Ecological Applications, 4(4), 1994, pp. 833–843

USING BIODIVERSITY DATA TO ASSESS SPECIES–HABITAT RELATIONSHIPS IN GLACIER NATIONAL PARK, MONTANA[1]

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Abstract. Biodiversity surveys are becoming increasingly popular. However, standard analysis techniques for these data have not yet been developed. This paper explores the use of multivariate ordination techniques for assessing species–habitat relationships using biodiversity data. The research was conducted in Glacier National Park, Montana, and birds and butterflies were chosen as the taxonomic groups of study. Biodiversity assessment sites were established throughout a range of habitats and monitored from 1987 through 1989. Presence/absence sampling over the total number of sampling sites was used to classify species commonness and rarity. Approximately 86% of the historically recorded butterflies and 70% of the historically recorded bird species have been observed in the 3 yr of sampling. During the 3 yr of this study there was a striking continuity of species richness per site. There was also a striking overlap between sites that support high species diversity and sites that support rare species. Principal components analysis and cluster analysis worked well in discerning species–habitat relationships. Elevation, structural diversity of the site, and moisture were the major factors explaining species distributions. A chi-square analysis also provided some insights into species–habitat relationships, showing birds were more habitat specific than butterflies. Habitat diversity analyses demonstrated a positive but nonsignificant correlation between remotely sensed spectral-class diversity of a site and species richness for both birds and butterflies. Aspect, slope, and elevation diversity had a negative or negligible relationship with species richness.

Key words: biodiversity; birds; butterflies; cluster analysis; environmental gradients; Glacier National Park, Montana; habitat specificity; multivariate analysis; PCA; species–habitat relationships; species richness.

INTRODUCTION

The recent interest in preservation of biodiversity, both in the U.S. and in tropical regions, has sent scientific teams to the task of collecting volumes of data on species, community, and genetic diversity. Government officials have also become involved (OTA 1987). However, if we are to conduct rigorous monitoring of species distribution patterns, it would be valuable to go a step beyond simply creating species lists. Understanding the environmental parameters that define species distributions is the second component of biodiversity assessments.

This paper is an example of the methods that can be used to survey species diversity and assess species–habitat relationships using Glacier National Park, Montana, USA, as a case study. Our research focused on evaluating the species diversity patterns of two taxonomic groups, birds and butterflies. The ultimate goal was to be able to track patterns of changing distribution and abundance in several "indicator" taxa into the future (see Kremen 1992). The immediate goals of this project were to choose representative taxa that could be inventoried and monitored and serve as indices or "indicator taxa" of the state of overall biological diversity in Glacier National Park and to establish an appropriate sampling regime and methodology (see Debinski and Brussard 1992). The secondary goal was to test the use of multivariate analysis in discerning relationships between species assemblages and environmental parameters (e.g., elevation, moisture, topography).

Vertebrate biologists have been using knowledge of an animal's habitat to predict its presence or absence for decades (e.g., Baker 1956, Armstrong 1972). More recently, Green (1971) used multivariate statistical approaches to identify significant ecological factors (e.g., sediment particle size, nutrient concentrations, and depth) separating species distributions for freshwater mollusks. James (1971) and Kikkawa et al. (1978) used similar techniques to describe the distribution of birds relative to habitat structure. Owen (1990) found elevation, productivity, and temperature to be good predictors of mammal species richness in Texas. These approaches have also been applied to bioclimatic models for predicting species distributions (Walker 1990, Lindenmayer et al. 1991). Here we limit our objectives to descriptive, rather than predictive, analyses of species relationships with environmental parameters.

[1] Manuscript received 3 March 1993; revised 15 October 1993; accepted 9 November 1993.

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Specific questions and issues regarding species diversity that were addressed in this study are: (1) What is the distribution of bird and butterfly species in Glacier National Park? (2) How adequate are current park species lists as historical species presence/absence documentation? (3) Are predictable species assemblages routinely found in certain habitat types? (4) Is there a relationship between high species diversity and the number of rare species present? (5) Is there a correlation between habitat diversity and species diversity? With respect to monitoring and management: (6) How much variation in species presence and absence is there between years? and (7) What areas of the reserve merit special protection, intervention, or efforts to manage biodiversity?

