonomic group meets those criteria.*

Keywords: climate change, indicator species, land cover, land use, monitoring and assessment, surrogate species, validation

Una Evaluación Realista del Potencial Indicador de Mariposas y Otros Grupos Taxonómicos Carismáticos

Resumen: *A menudo, los grupos carismáticos de animales y plantas son propuestos como centinelas del estatus y las tendencias ambientales. Sin embargo, muchas afirmaciones de que un cierto grupo taxonómico puede proporcionar información más general de la calidad ambiental no son evaluadas críticamente. Para abordar varias de las muchas definiciones de especies indicadoras, utilizamos mariposas para explorar en detalle los atributos que afectan la implementación de indicadores genéricamente. Probablemente hay pocas especies individuales, o conjuntos de especies, que pueden servir como medidas, científicamente válidas y rentables, del estatus o la tendencia de un fenómeno ambiental que es difícil de medir directamente. Sin embargo, hay especies con distribuciones, abundancias o características demográficas que responden a cambios ambientales conocidos. En este contexto, especies individuales o múltiples pueden servir como indicadores cuando los blancos son definidos explícitamente, las relaciones ecológicas entre el blanco y los indicadores putativos están bien entendidas y los datos son suficientes para diferenciar entre respuestas determinísticas y estocásticas. Aunque estas situaciones existen, son menos comunes de lo que pudiera parecer en una literatura extensa, y a menudo confusa, sobre indicadores. En su lugar, el reconocimiento público de los grupos carismáticos puede ser la causa de su reconocimiento como indicadores. El mismo taxón puede ser no apropiado para el mercadeo de una misión de conservación general y para inferir sobre cambios ambientales*

específicos. Para proporcionar una visión del progreso de los esfuerzos de conservación, es esencial identificar criterios científicos y prácticos para la selección y aplicación de indicadores y posteriormente examinar si un grupo taxonómico determinado cumple con esos criterios.

Palabras Clave: cambio climático, cobertura de suelo, especies indicadoras, especies sustitutas, monitoreo y evaluación, uso de suelo, validación

Introduction

Charismatic groups of animals and plants play critical roles at the nexus between environmental science and environmental action. Butterflies, birds, marine mammals, and other attractive organisms are perceived by a sympathetic public as beautiful, fragile, and especially ill suited to landscapes or waters that are experiencing a heavy human footprint. Consequently, certain taxonomic groups have been invoked as reflective beacons of environmental status and trend. Of course, functionality is not based on aesthetics. So, although “brightly colored insects” certainly “have the potential to be used as flagship groups in conservation programs,” evidence that flashy insects “can serve as indicators of environmental quality” is more equivocal (Lewinsohn et al. 2005). Perhaps because the ecology of taxonomic groups like butterflies and birds is so well known, many advocates of these organisms as “critical indicators of habitat quality for many plant and animal species” (Wallis DeVries & Raemakers 2001) seem not to have examined their claims critically.

The ability of researchers to measure similar phenomena in similar manners, and the ability of managers and decision makers to apply the results and inferences, is predicated on standardized definitions (Morrison & Hall 2002). Given the importance of the concept, it is unfortunate that the professional conservation community does not have a unanimous definition of an indicator. For that matter, scientists and managers frequently conflate indicator species and other categories of surrogates, such as umbrella species, keystone species, and flagship species (Lindenmayer et al. 2000). The confusion, or lack of precision, is apparent in many casual discussions and in the literature. Here, with the aim of encouraging more consistent and more useful application of indicators to management, we critically addressed at the species level two of the many definitions of indicators. We used butterflies to explore in some detail the attributes that affect application of indicators generically. Our concerns about indicators are not restricted to that taxonomic group, however, and we did not consider whether certain taxonomic groups or species can convey more information about broad environmental phenomena than other groups might.

Our preference is to define indicators as scientifically reliable, cost-effective measures of the status or trend of an environmental phenomenon that is scientifically

or logistically challenging to measure directly (also see Landres et al. 1988). In this context, indicators can serve a number of purposes. For example, small sets of species that exhibit presence or absence patterns that are correlated functionally with the species richness of a larger group of organisms might be defined as indicator species (Fleishman et al. 2005). According to the definition above, if a biotic or abiotic environmental change can be evaluated readily and directly, the use of indicators is moot. For instance, because macronutrients in lakes can be measured relatively accurately and cheaply, there is no need to use the population response of an organism as a surrogate measure. But we also recognize a second common definition, which is not mutually exclusive from the first: indicators are distributions, abundances, or demographic variables measured to assess responses to, or as correlates of, known environmental changes. In that context, many researchers have attempted to identify indicators of phenomena such as climate change or water pollution—metrics that are believed to reflect how species are responding to documented changes in, say, climate or contaminant loads.

