ASSESSING THE INDICATOR PROPERTIES OF SPECIES ASSEMBLAGES FOR NATURAL AREAS MONITORING

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Abstract. The diversity of organisms and complexity of ecosystems prevent thorough inventory and monitoring of protected areas, yet sound databases are needed to manage ecosystems for long-term persistence. One strategy is therefore to focus monitoring on indicator organisms, but guidelines are lacking for selecting appropriate species or groups. This paper presents a simple protocol based on ordination techniques for establishing the indicator properties of a group of organisms and for selecting an indicator species subset for more intensive monitoring. Use of ordination allows inclusion of many more taxa than have been traditionally used for natural areas monitoring, and need not rely on detailed knowledge of species biology. As an example, I studied the indicator properties of a butterfly taxocene in a rain forest in Madagascar. Butterflies have been suggested as particularly good environmental indicators due to their sensitivity to micro-climate and light level changes, and their interactions as larvae and adults with different sets of host plants. The indicator properties of butterfly assemblages were evaluated in this study with respect to a known pattern of environmental heterogeneity along topographic/moisture and disturbance gradients. Butterfly assemblages were found to be excellent indicators of heterogeneity due to the topographic/moisture gradient, limited indicators of heterogeneity due to anthropogenic disturbance, and poor indicators of plant diversity. The protocol defined in this study is widely applicable to other groups of organisms, spatial scales, and environmental gradients. By examining the environmental correlates of the distribution of species assemblages, this protocol can assess the indicator properties of target species groups.

Key words: diversity; dominance; ecological monitoring; indicator species assemblage; Madagascar; natural areas conservation; ordination; rarity; Satyrinae; tropical butterflies.

INTRODUCTION

Most ecosystems today are subject to one or more forms of anthropogenic disturbance, especially pollution and acidification, habitat modification and fragmentation, and invasions by introduced species (Soule and Wilcox 1980, Burgess and Sharpe 1981, Peters and Darling 1985, Soule 1986, Schreiber and Newman 1988, Carleton 1989, Fajer 1989, Fajer et al. 1989, Klein 1989). Given the pervasive spatial and rapid temporal scale of current anthropogenic environmental changes, methods are needed for choosing appropriate species or species assemblages for establishing conservation priorities and monitoring biotic responses to local and global environmental change (Kimball and Levin 1985, Soule 1990).

Outside of a substantial literature on single or multispecies indicators of specific environmental contaminants (Cairns 1985, 1986), few practical guidelines currently exist for selecting indicators for monitoring natural areas. A recent review critically evaluated selection of vertebrate indicators, concluding that no single traditional criterion (e.g., high sensitivity to habitat modification, large size, habitat specialization, low population or species turnover rates, or large area requirements) can be safely used for monitoring population trends or habitat quality (Landres et al. 1988). Given the difficulties inherent in using one or a few species as indirect assays of complex ecosystem structure and function (Ward 1978, Kimball and Levin 1985, Cairns 1986, Soule 1987, Landres et al. 1988, Noss 1990), further work is needed to establish and test criteria for selecting indicators.

Much previous work involving indicators has relied on utilizing one or a few species (e.g., Management Indicator Species of the Forest Service, Landres et al. 1988). The failing of this approach is its narrow focus, which can result in protection of one organism at the expense of others (Kushlan 1979, Landres et al. 1988). By contrast, use of a greater variety of indicator species could provide more fine-grained information (Noss 1990): the degree of detail gained would in turn depend on variation in microhabitat use, niche breadth, ecological function, and response to environmental change among members of the indicator assemblage. By using ordination techniques, one can easily examine the distributions of many species simultaneously and their relationship to environmental parameters (Gauch 1982a, Ter Braak 1987, Peet et al. 1988). These powerful multivariate tools allow assessment of the indicator properties of a much wider array of organisms, and could be used to broaden monitoring concepts to include detection of environmental patterns based on the response of a group of species.

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This paper presents an analytical method based on ordination techniques for assessing the indicator properties of a given species assemblage (guild, taxon, taxonomy, or community). The method first tests whether the distributional data from the chosen species assemblage indicate environmental patterns at the geographic scale of interest. It then determines which environmental parameters the species assemblage serves to indicate. Finally, it provides a framework for selecting the most important indicator species from within the original species assemblage.

**Butterflies as indicators**

The taxon Rhopalocera (butterflies and skippers) was the group chosen for this study of a rain forest habitat in Madagascar. Little ecological information exists on these species or their habitat, and some of the taxa are poorly defined at the species level. This study therefore required a method for choosing indicator species that did not depend on detailed knowledge of their biology. This property of the method developed below makes it particularly important for use in testing and selecting indicators in regions where the ecological information-base is poor.

In addition, the choice of the Rhopalocera allowed a test of the claim, advanced by several authors, that butterflies have a particular value as ecological indicators (Gilbert 1980, 1984, Pyle 1980, Brown 1982, Murphy et al. 1990). On a practical basis, butterflies (in comparison to other insect taxa) have a manageable level of diversity, are better known taxonomically, and can in many areas be reliably identified in the field (Pollard 1977, Thomas 1983, Thomas and Mallorie 1985, Murphy and Wilcox 1986). On biological grounds, it has been suggested that butterfly diversity could be used as an index of plant diversity (Pyle 1980), since coevolution between butterflies and their larval host-plants has in some cases led to high butterfly-plant specificity (Ehrlich and Raven 1964, Gilbert and Smiley 1978). However, positive correlations between butterfly and plant diversity may in fact be the exception (e.g., Thomas and Mallorie 1985) rather than the rule (e.g., this study, Sharp et al. 1974, Vane-Wright 1978; M. Singer, personal communication, P. Brussard, personal communication). Of perhaps more interest is that butterflies interact with plants both as larval herbivores and as adult pollinators, potentially influencing plant population dynamics in both interactions (Gilbert 1980, Rausher and Feeny 1989, Jennersten 1988).