METHODS

Census sites

During 1987 a pilot project was conducted for biodiversity assessment of butterflies and birds. A subset of the 84 areas surveyed in 1987 were chosen for more detailed study during 1988 and 1989: 35 sites for birds and 24 sites for butterflies. Each of the sampling sites was 1 km^2 in size and defined by Universal Transverse Mercator coordinates on United States Geological Survey (USGS) topographic maps. Sites were selected primarily on the basis of their position in the topographic/elevational gradients in Glacier National Park (GNP) and described within very broad habitat types (see *Habitat characterization in sample sites,* below).

This method of site selection was used for two reasons. First, temperature and moisture gradients, quite independent of habitat types defined by vegetation, are often of primary importance in determining the distribution and local abundance of most terrestrial plant and animal taxa (e.g., Whittaker 1952, Terborgh 1970, Brussard 1985). Temperature is correlated with elevation, and moisture is correlated with both elevation and topography (i.e., slope, aspect, and exposure); both factors affect the metabolic functions of animals either directly or indirectly. Second, vegetation is often distributed as a continuum, so it is very difficult to divide into discrete units, particularly at a scale that is biologically meaningful to each species in groups as diverse as birds and butterflies.

This procedure allowed each site to be located on two-dimensional graphs representing the available "ecological space" in GNP using elevation as the ordinate and moisture conditions (ranging from hydric to xeric on the flats and based on aspect, corrected for slope and exposure, on mountainsides) as the abscissa. Additional sites were then chosen to maximize the full range of topographic/elevation conditions in the park. Sample plots of 1 km^2 were chosen on the basis of field experiences in 1987 (Debinski 1991). For a description of each of the sites, see Debinski (1991).

Birds were censused aurally and visually at a given sample site by walking through the 1-km^2 area for 2 hr between 0500 and 1000. Butterflies were censused by netting for 20 min and releasing in three separate 50×50 m^2 subplots in the plot between 1000 and 1600. These sample periods were established empirically by plotting the number of species recorded against duration of sampling period. The average duration at which the species–effort curve flattened out (no more species added) was considered to be the optimal sampling period. Butterfly sites were sampled three times a year and bird sites were sampled twice. Questionable butterfly species assignments were verified by S. Kohler, and bird identifications were discussed by two or three observers at the time of census.

Although community ecology stresses sampling sites that are homogeneous in structure and composition (Gauch 1982), the methodology used herein maximized habitat diversity within the 1988–1989 sites. This was done for two reasons. First, this study was designed to inventory species occurrences across a very large area, so site homogeneity was sacrificed to maximize broad-scale coverage. Second, it was observed in 1987 that species diversity tended to be much higher along ecotones, so a number of ecotones were included in many of the sites. Nevertheless, broad habitat-type characterizations were still possible at each site.

This particular design produces a certain type of bias: vegetation types or "ecological space" defined by position on the topographic/elevational gradient are not sampled in direct proportion to their frequency of occurrence in GNP. In attempting to maximize the opportunity to sample rare species and to increase coverage of "ecological space" along temperature and moisture gradients, some of the rare habitats were overrepresented in our sample relative to their frequency in the park; a species which is rare in the sample may be even more rare within the park.

Habitat characterization in sample sites

Although several methods of habitat categorization were considered (Elton and Miller 1954, Bunce and Shaw 1973, Southwood et al. 1979), the technique eventually employed involved locating each site on a 7.5-minute scale USGS topographic map, recording its elevation, slope, and exposure, and making a brief and very general categorization of its habitat type. Terrestrial habitats usually are defined by vegetation, and vegetation can be classified either by structure (the horizontal and vertical occupation of space by plants) or by taxonomic composition. Our habitat classifications were very general, including only gross structural categories (e.g., forest, scrub, grassland), and consisted of the dominant plant species at each vegetation layer (e.g., upper canopy, lower canopy, shrub, and groundcover). Butterfly sites included mesic, hydric, and xeric meadows throughout a range of elevations from 2250 m to >4375 m. Bird sites included the areas described above in addition to riparian areas and lodgepole pine

(*Pinus contorta*), spruce–"fir" (*Picea engelmannii–Pseudotsuga menziesii*), aspen (*Populus tremuloides*), subalpine fir (*Abies lasiocarpa*), and "cedar"–hemlock (*Thuja plicata–Tsuga heterophylla*) forests.