When the term *indicator* is not defined and its use is ambiguous, cross referencing in the literature may compound misunderstandings of the information that may be provided by one or more species. Many publications that describe associations between a given taxonomic group and biotic or abiotic variables do not contend that the association is causal, yet subsequent authors frequently cite such work to bolster the contention that the taxonomic group has diverse and reliable applications in impact assessments (Lomov et al. 2006). References to one or multiple species of butterflies as indicators of land-use changes or anthropogenic landscape disturbances are frequent (e.g., Cleary 2004; Bobo et al. 2006; Poyry et al. 2006; Uehara-Prado et al. 2007). Where land uses are causing changes in vegetation structure or composition to which butterflies are responding, the allusion frequently can be accurate. But it is important to evaluate whether observed changes in vegetation may have been driven by natural phenomena, such as succession or extreme weather events, rather than by human activities. In other words a taxonomic group cannot be used to evaluate the biological effects of land use unless changes in its habitat can be unambiguously attributed to that use. Species richness and composition of dragonfly assemblages, for example, may be correlated with

the magnitude of disturbances in savannah river systems, but assemblages of dragonflies cannot be used to “pinpoint a specific type of disturbance or pollution . . . [or to] tell us whether that disturbance is natural or anthropogenic, save for obvious changes such as riparian vegetation removal” (Stewart & Samways 1998). To provide insights into the progress of conservation efforts, scientific and practical criteria for selection and application of indicators need to be identified and whether a given taxonomic group meets those criteria must be determined (Landres et al. 1988; Noss 1990; Wiens et al. 2008).

Relationships between Indicators and Targets

Indicators, whether implicit or explicit, are a feature of nearly all studies in ecology. Perhaps most often, estimates of population size are invoked as surrogate measures of fitness or habitat quality. The explicit use of an organism as an indicator presumes that the measurement or management of it can facilitate broader inferences or can guide management of an ecosystem. Accordingly, indicators require context. Indicators have no intrinsic value; they cannot provide useful information unless the biotic or abiotic target of conservation or assessment is articulated clearly and quantitatively. Ecological integrity and sustainability are appealing and generate affirmative responses among scientists and the general public, but those concepts do not have universal qualitative definitions, let alone universal quantitative definitions. Instead, environmental targets used as indicators need to be defined in the context of a given research project, assessment effort, or management program. To illustrate, the “health” of riparian woodlands—the target of an environmental assessment—might be diagnosed in terms of structural complexity of vegetation, with the proportional cover of canopy, shrubs, and understory forbs and grasses used to quantify that complexity. Then there must be a known or hypothesized functional relationship between the target and its indicator. If determining whether abundance of one or more species of butterflies can serve as an indicator of climate change is the goal, then one first needs to understand the direct and indirect mechanisms by which temperature, precipitation, cloud cover, and extreme weather events affect butterflies at the levels of populations and individuals (Dennis 1993; Hellmann 2002).

Ideally, the functional relationship between a target and a candidate indicator will be validated with observations or experimental data before the indicator is applied in a management or decision-making context. The hypothesis that the phenology of a given species of plant is an indicator of regional warming might be confronted with experimental data on relationships between flowering date and temperature, when variables such as soil

type and precipitation are controlled. Because relationships observed at a given place or time may not be transferable to others within the planning or implementation horizon, validation should use data from locations or time periods that were not used to build the model (external validation; Landres et al. 1988; Mac Nally et al. 2000). Nevertheless, internal validation (bootstrapping) is preferable to no validation. If the functional relationship between environmental change and indicator response has not been validated, then the presumed relationship should be grounded in a conceptual model, with an accompanying plan for using data to test the hypothesis that one or more attributes of one or more given species has indicator potential.

In principle, selection of candidate indicators is prospective, based on either empirical evidence or an informed assumption that measurable attributes of the indicators are correlated, if not causally linked, with the target of conservation or assessment. In practice, the retrospective identification of indicators has been far more common than not, and indicators frequently are chosen primarily for political reasons (Feest 2006). Greater Sagegrouse (*Centrocercus urophasianus*), a bird emblematic of sagebrush steppe ecosystems in the intermountain western United States, was proposed as an indicator of that ecosystem’s condition, and an umbrella species for other sagebrush-associated taxa, many years before those hypothesized relationships were evaluated with field data (Rowland et al. 2006). As with Sagegrouse, in many circumstances, animals or plants are proposed as indicators primarily because they are declining in abundance (and perhaps protected by law), are charismatic, or are biologically well understood—not because their status and trend conveys accurate information about changes in biotic or abiotic environmental phenomena of concern.

Drawing Inference from Butterflies

Butterflies are unusual among insects because they can be studied nearly worldwide (Thomas 2005). Assumptions have been made in the literature that the presence of all or selected species in a butterfly assemblage is indicative of general environmental attributes, such as conservation value (Mas & Dietsch 2004), environmental health (Nel 1992), and environmental quality (Gordon & Cobblah 2000; Brown & Freitas 2002; Lu & Samways 2002; Mouquet et al. 2005). These attributes often are not defined; authors typically do not clarify how excellent, good, or poor environmental condition should be measured. As a result, it is difficult to evaluate whether the presence of one or more species of butterflies or any other taxonomic group is correlated, if not causally linked, with specific environmental targets.

Species richness and patterns of land cover and land use recur as the dominant environmental phenomena that drive conservation planning and management. Conservation professionals frequently take for granted that the conservation value of a geographic area increases as the number of species (or native species) increases (Meir et al. 2004). In addition, there is a common assumption that protection of locations with high species richness is an effective and efficient way to conserve biotic diversity and sustain ecological function (Scott et al. 1987; Myers et al. 2000). We do not want to debate these assumptions here but accept that they exist and consider whether butterflies actually provide information on species richness.