Thus, with sufficient system-specific knowledge, one might be able to predict changes in plant populations from knowledge of butterfly population changes. Finally, populations of butterflies are strongly influenced by local weather, microclimates and light levels acting in a variety of ways at all stages of the life cycle (e.g., oviposition site selection and larval development, Rausher 1979; larval development and host plant phenology, Weiss et al. 1987, 1988; availability of flight time for adult courtship and oviposition, Watt et al. 1968, Kingsolver 1983a, b; severe climate and population extinction, Ehrlich et al. 1972). Since butterfly populations respond to habitat modifications affecting local climates and light levels, it has been suggested that changes in butterfly populations could serve to herald local or global climate change (Murphy et al. 1990).

While studies of butterflies have contributed to conservation biology in both a population and community context (e.g., Brown 1982, Ehrlich and Murphy 1987, Murphy et al. 1990, Singleton and Courtney 1991), no studies to date have evaluated the indicator properties of butterfly species or assemblages. This study examines the ability of butterfly community data to reveal patterns of habitat heterogeneity due to topography and anthropogenic disturbance. Variation related to these two parameters strongly influences micro-climate and plant community composition (Swanson et al. 1988), and thus provides one appropriate assay of some of the proposed indicator properties of butterflies.

**METHODS**

**Field site**

The field site was located in the southeastern montane rain forest of Madagascar, 7 km southwest of Ranomafana on route 45 in the province of Fianarantsoa. The area is topographically diverse, with steeply wooded hills, dissected by numerous streams draining into the Namorona River. The site had a tree species richness on the order of 95 species/0.2 ha (D. Overdorff, unpublished data) including Ficus spp. (Moraceae), Eugenia spp. (Myrtaceae), Weinmannia spp. (Cunoniaceae), Symploca spp. (Guttiferae), Ravensara and Ocotea spp. (Lauraceae), Pittosporum spp. (Pittosporaceae), and many others. Common understory plants include many Psychotria and other Rubiaceae, Pandanus (Pandanaceae), palms, grasses and bamboos, treeferns, and ferns. The forest is rich in lianas and epiphytes, and receives a total rainfall of ≈2300–2600 mm per year. The soils are acid, and of low natural fertility (P. Sanchez, personal communication). Much of the forest at the study site experienced a patchwork cycle of slash and burn farming within the past 50–100 yr. Slash field sizes were small (50 × 50 m) and regeneration of a diverse rain forest community in the absence of further disturbance has been rapid (C. Kremen, unpublished observations). For example, the site supports 12 species of lemur, one of the highest levels of primate diversity anywhere in the world (P. Wright, personal communication). The understory vegetation is also relatively sparse, except where recent disturbance has led to the invasion of the introduced guayava, Psidium cattleianum.

In this study, two forest types were studied within a distance of 4.2 km: forest at Vatoharanana that had been selectively logged 25 yr previously (referred to from now on as “old forest”), and forest at Talatany
that had been selectively logged within the previous 2 yr ("new forest"). The old forest was farther from the main road, and probably never experienced the same intensity of logging as the new forest. In both forest types, 100-m transects were situation along trails on ridges (new forest, \(N = 3\); old forest, \(N = 2\)) and stream banks (new forest, \(N = 3\); old forest, \(N = 2\)). Three additional transects were located within the new forest in highly disturbed areas slashed to provide logging trails. In addition to disturbance regime, the old forest was found at a slightly higher elevation than the new forest (50 to 100 m) and may receive higher rainfall (D. Overdorff, personal communication). Both forest types had closed canopy, but the old forest contained a much higher proportion of trees >20 m in height (11.5%) than the new forest (2.5%) (F. White and D. Overdorff, unpublished data).

**Butterfly sampling**

The study was begun at the end of the cool, low-rainfall "winter." Increasing mean daily temperatures and monthly rainfall at this time appeared to stimulate eclosion in a wide variety of butterfly species. During each of five 10-d sampling periods between the end of August and the beginning of November, each of the 13 transects was sampled for butterflies twice, 1 h during a morning time period (1000-1200) and 1 h during an afternoon time period (1200-1400). Morning and afternoon collecting dates were randomized between sites in any one sampling period, and transects were only sampled under sunny conditions. An equal sample effort was thereby devoted to each transect, for a total of 130 person-hours of sampling time.

Sampling was conducted by continuously walking back and forth along the transect for 1 h, collecting all butterflies that were observed within a 5-m band on either side of the transect (modification of Pollard 1977, Thomas 1983). The sampling method assessed the relative abundance of understory butterfly species. While it ignored the canopy (i.e., Charaxides species) and underestimated the fast-flying mid-level to canopy species (most pavilionids, some nymphalids), it was consistent between transects. Observations and understory and canopy trap-data collected during the same sampling period permitted an assessment of which species were not quantitatively represented in these samples.

**Butterfly identification**

Butterflies in most families were identified by the author using D’Abrera (1980), Paulian (1956), and Paulian and Viette (1968). Dr. Robert K. Robbins and Dr. Donald Harvey (National Museum of Natural History, Washington, D.C.) assisted with identifications of lycaenid and rodinid species, respectively. Dr. Jacques Pierre (Musee Nationale d’Histoire Naturelle, Paris) assisted with identifications in the family Acreaiidae. Skippers were identified by the author using Viette (1956) and Evans (1937).

Taxonomy of the Malagasy Satyrinae (Nymphalidae) is poorly established; hence morpho-species were designated according to characteristics of the male genitalia, a standard character set for defining taxa in this subfamily (Miller 1968; R. Robbins, personal communication). Once morpho-species were resolved according to genitalic characteristics, the remaining specimens were identified by associated wing pattern characteristics. Names given to morpho-species are preceded by question marks, and represent an attempt to synonymize this species with established names.