Many researchers have examined whether species richness or the occurrence of a subset of a butterfly assemblage—typically identified a priori on the basis of taxonomy, ecological similarity, or rarity—is correlated with species richness of an entire assemblage of butterflies. Authors generally report a positive correlation between the two (Beccaloni & Gaston 1995; Swengel & Swengel 1997; Horner-Devine et al. 2003, but see Schulze et al. 2004). For example, the presence and relative abundance of *Maculinea* butterflies is associated with species richness and abundance of the local butterfly assemblage (Skorka et al. 2007). In addition, nestedness analyses have yielded positive associations between the occurrence of a subset of a butterfly assemblage and an assemblage as a whole (Franzen & Ranius 2004). Nevertheless, we are aware of few studies in which a rigorous, objective process was used to identify a small set of butterfly species or, for that matter, any other species, which exhibit occurrence patterns that have a statistical relationship to the species richness of a larger assemblage (Mac Nally & Fleishman 2002).

Numerous investigations have focused on whether the presence or abundance of some or all species in a given assemblage is correlated with species richness or abundance of other taxonomic groups (Williams & Gaston 1998; Ricketts et al. 1999; Maes et al. 2005). The synthetic answer for butterflies, as it is for virtually all taxonomic groups, is that it depends—on spatial or temporal grain and extent, biogeographic history, or the specific groups under comparison (Murphy & Wilcox 1986; Pearson & Carroll 1998; Vessby et al. 2002; Grill et al. 2005). Swengel and Swengel (1999) found correlations between the abundance of butterflies restricted to prairies and several species of songbirds that also are found there. Furthermore, species richness or distribution of butterflies correlates well with the distribution of plants (Niemela & Baur 1998) and hymenoptera (Kerr et al. 2000). Nevertheless, a number of researchers have reported low degrees of correlation between the distribution of butterflies and the distribution of plants (Kremen 1992; Kleintjes et al. 2004), moths (Ricketts et al. 2002), or broader arrays of taxonomic groups (Abensperg-Traun 1996; Lawton et al.

1998; Niemela & Baur 1998; Hess et al. 2006). Again, few studies apply objective statistical methods to identify, let alone validate, species of butterflies that may be linked with the species richness of other taxonomic groups (Fleishman et al. 2005).

Researchers long have referred to one or more species of butterflies as indicators of the distributions of one or more vegetation or land-cover types (Ross 1976; Erhardt 1985; De Benedictis et al. 1990). Butterflies also have been characterized as indicators of life zones (Garth & Tilden 1963) and woodland (Viejo et al. 1989) and river-valley types (Thiele 2000). The basis for this characterization—an assumption that butterflies have predictable associations with the composition and structure of vegetation communities (Hermy & Cornelis 2000)—can be surprisingly tenuous. At a local level, the larvae of many species of butterflies are restricted to one or a few closely related species of larval host plants, and adults of some species are linked closely with particular species of plants from which they derive nectar. Nevertheless, the breadth of host-plant use and preferences for individual species sometimes differs dramatically in space, time, and even among individuals in the same population (Singer 1983; Boughton 1999). Furthermore, in temperate regions, let alone the tropics, the identities of larval host plants for many butterflies still are not known at the species level, and the geographic distribution of a given butterfly species typically is less extensive than the geographic distribution of its larval host plants and nectar sources (Ehrlich & Hanski 2004; Scott 1986). As a result, the presence of a given species of butterfly does not always allow us to infer whether certain species of plants are present. In addition, although presence of a butterfly may provide information about presence of certain plants, absence can be less informative; a butterfly that generally is associated with a given vegetation type rarely is present in all patches of that vegetation type.

Results of many studies show correlations between the distribution of butterflies and different land uses or intensities of land uses (Lomov et al. 2006). For example, butterflies have been proposed as indicators of the biological effects of logging (Hill et al. 1995; Brown 1997; Cleary 2004), other human uses of forests (Hamer et al. 1997; Hammond & Miller 1998; Bobo et al. 2006; Uehara-Prado et al. 2007), grazing by domestic livestock (Bachelard & Descimon 1999; Poyry et al. 2006), and air pollution (Kula & Kralicek 1995). But the metrics of butterfly distributions do not appear to be reliable indicators of forest disturbance (Ghazoul 2002; Nummelin & Kaitala 2004) or the success of reclamation following surface mining (Holl 1995, 1996). Most apparent associations between butterflies and a given type of land use are mediated through the structure or composition of vegetation, rather than land use per se. In some cases either a natural or an anthropogenic disturbance may drive a vegetation community

to a similar state. For example, wildfire and some timber-harvest regimes can have similar effects (Hunter 1993; although see Schmiegelow et al. 2006), and colonization of the non-native annual plant cheatgrass (*Bromus tectorum*) in the western United States can be facilitated by fire, construction of roads, agriculture, and other sources of soil disturbance (Bradley & Mustard 2006). Especially when years have elapsed since a given disturbance, it may be difficult to infer the ultimate cause of a change in vegetation structure or composition. In cases like these, butterflies may be less reliable indicators of land use.

Candidate indicators of a given target of conservation or assessment must be evaluated against practical criteria as well as scientific criteria. Butterflies generally meet reasonable standards of measurement tractability, but there can be substantive caveats. For example, indicators should be easy to observe. Although butterflies are diurnal, often colorful, and typically readily detected, phenologies of butterfly populations can vary dramatically among locations and years and are affected by short-term weather conditions. These attributes are a challenge in conducting, and analyzing data from, annual surveys of butterfly populations. Estimation of population size and emergence curves can require intensive surveys or mark-recapture efforts by trained personnel (Weiss et al. 1993; Haddad et al. 2008). It is generally appreciated that indicators also should be easy to identify. Certainly many species of butterflies can be identified on the wing or in the net by experienced observer, but morphological similarities among species in some species-rich genera (e.g., *Speyeria*, *Euphydryas*, and *Euphilotes*) confound reliable identification, even by seasoned lepidopterists. In addition, many small-bodied species of butterflies, especially hesperiids and lycaenids, are difficult to capture and handle without injuring the animals.

Some have suggested that butterflies can serve as indicators of environmental phenomena because they have short generation times, which allow for rapid changes in demography or distribution in response to environmental change (van Swaay et al. 2006). But the population dynamics of butterflies actually may be too responsive to minor variations in ecological conditions to signal meaningful environmental trends. Rates of birth, death, emigration, and immigration of butterflies are highly sensitive to daily and seasonal weather. Changes in local butterfly abundances over orders of magnitude regularly are observed in the absence of obvious deterministic environmental changes, whether natural or anthropogenic. Thus, it can be remarkably difficult to separate environmental signals from environmental noise and to attribute causation to actual variability in population dynamics or occurrences of butterflies (McLaughlin et al. 2002; Fleishman & Mac Nally 2003). Butterflies may be among the first organisms to decline dramatically or to be extirpated as a local environment changes, but shifts in the population dynamics of butterflies are not necessarily a direct

reflection, let alone an early warning, of environmental changes of concern. For example, we might be able to explain a decline in abundance based on precipitation, but it is not true that a decline in abundance of a species necessarily reflects a certain pattern of precipitation. Furthermore, changes in abundance of any organism rarely are triggered by a change in an individual environmental attribute; instead, those changes tend to reflect suites of interacting or cascading changes in the biotic and abiotic environment.

Butterflies are among the best-known groups of invertebrates in terms of their ecology and, in some regions, such as Great Britain, historical distributions and population trends. Although most species are resilient to moderate levels of human activity (in the case of climate change, this reduces the number of likely drivers of a population response) and have rapid response times (Parmesan 2003), "there is much information still to be gathered before it can be advised of just what in ecological conditions and environmental changes each species is precisely an indicator" (Dennis 2004). Butterflies do not often indicate environmental change in the sense that they are conveying elusive information, and there is little evidence on which to base the sweeping statement that butterflies "can be used as rapid indicators of different types of change in the community, its environment, and the landscape" (Brown & Freitas 2000).

If the context is carefully articulated, we think certain species or sets of species of butterflies might be used to evaluate the direct and indirect effects of environmental change, especially changes in climate, on butterfly populations and assemblages. Known mechanisms by which the abiotic environment affects butterflies can allow generation of specific, testable predictions related to climate change (Hellmann 2002; Parmesan 2003). In that case, if long-term data on the distribution and abundance of butterflies are available and can be coupled with comprehensive data on means and variance in temperature and precipitation, it may be possible to separate the signal of climate change from the noise of weather.

Drawing Inference from Indicators

There probably are few individual species, or sets of species, that can serve as a scientifically reliable, cost-effective measure of the status or trend of an environmental phenomenon that is not scientifically or logistically tractable to measure directly. In at least some systems, indicators of species richness can be identified using objective, quantitative methods, but experienced observers usually can detect all species in well-known taxonomic groups (e.g., birds, butterflies, angiosperms) without expending substantially more effort than would be necessary to detect a subset of species in those groups.

A validated indicator (e.g., one or multiple species) might provide information on biotic factors or abiotic environmental factors of conservation concern. From a scientific perspective, we suggest that it may be more tractable to establish indicators of abiotic factors because those environmental attributes generally are the ultimate drivers of responses in the distributions and abundances of plants and animals. The proximate driver of a decline in the abundance of a given species of butterfly may be a change in the abundance or phenology of its larval host or an increase in larval parasitism, but the ultimate driver is likely to be stochastic changes in weather or deterministic changes in climate. In this context we are referring to indicators as distributions, abundances, or demographic variables that are measured to assess responses to, or as correlates of, known environmental changes. We recognize it is usually easier and cheaper to measure an abiotic variable than a biotic surrogate.

There are species with distributions, abundances, or demographic characteristics that are responsive to known environmental changes (Batalden et al. 2007; Hellmann et al. 2008; Merrill et al. 2008). In this context, single or multiple species can serve as indicators when targets are defined explicitly, ecological relationships between the target and the putative indicators are well understood, and data are sufficient to differentiate between deterministic and stochastic responses. Although these situations exist, they are less common than might be apparent from the extensive literature proclaiming that certain appealing taxa are “indicators of the health of terrestrial ecosystems” (Nel 1992; Lindenmayer et al. 2000).