**Habitat characterization**

At each transect, three randomly located plots of 25 m² each were established for plant sampling. All plants within these plots >1 cm diameter at breast height (dbh) were identified by a local guide using common Malagasy names. Voucher collections made in this area since 1986 have allowed the identification of many of these species (D. Overdorff and P. Wright, personal communication). Measurements of dbh and estimates of height to top of crown were taken on all plants >1 m in height. These measurements and the plant identifications were used to determine average transect values for plant species diversity, plant basal area, and height of the canopy. Altitudes at each transect were measured with an altimeter.

Flowing phenology was examined at each transect four times during the study. Flower abundance and richness were assessed along the length of the transect in ten 10 m wide by 5 m deep plots, spaced alternately every 10 m on either side of the transect. All flowers (whether lianas, epiphytes, herbs, shrubs, or trees) were noted by three observers equipped with 7 × 35 power binoculars. Species were identified by Malagasy names, and detailed notes on floral characteristics were taken to ensure consistent identifications between plots. The number of flowering individuals was counted for each flower type in each plot to derive an estimate of floral abundance (number of individuals in flower at a given time) and floral richness (number of types of plants in flower at a given time). In general, few flowers were observed in any one of the ten 50-m² plots; therefore the data for the 10 plots were pooled at each site. Average floral abundance and richness at a site refer to these measurements averaged over time.

**Analysis**

**Ordination.**—Species abundance matrices for butterfly or plant data were analyzed by ordination, using Detrended Correspondence Analysis (DCA; detrended by polynomials, CANOCO program, Ter Braak 1988). DCA displays the patterns of covariation in species distributions, by reducing the dimensionality of \(N\) species among \(M\) samples to just a few ordination axes (Knox and Peet 1989). The eigenvalue associated with each axis can be thought of as the proportion of vari-
ation in sample or species dispersion explained by that axis (Gauch 1982a). Detrended correspondence analysis was chosen over other available techniques because: (1) this algorithm removes several artifacts such as the arch effect and compression of gradients at ends, (2) it ordinates sites and species simultaneously within the same ordination space by reciprocal averaging, and (3) it requires no a priori assumptions about directions of environmental gradients or weighting of species or sites (Gauch 1982a, Peet et al. 1988, Knox and Peet 1989). DCA, an indirect gradient analysis technique, ordinates samples based only on the distribution of species abundance values. In the absence of other information, it is therefore a good preliminary technique for assessing the ability of floral or faunal distributional data to indicate a particular environmental pattern.

For analysis of the butterfly data set by DCA, the abundance of each species was partitioned into male and female abundances, since males and females of a species may fly in different habitats (e.g., oviposition vs. feeding habitat). Relative abundance was estimated as the sum of individuals of each sex of each species captured during the five sampling periods at each site. Relative abundances for the plant data set were estimated as the total number of individuals of a morphospecies >1 cm dbh observed at a site (the sums of abundance measures from the three separate quadrants totaling 75 m²).

Axis interpretation.—Canonical Correspondence Analysis (CCA) was used to examine the relationship between species distributions and environmental parameters. In CCA, a direct gradient analysis technique, axis interpretation is performed within the ordination algorithm using a set of supplied environmental variables (Ter Braak 1987). A major difference between CCA and DCA is that ordination of species and samples are constrained to lie along axes determined by the environmental variables. The significance of a particular environmental variable can be assessed through Monte Carlo testing (bootstrapping) of the axis associated with that variable, using the axis eigenvalue as the test statistic (Ter Braak and Prentice 1988). Thus, in CCA, one can test the significance of an environmental variable in establishing the ordination pattern.

Environmental variables included in the CCA analysis of butterfly data were altitude, topography, and level of disturbance (see Table 1 for scoring systems for disturbance and topography). Vegetative and plant community characteristics were canopy height, stem basal area per square metre, plant species richness, DCA site ordination scores based on plant community data, and average richness and abundance of plants in flower. A characteristic of butterfly species assemblages was dominance (Berger-Parker index, $d = N_{max}/N$, where $N_{max}$ is the number of individuals of the most abundant species, Magurran 1988). For axis interpretation of the plant DCA analysis, environmental variables considered were topography and level of disturbance.

<table>
<thead>
<tr>
<th>Table 1. Environmental variables used in Canonical Correspondence Analysis (CCA) of butterfly data.</th>
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<tbody>
<tr>
<td><strong>Environmental variable</strong></td>
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<tr>
<td>Topography*</td>
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<td>Disturbance*</td>
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<tr>
<td>Altitude</td>
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<tr>
<td>Floral abundance</td>
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<tr>
<td>Floral richness</td>
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<td>Butterfly dominance</td>
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* Variables also used in CCA of plant community data.

**Results**

Sample effort

Cumulative species diversity began leveling off under the sampling scheme used in this study after the fifth sample period (a total of 10 person-hours of sampling time per transect). Fig. 1, which shows a sample effort curve for the five sample periods of the study, includes additional data from a sixth and seventh period sampled at 9 of the 13 sites. When different habitat types were considered separately, cumulative species diversity also began to level off at the fifth sample periods (Fig. 1). This suggests that sampling effectiveness was similar in each of the habitat types despite topographic and vegetative differences that might have rendered certain habitat types easier to sample than others.

The possibility that sample curves would rise again with continued sampling cannot be excluded, since a new phenological guild of species could begin flying later in the season. However, inventory taken during a January–March field season (C. Kremen, unpublished data from 1990) added only a few more species to the list compiled from July to November (1988 data), despite distinct increases in temperature and rainfall during this period.