If long time-series data like those from the British Butterfly Monitoring Scheme or North American Breeding Bird Survey are available, distributions and abundances of well-known taxonomic groups appear most promising for assessing responses to documented changes in climate, resource extraction, or expansion of invasive species. Abundances of Lepidoptera from 1864 to 1952 were correlated with various measures of current-year and previous temperatures and precipitation and with the North Atlantic Oscillation index (Dennis & Sparks 2007). Mean dates of appearance of butterflies also have been related to changes in temperature (Sparks & Yates 1997). Similarly, the spring phenology of a subset of Nearctic-Neotropical migratory songbird species in California (U.S.A.) has been associated with temperature and large-scale climate oscillation indices (Macmynowski et al. 2007), and the abundance and dispersal of Magellanic penguins over many decades likely reflects both climate-induced changes in the distribution of their prey and cascading effects from commercial fishing (Boersma 2008). Trends in abundance of some breeding birds also correspond to movement of West Nile virus across North America (LaDeau et al. 2007). Multiple taxonomic groups also can be used to design networks of protected areas

under the assumption that conservation of locations with high species richness is an effective mechanism to sustain biological diversity in its broadest sense (e.g., Kremen et al. 2008).

During the past several decades, we have witnessed a proliferation in claims that charismatic taxonomic groups provide information on the status and trends of biological diversity and ecological function. In a majority of cases—examples in the preceding paragraph notwithstanding—these statements have been linked to few caveats and have not been supported with data. There are circumstances in which butterflies can serve effectively as indicators, especially at the assemblage level, but we are not aware of an example in which a single species has provided environmental information that cannot be measured more directly. We suggest that the public appeal of these groups of organisms and the fact that there is a substantial body of literature on their ecology have driven much of their acclaim as indicators. Marketing and science are equally important to conserving Earth’s biological diversity, but a taxon used to market a general conservation mission and a taxon used to draw strong inference about specific environmental changes may not be the same. We need to be exacting in our definitions of indicators and scrupulous in our validation.

Acknowledgment

Thanks to E. Main and several anonymous reviewers for comments that improved the manuscript.

Literature Cited

- Abensperg-Traun, M., G. W. Arnold, D. E. Steven, G. T. Smith, L. Atkins, J. J. Viveen, and M. Gutter. 1996. Biodiversity indicators in semi-arid, agricultural Western Australia. *Pacific Conservation Biology* 2:375–389.
- Bachelard, P., and H. Descimon. 1999. *Lycaena belle* (Denis and Schiffermuller, 1775) from the Central Massif (France): an ecogeographical analysis (Lepidoptera: Lycaenidae). *Linneana Belgica* 17:23–41.
- Batalden, R. V., K. Oberhauser, and A. T. Peterson. 2007. Ecological niches in sequential generations of eastern North American monarch butterflies (Lepidoptera: Danaidae): the ecology of migration and likely climate change implications. *Environmental Entomology* 36:1365–1373.
- Beccaloni, G. W., and K. J. Gaston. 1995. Predicting the species richness of Neotropical forest butterflies: Ithomiinae (Lepidoptera: Nymphalidae) as indicators. *Biological Conservation* 71:77–86.
- Bobo, K. S., M. Waltert, H. Fermon, J. Njokagbor, and M. Muhlenberg. 2006. From forest to farmland: butterfly diversity and habitat associations along a gradient of forest conversion in southwestern Cameroon. *Journal of Insect Conservation* 10:29–42.
- Boersma, P. D. 2008. Penguins as marine sentinels. *BioScience* 58:597–607.
- Boughton, D. A. 1999. Empirical evidence for complex source–sink dynamics with alternative states in a butterfly metapopulation. *Ecology* 80:2727–2739.

- Bradley, B. A., and J. F. Mustard. 2006. Characterizing the landscape dynamics of an invasive plant and risk of invasion using remote sensing. *Ecological Applications* **16**:1132–1147.
- Brown, K. S., Jr. 1997. Diversity, disturbance and sustainable use of Neotropical forests: insects as indicators for conservation monitoring. *Journal of Insect Conservation* **1**:25–42.
- Brown, K. S., Jr., and A. V. L. Freitas. 2000. Atlantic forest butterflies: indicators for landscape conservation. *Biotropica* **32**:934–956.
- Brown, K. S., Jr., and A. V. L. Freitas. 2002. Butterfly communities of urban forest fragments in Campinas, Sao Paulo, Brazil: structure, instability, environmental correlates, and conservation. *Journal of Insect Conservation* **6**:217–231.
- Cleary, D. F. R. 2004. Assessing the use of butterflies as indicators of logging in Borneo at three taxonomic levels. *Journal of Economic Entomology* **97**:429–435.
- De Benedictis, J. A., D. L. Wagner, and J. B. Whitfield. 1990. Larval hosts of microlepidoptera of the San Bruno Mountains, California. *Atala* **16**:14–18.
- Dennis, R. L. H. 1993. Butterflies and climate change. Manchester University Press, Manchester, United Kingdom.
- Dennis, R. L. H. 2004. Butterfly habitats, broad-scale biotope affiliations, and structural exploitation of vegetation at finer scales: the matrix revisited. *Ecological Entomology* **29**:744–752.
- Dennis, R. L. H., and T. H. Sparks. 2007. Climate signals are reflected in an 89 year series of British Lepidoptera records. *European Journal of Entomology* **104**:763–767.
- Ehrlich, P. R., and I. Hanski. 2004. On the wings of checkerspots. Oxford University Press, New York.
- Erhardt, A. 1985. Diurnal lepidoptera, sensitive indicators of cultivated and abandoned grassland. *Journal of Applied Ecology* **22**:849–862.
- Feest, A. 2006. Establishing baseline indices for the quality of the biodiversity of restored habitats using a standardized sampling process. *Restoration Ecology* **14**:112–122.
- Fleishman, E., and R. Mac Nally. 2003. Distinguishing between signal and noise in faunal responses to environmental change. *Global Ecology and Biogeography* **12**:395–402.
- Fleishman, E., J. R. Thomson, R. Mac Nally, D. D. Murphy, and J. P. Fay. 2005. Using indicator species to predict species richness of multiple taxonomic groups. *Conservation Biology* **19**:1125–1137.
- Franzen, M., and T. Ranius. 2004. Occurrence patterns of butterflies (Rhopalocera) in semi-natural pastures in southeastern Sweden. *Journal for Nature Conservation* **12**:121–135.
- Garth, J. S., and J. W. Tilden. 1963. Yosemite butterflies: an ecological survey of the butterflies of the Yosemite sector of the Sierra Nevada, California. *Journal of Research on the Lepidoptera* **2**:1–96.
- Ghazoul, J. 2002. Impact of logging on the richness and diversity of forest butterflies in a tropical dry forest in Thailand. *Biodiversity and Conservation* **11**:521–541.
- Gordon, I., and M. Cobblah. 2000. Insects of the Muni-Pomadze Ramsar site. *Biodiversity and Conservation* **9**:479–486.
- Grill, A., B. Knoflach, D. F. R. Cleary, and V. Kati. 2005. Butterfly, spider, and plant communities in different land-use types in Sardinia, Italy. *Biodiversity and Conservation* **14**:1281–1300.
- Haddad, N. M., B. Hudgens, C. Damiani, K. Gross, D. Kuefler, and K. Pollock. 2008. Determining optimal population modeling for rare butterflies. *Conservation Biology* **22**:929–940.
- Hamer, K. C., J. K. Hill, L. A. Lace, and A. M. Langan. 1997. Ecological and biogeographical effects of forest disturbance on tropical butterflies of Sumba, Indonesia. *Journal of Biogeography* **24**:67–75.
- Hammond, P. C., and J. C. Miller. 1998. Comparison of the biodiversity of Lepidoptera within three forested ecosystems. *Annals of the Entomological Society of America* **91**:323–328.
- Hellmann, J. J. 2002. Butterflies as model systems for understanding and predicting climate change. Pages 93–126 in S. H. Schneider and T. L. Root, editors. *Wildlife responses to climate change*. Island Press, Washington, D.C.