The data from the five sample periods used in the ordination analysis contained a total of 57 species of Rhopalocera (Appendix) among 659 specimens. Using the maximum likelihood method of Cohen (1959, 1961, in Krebs 1989), the distribution of species’ abundances was not significantly different from a lognormal, with a mode of 13 species in the 4th octave of abundance (data analyzed included all seven sample periods with 59 species distributed among 8 octaves of abundance, $N = 882$, $\chi^2 = 5.852$, df = 5, $P > .5$).
Environmental patterns indicated by butterfly species abundances

Detrended Correspondence Analysis (DCA) of the butterfly species abundance by samples matrix resulted in strong clustering of the samples along the first axis into two clusters at either ends of the axis, representing ridge and stream groups, and a third, middle, cluster of highly disturbed logging trails (D sites) (Fig. 2A). Within ridge and stream clusters, samples also clustered according to whether they were located in the forest selectively logged 25 yr ago (old forest) vs. forest selectively logged within the previous 2 yr (new forest). Eigenvalues for the first two principal axes were high (0.676, 0.436). The ordination based on butterfly data effectively clustered sites according to the patterns of known environmental heterogeneity due to the topographic/moisture and disturbance gradients.

In the above ordination, sexes of each species were considered separately. When DCA was run on data in which male and female abundance values were combined for each species, the first eigenvalue declined from 0.676 to 0.618, although the overall ordering of sites along this axis was qualitatively similar (data not shown). Thus, the separation of species abundance data by sex resulted in a slightly better ordination of the sites, suggesting that the distribution of males vs. females among sites conveyed additional information. All subsequent ordination analyses therefore separated species abundance values by sex.

The size effect

Previous studies have questioned whether ordination and clustering techniques reveal actual covariation of species distributions or result from a sampling artifact in which species cluster according to their frequency of occurrence among samples (the “size effect” of Jackson et al. 1989). In DCA, ordination of samples and species occurs simultaneously by reciprocal averaging; thus the “size effect,” if present, could influence the clustering of sites and affect the environmental interpretation. Prior to axis interpretation, it was important to determine whether such an artifact had contributed to establishing the ordination pattern.

For each of the DCA axes, I ran Spearman’s rank correlation analyses (Statgraphics 4.0; Statistical Graphics Corporation 1989) between species’ frequencies of occurrence among sites and species’ DCA scores. No significant correlations were observed, although the second axis showed a weak trend toward a negative correlation ($r = -0.1802, P = .0877$). Similarly, no significant correlations were observed between species’ overall masses and species’ DCA scores on either axis. These analyses therefore rule out the possibility of the DCA ordination being trivially based on a “size effect.”

Axis interpretation: topography

To interpret the axes produced by DCA, I ran canonical correspondence analysis, a direct gradient anal-

ysis ordination technique. Out of eight supplied environmental variables (including one descriptor of butterfly species assemblages, see Table 1), only the nominal variables defining the topographic/moisture gradient significantly explained the variation along the first CCA axis ($P = .01$, exact probability from 99 Monte Carlo runs). This axis had an eigenvalue of 0.616, and the relative ordering of sites closely resembled that produced by DCA (Fig. 2B, note orientation of the axes appears reversed in CCA relative to DCA, but axis orientation is arbitrary [Knox and Peet 1989]). Given the similarity between the ordering of sites along the first axis in both ordinations, one can assume that topography also significantly explains variation among sample and species scores in the first axis of the DCA ordination.

Axis interpretation: disturbance

In Fig. 2B, the significant first axis is plotted for ease of viewing against a nonsignificant axis. The vectors indicate the strength and direction of the topographic/moisture and disturbance gradients. Lack of significance of the axis defined principally by disturbance in the CCA analysis may be due to the coding of disturbance, which was based only on known anthropogenic effects (time since selective logging or clearing), and did not consider the contribution of natural disturbance (e.g., size and shape of stream beds and treefall gaps).

Ridge areas are likely to experience different natural disturbance regimes from stream areas (Swanson et al. 1988), and the intensity of anthropogenic disturbance from selective logging probably also differed between these two habitats. In addition, the large separation of

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**Fig. 1.** Sample effort curves for all habitats, disturbed habitats (logging trails), stream habitats, and ridge habitats. Curves began to level off in all habitat types after 20 person-hours of sampling time per transect (five sample periods consisting of one morning and one afternoon hour).
ridge vs. stream sites in the DCA ordination in Fig. 2A indicates that the butterfly assemblages occupying ridge vs. stream sites are distinct. Given these considerations, a separate CCA analysis was conducted for each of two site clusters defined empirically by DCA axis 1 (Fig. 2A); sites with values $<-100$ (ridge cluster) and sites with values $>+100$ (stream cluster).

The ridge cluster contained all of the new and old ridge sites, plus one of the logging trail sites (D1). The first axis of CCA of the data from these sites alone was significantly related to the disturbance variables ($\lambda = 0.469, P = .01$), but not to the six other environmental variables. In contrast, the stream cluster, containing two of the new stream sites and all of the old stream sites, showed no significant relationship to disturbance in CCA analysis ($\lambda = 0.541, P = .32$), or to any of the other environmental variables.

Identifying butterfly indicator species assemblages

In correspondence analysis, species ordination scores represent the optimal localization of the species within the ordination space, and the abundance or probability of occurrence of a species decreases with distance from the location of its score. I used the DCA species ordination diagram as an aid to find assemblages of species characteristic of points along the topographic/moisture and disturbance gradients.