- Hellmann, J. J., S. L. Pelini, K. M. Prior, and J. D. K. Dzurisin. 2008. The response of two butterfly species to climatic variation at the edge of their range and the implications for poleward range shifts. *Oecologia* **157**:583–592.
- Hermly, M., and J. Cornelis. 2000. Towards a monitoring method and a number of multifaceted and hierarchical biodiversity indicators for urban and suburban parks. *Landscape and Urban Planning* **49**:149–162.
- Hess, G. R., R. A. Bartel, A. K. Leidner, K. M. Rosenfeld, M. J. Rubino, S. B. Snider, and T. H. Ricketts. 2006. Effectiveness of biodiversity indicators varies with extent, grain, and region. *Biological Conservation* **132**:448–457.
- Hill, J. K., L. A. Lace, and W. M. T. Banham. 1995. Effects of selective logging on tropical forest butterflies on Buru, Indonesia. *Journal of Applied Ecology* **32**:754–760.
- Holl, K. D. 1995. Nectar resources and their influence on butterfly communities on reclaimed coal surface mines. *Restoration Ecology* **3**:76–85.
- Holl, K. D. 1996. The effect of coal surface mine reclamation on diurnal lepidopteran conservation. *Journal of Applied Ecology* **33**:225–236.
- Horner-Devine, M. C., G. C. Daily, P. R. Ehrlich, and C. L. Boggs. 2003. Countryside biogeography of tropical butterflies. *Conservation Biology* **17**:168–177.
- Hunter, M. L., Jr. 1993. Natural fire regimes as spatial models for managing boreal forests. *Biological Conservation* **65**:115–120.
- Kerr, J. T., A. Sugar, and L. Packer. 2000. Indicator taxa, rapid biodiversity assessment, and nestedness in an endangered ecosystem. *Conservation Biology* **14**:1726–1734.
- Kleintjes, P. K., B. F. Jacobs, and S. M. Fettig. 2004. Initial response of butterflies to an overstorey reduction and slash mulching treatment of a degraded pinon-juniper woodland. *Restoration Ecology* **12**:231–238.
- Kremen, C. 1992. Assessing the indicator properties of species assemblages for natural areas monitoring. *Ecological Applications* **2**:203–216.
- Kremen, C., et al. 2008. Aligning conservation priorities across taxa in Madagascar with high-resolution planning tools. *Science* **320**:222–226.
- Kula, E., and M. Kralicek. 1995. Occurrence of melanism with butterflies in polluted area Decinsky Sneznik. *Lesnictvi* **41**:257–264.
- LaDeau, S. L., A. M. Kilpatrick, and P. P. Mara. 2007. West Nile virus emergence and large-scale declines of North American bird populations. *Nature* **447**:710–713.
- Landres, P. B., J. Verner, and J. W. Thomas. 1988. Ecological uses of vertebrate indicator species: a critique. *Conservation Biology* **2**:316–328.
- Lawton, J. H., et al. 1998. Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. *Nature* **391**:72–76.
- Lewinsohn, T. M., A. V. L. Freitas, and P. I. Prado. 2005. Conservation of terrestrial invertebrates and their habitats in Brazil. *Conservation Biology* **19**:640–645.
- Lindenmayer, D. B., C. R. Margules, and D. B. Botkin. 2000. Indicators of biodiversity for ecologically sustainable forest management. *Conservation Biology* **14**:941–950.
- Lomov, B., D. A. Keith, D. R. Britton, and D. F. Hochuli. 2006. Are butterflies and moths useful indicators for restoration monitoring? A pilot study in Sydney's Cumberland Plain Woodland. *Ecological Management and Restoration* **7**:204–210.
- Lu, S.-S., and M. J. Samways. 2002. Behavioural ecology of the Karkloof blue butterfly *Orachrysoptis ariadne* (Lepidoptera: Lycaenidae) relevant to its conservation. *African Entomology* **10**:137–147.
- McLaughlin, J. F., J. J. Hellmann, C. L. Boggs, and P. R. Ehrlich. 2002. Climate change hastens population extinctions. *Proceedings of the National Academy of Sciences of the United States of America* **99**:6070–6074.
- Macmynowski, D. P., T. L. Root, G. Ballard, and G. R. Geupel. 2007. Changes in spring arrival of Nearctic-Neotropical migrants attributed to multiscalar climate. *Global Change Biology* **13**:2239–2251.