Fig. 3 shows the DCA species scores for the 12 most abundant species (the scores are separated by sex as in the analysis, but only the male score is shown if male and female scores are side by side). The ordination space is identical to that shown for the sites ordination (Fig. 2A), and the location of habitat clusters (new stream, old stream, etc.) is indicated in the diagram. A complex of species, including *Henotesia* ?iboina and *Strabena andriana* (Nymphalidae: Satyrinae) and *Sarbia* ?perroti (Riodinidae) had ordination optima within the ridge cluster. Another species complex, including *Henotesia* ?angulifascia, *H. ?undulosa* (male), *H. ?subsimilis* (male), *H. ?anceps* and *H. ?pauper*, had ordination optima within the stream cluster.

The relationship between the DCA ordination scores and species distributional data can be seen by comparing Table 2 with Fig. 3. *Henotesia* species ?anceps, ?subsimilis, and ?pauper were each consistently found at the new stream sites, but were almost never found at the old stream sites. Their ordination optima fall within the domain of the new stream sites. Male *H.

<table>
<thead>
<tr>
<th>Species†</th>
<th>S1</th>
<th>S2</th>
<th>S3</th>
<th>OS1</th>
<th>OS2</th>
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<tr>
<td><em>Henotesia</em> ?anceps</td>
<td>18</td>
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<tr>
<td><em>Henotesia</em> ?undulosa</td>
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<td>0</td>
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<td>6</td>
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<tr>
<td><em>Henotesia</em> ?angulifascia</td>
<td>5</td>
<td>5</td>
<td>3</td>
<td>29</td>
<td>18</td>
</tr>
</tbody>
</table>

* S1–S3: new stream sites; OS1–OS2: old stream sites.
† See Appendix footnote † for information on Malagasy butterfly taxa.
?undulosa were most frequently observed at new stream sites, but also regularly occurred at old stream sites, and its ordination optimum is intermediate in position between the new and old stream domains. The female also frequented disturbed sites, and its optimum reflects this. While H. ?angulifascia was observed frequently at new stream sites, its position within the old stream domain reflects its extreme dominance at these sites (comprising 44–66% of the total butterfly abundance).

Interpreting the species ordination diagram

Typically, many of the species found at the center of the DCA ordination are ubiquitous species, bimodally distributed otherwise departs from a unimodal response curve (Ter Braak and Prentice 1988). In Fig. 3, Mylothis phileris Pieridae is a good example of this phenomenon. Despite its placement in the domain of the disturbed sites, this species occurred abundantly in all of the habitat types sampled.

In contrast, species found at the edges of the ordination diagram are frequently “rare” species, and occur there because they are associated with “extreme” environmental conditions (Ter Braak and Prentice 1988). In Fig. 4, the species scores of the “rare” species (i.e., species individually contributing <1% of the total sample abundance) are plotted. Fig. 4A shows scores for those species whose “rarity” was known by independent observations to be due to sampling error (i.e., species that were frequently observed in one or more of the habitat types at the study site but were not frequently captured during the study sample periods; C. Kremen, personal observations). As expected, ordination scores for these species were spread over the entire ordination diagram due to random sampling error.

Ordination scores for the remaining “rare” species (those that appeared to be low in abundance during both 1988 and 1990 field seasons) are plotted in Fig. 4B. A subset of these species had scores at the edges of the ordination diagram. In particular, several Henotesia species were noted that were found only at either old or new ridge sites (see H. ?parva, H. ?obscura, and H. ?turbans). The distributions of these species between sites were consistent although the number of observations was small, and independent records of these species support their habitual occurrence at these or similar sites. H. ?parva and H. ?obscura occurred at both the old ridge sites, and nowhere else, while H. ?turbans occurred at two out of three of the new ridge sites, and nowhere else. These species might qualify as either genuinely rare species characteristic of these habitats, or as species that were sampled at the edges of their range. In the latter case, the two species found only at the old ridge sites (H. ?parva and H. ?obscura) may have optima under less disturbed conditions (e.g., primary forest). Further work could distinguish between these two hypotheses to determine whether these species would make good indicators of undisturbed conditions.

**Dominance and diversity characteristics relative to DCA ordination**

Characteristic levels of dominance were associated with different site types. In and of itself, ranking sites by dominance (Berger-Parker index) organized the sites: low dominance characterized newly disturbed sites plus new stream sites; and high dominance characterized new ridge, old ridge, and old stream sites (Fig. 5A). Species richness was negatively correlated with dominance (Fig. 5B, r = −0.56, P = .047). No density compensation was observed; sites that were low in species richness did not have a compensatory increase in abundance of one or more species (Fig. 5C).

The dominance index distinguished significantly (ANOVA, Berger-Parker, F = 15.504, P = .0292) between butterfly species assemblages found at old vs. new stream sites, although species richness did not distinguish between the two types of sites (F = 1.681, P = .2856). In contrast, dominance did not distinguish between old and new ridge sites (F = 2.516, P = .2109), although species richness did (F = 30.943, P = .0115).
Environmental patterns indicated by plant species abundance data

In comparison with the butterfly DCA ordination, the plant DCA ordination was less successful in revealing the known environmental gradients (Fig. 6). To test whether plant community data were significantly related to the two known gradients, a CCA was performed using the topographic and disturbance variables (Table 1). The first CCA axis was not significantly related to either of these variables ($r = 0.399$, $P = .47$), and there was therefore no need to look at subsequent axes.

Relationship between butterfly species assemblages and plant communities

To examine the relationship between the butterfly and the plant ordinations, DCA site scores from the plant ordination were also included as one of the environmental variables for CCA analysis of the butterfly data; however, no significant relationship was found. As noted earlier, none of the other environmental variables related to vegetative diversity or structure were found to explain significantly the variation along CCA axes of the butterfly data.

To see whether local butterfly diversity was a good indicator of plant species richness or diversity, I used linear regression. Butterfly species richness was not a good predictor of either plant species richness (Margalef’s index, $F = 0.608$, $r^2 = -0.05$, $P = .45$) or plant species diversity (Shannon’s index, $F = 0.257$, $r^2 = 0.02$, $P = .62$). However, butterfly richness showed a weak relationship with average floral abundance ($F = 4.349$, $r^2 = 0.28$, $P = .061$) and was significantly related to average floral richness ($F = 18.65$, $r^2 = 0.63$, $P = .0012$) (Fig. 7). Floral richness and abundance were both highest in sunny regions by the larger streams (S2 and S3) and the logging trails (D1–D3), which also had the greatest butterfly species diversity and abundance (Fig. 5C).

DISCUSSION

Ordination techniques are exploratory tools that have frequently been used in community ecology to reveal environmental patterns and to generate ecological hypotheses based on the covariation of species distributions (Gauch 1982a, b, Digby and Kempton 1987). As techniques that examine the relationship between species distributions and environmental gradients, they are inherently useful for testing the indicator properties.
of a group of organisms, especially in poorly known systems. However, limitations of these techniques, including ambiguity of interpretation (Gauch 1982a) and lack of statistical tests, have perhaps prevented a greater utilization (Ter Braak and Prentice 1988). Recent advances that allow bootstrapping of DCA (Knox and Peet 1989 and R. G. Knox, personal communication) and CCA (Ter Braak and Prentice 1988) ordination axes have opened the door for significance testing, and can now be used creatively for testing as well as generating hypotheses. In particular, this facility greatly enhances the utility of ordination techniques for testing

the indicator properties of an assemblage of species and selecting appropriate sets of indicators from within the larger group.

Why and what to monitor?

Before elaborating on a protocol for testing and selecting indicators for natural areas monitoring (see below), it is important to establish the goals of a monitoring program and the desirable qualities of indicators. The general function of a monitoring program is to provide data that can be used for the scientific management of reserves for restoration or maintenance of the composition, structure, and function of natural ecosystems (Franklin et al. 1981, Noss 1990). An ideal monitoring program should therefore be made up of two components: (1) a descriptive component that establishes the baseline in a large, buffered, “pristine” natural area, including study of “normal” fluctuations over time, and (2) an experimental component that evaluates the effects of specific management activities over time using standard ecological experimental design. The details of a monitoring program will be highly specific to a given reserve, depending, for example, on its “naturalness” (how different it is from baseline), size, shape, biotic and physiographic heterogeneity, and on the impacts of anthropogenic and natural disturbance regimes, global changes, and management practices.

Properties of species or species assemblages can serve as indicators at genetic, population–species or community–ecosystem levels for monitoring composition, structure, and function in natural areas; however, many other indicators, both biotic and abiotic, are available for monitoring natural ecosystems at all biological levels (genetic to landscape) (Noss 1990). It is therefore important to determine the unique value of monitoring properties of species or species assemblages. First, monitoring species or species assemblages allows the most direct assessment of fundamental management goals such as the maintenance of viable populations and native biodiversity (Noss 1990). Second, monitoring at this level can provide direct or indirect assessments of ecological function (Gilbert 1980), although such information is likely to be narrowly focused (e.g., studies of specific ecological interactions, as in a predator–prey cycle) as compared with ecosystem studies at the landscape level (e.g., studies of functional processes, as in nutrient cycling).

When monitoring of populations or communities is conducted within the context of known environmental change (e.g., due to human or natural disturbances, global changes, or management practices), it can then provide a basis for improved management decision-making. There is little point in using indicators to measure an environmental change that can be measured directly using a pH scale, thermometer, or LANDSAT image, for example; instead, the purpose and value of using indicator organisms is to observe the biotic re-

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**Fig. 5.** Characteristics of butterfly diversity and structure of species assemblages at each site. (A) Dominance (Berger-Parker index) is lowest in the sunniest sites: streams in new forest (S) and disturbed sites (D). R = ridge sites; OR = old ridge sites; OS = old stream sites. (B) Species richness is negatively correlated with dominance \((r = -0.56, P = .041)\); sunny new streams and disturbed sites have the highest species richness. (C) Species richness is positively correlated with the total relative abundance of butterflies at each site \((r = 0.786, P = .001)\). At the spatial scale of this study, no density compensation for butterfly abundance was observed.
sponse to environmental stress, and especially to provide early warnings of natural responses to environmental impacts (Noss 1990). If studies are well designed, such information should also be useful in developing or refining restoration or management plans, and in monitoring the success of these efforts.

An indicator should "be capable of providing a continuous assessment over a wide range of stress" (Noss 1990: 357). Inherently, species assemblages should provide finer gauges of biotic responses than single species, just as precision is increased by placing finer gradations upon a scale. Certain properties of assemblages can be defined that might enhance the likelihood of wide-scale sensitivity to a specific environmental stress. For example, assemblages that include species covering a wide range of spatial heterogeneity (low to high vagility, narrow to broad distribution) and micro-habitat specificity (specialist to generalist), and that collectively occupy a broad range of micro-habitats, might be expected to display a greater range of sensitivities to habitat fragmentation and/or modification over time (Terborgh 1974).

For completeness, a monitoring program might use separate indicator species assemblages representing different taxonomic and/or functional groups to monitor different environmental impacts, as will be dealt with more fully in a separate paper. This paper is concerned instead with testing the indicator properties of a uniform taxonomic-functional group, and selecting a subset of appropriate indicators from within the group for addressing a specific management problem. As the protocol summarized below is widely applicable to different species groups, as well as different spatial scales and environmental gradients, its objective is to encourage the testing, selection, and monitoring of multi-species indicator groups from among a broad range of taxonomic groups. This protocol can be used in the absence of detailed autoecological or community data, and is probably most appropriate to situations where such data are lacking.