- Mac Nally, R., and E. Fleishman. 2002. Using 'indicator' species to model species richness: model development and predictions. *Ecological Applications* **12**:79-92.
- Mac Nally, R., A. F. Bennett, and G. Horrocks. 2000. Forecasting the impacts of habitat fragmentation. Evaluation of species-specific predictions of the impact of habitat fragmentation on birds in the box-ironbark forests of central Victoria, Australia. *Biological Conservation* **95**:7-29.
- Maes, D., D. Bauwens, L. De Bruyn, A. Anselin, G. Vermeersch, W. Van Landuyt, G. De Knijf, and M. Gilbert. 2005. Species richness coincidence: conservation strategies based on predictive modelling. *Biodiversity and Conservation* **14**:1345-1364.
- Mas, A. H., and T. V. Dietsch. 2004. Linking shade coffee certification to biodiversity conservation: butterflies and birds in Chiapas, Mexico. *Ecological Applications* **14**:642-654.
- Meir, E., S. Andelman, and H. P. Possingham. 2004. Does conservation-planning matter in a dynamic and uncertain world? *Ecology Letters* **7**:615-622.
- Merrill, R. M., D. Gutiérrez, O. T. Lewis, J. Gutiérrez, S. B. Díes, and R. J. Wilson. 2008. Combined effects of climate and biotic interactions on the elevational range of a phytophagous insect. *Journal of Animal Ecology* **77**:145-155.
- Morrison, M. L., and L. S. Hall. 2002. Standard terminology: toward a common language to advance ecological understanding and application. Pages 43-52 in J. M. Scott, P. J. Heglund, M. L. Morrison, J. B. Hauffer, M. G. Raphael, W. A. Wall, and F. B. Samson, editors. *Predicting species occurrences: issues of accuracy and scale*. Island Press, Washington, D.C.
- Mouquet, N., V. Belrose, J. A. Thomas, G. W. Elmes, R. T. Clarke, and M. E. Hochberg. 2005. Conserving community modules: a case study of the endangered lycaenid butterfly *Maculinea alcon*. *Ecology* **86**:3160-3173.
- Murphy, D. D., and B. A. Wilcox. 1986. Butterfly diversity in natural habitat fragments: a test of the validity of vertebrate-based management. Pages 287-292 in J. Verner, M. L. Morrison, and C. J. Ralph, editors. *Wildlife 2000: modeling habitat relationships of terrestrial vertebrates*. University of Wisconsin Press, Madison, Wisconsin.
- Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. daFonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. *Nature* **403**:853-858.
- Nel, J. 1992. On the ecological plasticity and the biology of some Lepidoptera (Rhopalocera) of the southwest Mediterranean area of France. *Linneana Belgica* **13**:287-338.
- Niemela, J., and B. Baur. 1998. Threatened species in a vanishing habitat: plants and invertebrates in calcareous grasslands in the Swiss Jura mountains. *Biodiversity and Conservation* **7**:1407-1416.
- Noss, R. F. 1990. Indicators for monitoring biodiversity: a hierarchical approach. *Conservation Biology* **4**:355-364.
- Nummelin, M., and S. Kaitala. 2004. Do species dominance indices indicate rain forest disturbance by logging? *Biotropica* **36**:628-632.
- Parmesan, C. 2003. Butterflies as bioindicators for climate change effects. Pages 541-560 in C. L. Boggs, W. B. Watt, and P. R. Ehrlich, editors. *Butterflies: ecology and evolution taking flight*. University of Chicago Press, Chicago, Illinois.
- Pearson, D. L., and S. S. Carroll. 1998. Global patterns of species richness: spatial models for conservation planning using bioindicator and precipitation data. *Conservation Biology* **12**:809-821.
- Poyry, J., M. Luoto, J. Paukkunen, J. Pykala, K. Raatikainen, and M. Kuussaari. 2006. Different responses of plants and herbivore insects to a gradient of vegetation height: an indicator of the vertebrate grazing intensity and successional age. *Oikos* **115**:401-412.
- Ricketts, T. H., E. Dinerstein, D. M. Olson, and C. Loucks. 1999. Who's where in North America? Patterns of species richness and the utility of indicator taxa for conservation. *BioScience* **49**:369-381.
- Ricketts, T. H., G. C. Daily, and P. R. Ehrlich. 2002. Does butterfly diversity predict moth diversity? Testing a popular indicator taxon at local scales. *Biological Conservation* **103**:361-370.
- Ross, G. N. 1976. An ecological study of the butterflies of the Sierra de Tuxtla in Veracruz Mexico. *Journal of Research on the Lepidoptera* **15**:225-240.
- Rowland, M. M., M. J. Wisdom, L. H. Suring, and C. W. Meinke. 2006. Greater sage-grouse as an umbrella specie for sagebrush-associated vertebrates. *Biological Conservation* **129**:323-335.
- Schmiegelow, F. K. A., D. P. Stepnisky, C. A. Stambaugh, and M. Koivula. 2006. Reconciling salvage logging of boreal forests with a natural-disturbance model. *Conservation Biology* **20**:971-983.
- Schulze, C. H., et al. 2004. Biodiversity indicator groups of tropical land-use systems: comparing plants, birds, and insects. *Ecological Applications* **14**:1321-1333.
- Scott, J. A. 1986. *The butterflies of North America*. Stanford University Press, Stanford, California.
- Scott, J. M., B. Csuti, J. D. Jacobi, and J. E. Estes. 1987. Species richness. *BioScience* **37**:782-788.
- Singer, M. C. 1983. Determinants of multiple host use by a phytophagous insect population. *Evolution* **37**:389-403.
- Skorka, P., J. Settele, and M. Woyciechowski. 2007. Effects of management cessation on grassland butterflies in southern Poland. *Agriculture Ecosystems and Environment* **121**:319-324.
- Sparks, T. H., and T. J. Yates. 1997. The effect of spring temperature on the appearance dates of British butterflies 1883-1993. *Ecography* **20**:368-374.
- Stewart, D. A. B., and M. J. Samways. 1998. Conserving dragonfly (Odonata) assemblages relative to river dynamics in an African savanna game reserve. *Conservation Biology* **12**:683-692.
- Swengel, A. B., and S. R. Swengel. 1997. Co-occurrence of prairie and barrens butterflies: applications to ecosystem conservation. *Journal of Insect Conservation* **1**:131-144.
- Swengel, S. R., and A. B. Swengel. 1999. Correlations in abundance of grassland songbirds and prairie butterflies. *Biological Conservation* **90**:1-11.
- Thiele, V. 2000. To the knowledge of the Lepidoptera-fauna of different types of river valley in Mecklenburg-West Pomerania (Lep.). *Entomologische Nachrichten und Berichte* **44**:137-144.
- Thomas, J. A. 2005. Monitoring change in the abundance and distribution of insects using butterflies and other indicator groups. *Philosophical Transactions of the Royal Society B* **360**:339-357.
- Uehara-Prado, M., K. S. Brown Jr., L. Freitas, and A. Victor. 2007. Species richness, composition and abundance of fruit-feeding butterflies in the Brazilian Atlantic Forest: comparison between a fragmented and a continuous landscape. *Global Ecology and Biogeography* **16**:43-54.
- van Swaay, C., M. Warren, and G. Lois. 2006. Biotope use and trends of European butterflies. *Journal of Insect Conservation* **10**:189-209.
- Vessby, K., B. Soderstrom, A. Glimskar, and B. Svensson. 2002. Species-richness correlations of six different taxa in Swedish seminatural grasslands. *Conservation Biology* **16**:430-439.
- Viejo, J. L., M. G. De Viedma, and E. Martinez Falero. 1989. The importance of woodlands in the conservation of butterflies (Lepidoptera: Papilionoidea and Hesperioidea) in the center of the Iberian Peninsula. *Biological Conservation* **48**:101-114.
- Wallis DeVries, M. F., and I. Raemakers. 2001. Does extensive grazing benefit butterflies in coastal dunes? *Restoration Ecology* **9**:179-188.
- Weiss, S. B., D. D. Murphy, P. R. Ehrlich, and C. F. Metzler. 1993. Adult emergency phenology in checkerspot butterflies: the effects of macroclimate, topography, and population history. *Oecologia* **96**:261-270.
- Wiens, J. A., G. D. Hayward, R. S. Holthausen, and M. J. Wisdom. 2008. Using surrogate species and groups for conservation planning and management. *BioScience* **58**:241-252.
- Williams, P. H., and K. J. Gaston. 1998. Biodiversity indicators: graphical techniques, smoothing and searching for what makes relationships work. *Ecography* **21**:551-556.