Establishing the indicator properties of a species assemblage

The first step in establishing the indicator properties of a species assemblage is to ask whether the chosen group of species is appropriate for indicating a specific ecological pattern at the desired spatial and/or temporal scale. This can be accomplished using indirect gradient analysis techniques such as DCA, which are based simply on patterns of species covariation (Knox and Peet 1989). The pattern of species covariation ei-

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Fig. 6. Detrended Correspondence Analysis (DCA) ordination of sampling sites by plant community data. As in Fig. 2, = sites located in the old forest; OR = old ridge, OS = old stream. = sites in the new forest; R = ridge, S = stream. = sites along logging trails; D = disturbed. Eigenvalues are: axis 1, \( \lambda = 0.483 \); axis 2, \( \lambda = 0.444 \). Canonical correspondence constrained along topographic and disturbance variables did not produce a significant first axis.

Fig. 7. Butterfly richness in relation to floral abundance and richness. Floral abundance and richness values are averages of four phenological samples taken during the study period. D = disturbed areas (logging trails), R = new ridge sites, OR = old ridge sites, OS = new stream sites, OS = old stream sites. (A) Butterfly richness was weakly dependent on average floral abundance (\( r^2 = 0.28, P = .061 \)). Sunny areas (D1–D3 and S1–S2) had the greatest floral abundance. (B) Butterfly richness was significantly related to average floral richness (\( r^2 = 0.63, P = .0012 \)). Sunny areas had the greatest floral richness.

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ther will or will not reflect the ecological pattern or environmental impact of interest. More than one potential indicator property can be assessed simultaneously, dependent on the sampling design, as for topography and disturbance in this study. In addition, the results of a DCA ordination analysis may suggest other indicator properties of the assemblage associated with environmental gradients or factors not explicitly considered within the study design.

Alternative hypotheses of indicator properties can be tested in the second step, replacing the need for ad hoc arguments to justify indicator properties. A direct gradient analysis technique such as CCA can be used to interpret the ordination axes by looking at the significance of correlations between species and environmental data. The CCA analysis can be used to match a species assemblage to environmental factor(s) for which it is a good indicator.

Once the indicator properties of an assemblage are established, the ordination analyses can be employed at two biological levels for monitoring over time. At the community level, the entire assemblage can be monitored, and CCA ordination analysis used to track the community response to the environmental factor of interest (for an example of time-series analysis using ordination, see Wiegleb et al. 1989). For example, bird assemblages known to be good indicators of habitat heterogeneity associated with elevation could be monitored in permanent plots along an elevational gradient over a period of years. Each year’s data from a sample plot would then be ordinated as a point in sample space. Imagine that with time each plot shifted along the first CCA axis in the direction of an elevation loss. Therefore, as the true elevation at a plot is unchanged, this indicates that the new species composition at the plot is more similar to lower elevation sites from earlier years. Such a result might be predicted, for example, due to the effects of global warming. As temperatures increase, low-elevation faunas adapted to warmer climates can be expected to replace high-elevation faunas (Murphy and Weiss 1991). The effect of year on changes in species composition along the gradient can also be tested for significance.

At the population/species level, the ordination diagrams can be used to select a subset of the species as indicators for more intensive monitoring (e.g., studies of spatial dispersion, population fluctuations, adaptation, gene flow, Noss 1990). In DCA and CCA ordination diagrams, species placements within a plot represent the optima of unimodal species distributions with respect to environmental gradients (Ter Braak and Prentice 1988). In choosing potential indicator species, one looks for species whose optima fall at reference points for the environmental gradient of interest. The use of indirect (DCA) vs. direct (CCA) gradient ordinations should depend on knowledge of the system. CCA ordination plots should be chosen if the importance of a particular gradient is well established, since species ordination values would then be constrained along the gradient of interest. However, if knowledge of environmental gradients is minimal, DCA plots might be preferred, because this unconstrained ordination may show the response of species to environmental gradients not explicitly considered within the study design.

The selection of indicator species from an ordination diagram of species scores represents a hypothesis about the properties of these species in relation both to the entire assemblage and to environmental gradients. The reliability of these choices can be assessed through either spatial or temporal replication of the study, or through autocorrelational studies.

Rare species contribute little to establishing the ordination axes (Ter Braak and Prentice 1988). However, it may be useful to identify such species, because their “rarity” may result from being sampled far from their own environmental optima. Presence, in this case, may indicate the existence of a longer gradient or a rare habitat type (Terborgh 1974, Rabinowitz et al. 1986). In an ordination diagram, such species tend to be found at the edges of the diagram (e.g., Fig. 4B). In contrast, ordination scores of species whose rarity results simply from random sampling error will be randomly spread across the diagram (e.g., Fig. 4A). In this study, several uncommon species associated only with old ridge sites (Henotesia ?parva and H. ?obscura) were located at the edges of the ordination diagram (Fig. 4B). These species may prove to be indicators for more undisturbed conditions (e.g., primary forest) than were included in this study.

**Indicator properties of a butterfly species assemblage**

I used the protocol described above to assess the indicator properties of a butterfly assemblage from a rainforest habitat in Madagascar. The study looked at the response of butterfly communities to variation along topographic/moisture and disturbance gradients in space. Potential indicator properties established in this “snapshot” spatial study would, by inference, be likely to be valid for temporal variation in these same environmental factors.

The DCA ordination of the butterfly data reflected local patterns of habitat heterogeneity associated with both the topographic/moisture and disturbance gradients, which suggests that this assemblage could be considered as an appropriate indicator of these types and this spatial scale of habitat heterogeneity. However, Monte Carlo tests of CCA axes were significant only for the axis principally defined by topography/moisture. Since the influence of topography was so strong, it may have masked less obvious gradients related to disturbance at each end of the topographic scale. For example, in the DCA ordination shown in Fig. 2A, “gradients” of disturbance ran in opposite directions in the ridge vs. the stream clusters. By an-
alyzing each cluster separately using CCA, it was possible to assess the significance of disturbance in isolation from topography. Disturbance was then found to be a significant variable in CCA ordinations of the ridge cluster, although not for the stream cluster.

To select indicator species I used the DCA ordination, since the knowledge of one gradient of interest, disturbance due to anthropogenic effects, was limited to the historical record of length of time since selective logging. In general, small assemblages of species rather than individual species could be said to characterize a particular point on a gradient (see the Appendix for species names). Similarly, taxocene composition, including level of dominance, identity of dominant species, and species richness, were more characteristic of particular habitat types than were individual species.

Many of the species identified as potential indicators (Fig. 3, 4B, and Appendix) are members of the genus Henotesia (Satyrinae), a species-rich genus containing 41 endemic and one nonendemic species in Madagascar (D'Abrera 1980). The members of this genus and its tribe (Mycalesini) exhibit some primitive characteristics in Madagascar linking them with Indo-Malayan rather than African relatives, and suggesting an early arrival in Madagascar (late Cretaceous or early Tertiary), followed by a long period of evolution in isolation (Miller 1968). This genus appears to have experienced an extensive evolutionary radiation in Madagascar and exhibits high beta-diversity. Many species appear to be restricted to particular forest micro-habitats (canopy vs. understorey, ridge vs. riparian), elevational zones, and successional stages, while others are more widely distributed, both in range and habitat type (this study, R. Van Buskirk and C. Kremen, unpublished data). This range of habitat specificity and the diversity of micro-habitats occupied by members of this genus may allow them to serve as an indicator assemblage with a wide range of sensitivities to habitat fragmentation and/or modification. Species-rich genera resulting from evolutionary radiations and having high beta-diversity may frequently make good indicator assemblages, as will be elaborated more fully elsewhere.

Butterflies as ecological indicators

Other authors have suggested that butterfly diversity could provide an index of plant diversity, since larval host-plant relationships are frequently so specific (Murphy and Wilcox 1986). Interestingly, in this study, butterfly community data were not found to be a good indicator of any environmental gradients related to measured parameters of vegetation structure, plant diversity, or community composition. Nor was butterfly species richness a good predictor of plant richness or diversity at the spatial scale of this study.

While butterfly diversity was not correlated with plant diversity in general, it was strongly correlated with the average diversity of plants in flower. Regions of high floral and butterfly diversity also supported a higher total abundance of butterflies (compare Figs. 5C and 7B). Not surprisingly, these sites corresponded to the sunniest, most disturbed areas (logging trails and good-sized streams). Judging by both abundance and species composition of butterflies at these sites, these abundant and diverse nectar resources may have attracted forest species to the forest edge (Lovejoy et al. 1986; Brown, personal communication), so that the pool of species observed to occur there included both resident disturbed area species (Pieridae: Eurema floricola; Lycaenidae: Cacyreus darius, Leptotes rabenafer; Nymphalidae: Junonia eurodeo) and visiting forest species (Papilionidae: Papilio delalandei, P. oribazus; Nymphalidae: Pseudacraea lucretia). While forest edges had higher diversity than either disturbed or forest habitat alone, massive, widespread clearing of forests to create edges would not enhance landscape-level diversity, since it reduces habitat area for forest specialists (e.g., Henotesia lanceps, H. ?parva; see also Wilcove et al. 1986).

In this study, significance tests of CCA ordination axes allowed evaluation of the hypothesis that butterflies are good ecological indicators (Gilbert 1980, 1984, Pyle 1980, Brown 1982, Murphy et al. 1990). Are butterflies in fact good ecological indicators? In some sense, the presence, absence or abundance level of any organism must always indicate something about the biotic or abiotic environment, and the question is therefore trivial. The question should be: what does the presence/absence/abundance of species $X$ or the composition of species assemblage $Y$ indicate? In this study, butterfly taxocene composition proved to be an excellent indicator of heterogeneity due to anthropogenic disturbance by logging (although coding of disturbance levels may have been a factor obscuring the relationships between the disturbance gradient and butterfly data), and a poor indicator of plant species richness and diversity. Given their strong response to topographic/moisture effects, one likely utility of butterflies as ecological indicators will be for monitoring the biotic response to climate change, as has also been suggested elsewhere (Weiss and Murphy 1988, Murphy et al. 1990).

Conclusion

The modification of natural environments is accelerating at an alarming rate, and the responses of organisms to these changes provide information not only on the viability of global life support systems, but also on the efficacy of our protected area networks in maintaining biological diversity. A substantial research effort is needed to select appropriate indicators and to design monitoring programs. Ordination techniques provide a simple method for establishing the indicator properties of target assemblages of organisms. Continued use of these techniques in testing properties of assemblages and selecting multi-species indicator groups for intensive monitoring could increase the tax-
ic diversity and sensitivity of natural areas monitoring programs.

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### APPENDIX

Butterfly and skipper species list for the study.

<table>
<thead>
<tr>
<th>Species</th>
<th>Potential indicator*</th>
<th>Species</th>
<th>Potential indicator*</th>
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<tr>
<td>Papilionidae</td>
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<td>Graphium cyrus</td>
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<td>Acraea strattipocles</td>
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<td>Catopilia thauruma</td>
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<td>Neptis kikideli</td>
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<td>Neptis saclava saclava</td>
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<td>Leptosia mupta viettei</td>
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<td>Satyrinae†</td>
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* S = stream; OS = old stream; R = ridge; OR = old ridge.
† The taxonomy of some Malagasy butterfly taxa is poorly established. Species names preceded by a question mark refer to morphospecies and represent an attempt to synonymize these forms with established names.