The moisture gradient classification was as follows: meadows with standing water or water flowing through them throughout most of the summer were classified as "hydric" (most of these are early successional meadows, previously ponds or lakes); "mesic" meadows had no standing water after spring snow melt, and usually had a diverse group of flowering plants and grasses; and dry, open meadows, characterized by open ground and sagebrush as the primary vegetation, were classified as "xeric."

Presence/absence sampling

Species diversity in a given area consists of two components: richness (the number of species present) and equitability (the evenness of their relative abundances) (Magurran 1989). In taxonomically well-known groups richness is relatively easy to estimate by a direct count of the species encountered, provided that the sampling effort is sufficient. However, most taxa are very difficult to sample in such a way that the proportions of individuals per species in a sample are representative of their true abundances in the community (e.g., Shapiro 1975, Verner 1983), making an accurate estimation of equitability difficult. This is particularly true in extensive surveys where habitat differences exacerbate differences in detectability. For these reasons only species occurrences were recorded at a sampling site. Thus, the diversity index was "*S*," the observed number of species.

Presence/absence data have many advantages for extensive surveys. First, the bulk of the information lies in qualitative differences in species composition (Greig-Smith 1971). Second, sampling for absolute, or even relative, species abundances requires so much time that the number of samples obtainable drops drastically (Poore 1962). Finally, there seems to be general agreement that the observed number of species is the simplest, most practical, and most objective measure of species diversity (Hurlbert 1971, Whittaker 1972, Peet 1974).

Evaluating biodiversity data

Species lists.—Our construction of species lists followed four steps. (1) A data base was constructed detailing baseline distributional data on all species relative to each sampling site and each census.

(2) Historic species lists were compared to current biodiversity census results to identify any discrepancies (e.g., species not seen in our sampling or species never previously observed in the park). Park records were compared to our species lists to determine whether species diversity has changed over time. The historic species lists were *Glacier National Park Birds—Field Checklist* (Shea 1983), *Butterflies of Glacier National Park* (S. Kohler, *unpublished manuscript* [1980]), and a list of butterflies compiled by a naturalist in 1950. Butterfly species lists were taxonomically standardized using Scott (1986).

(3) Frequency of occurrence data were analyzed to identify species that are restricted to specific habitats (e.g, alpine, riparian, or successional habitats).

(4) Sites were compared to identify "hot spots," sites that support the highest species richness. Initial analysis of site-specific species diversity was conducted by combining all temporal replicate censuses at each of the sites.

Species assemblages and habitat.—(1) Principal components analysis (PCA) is an ordination technique that is used to identify major axes in a multidimensional "swarm of data points" (Pielou 1984). Each axis is based upon the Euclidean distance metric, the sum of the squared distance from the axis projected through the data points (Wartenberg et al. 1987). PCA was conducted to determine some of the environmental variables affecting species distributions using the presence/absence data of species (all replicates during a year combined for a site) as variables and census sites as observations. The principal component (PC) site scores were then plotted as two-dimensional scatter plots. Using habitat types of site groupings and knowledge of habitat requirements of high-ranking species at the extremes of the axes names for the axes were inferred. For example, if high-elevation sites were found at one extreme of an axis and low-elevation sites were found at the opposite end of the axis, the axis was inferred to be elevation. If our subjective axis descriptions represented quantifiable variables, correlations between site scores and these quantifiable factors (e.g., elevation) were calculated to test our interpretations (Ter Braak and Prentice 1988). Cluster analysis of PC scores for sites was also conducted to construct dendrograms of site relationships. Due to the difference in methods between 1987 and 1988–1989, the statistical analyses focus upon the 1988 and 1989 data. Plots are included for the 1988 data, while the 1989 data are described verbally.

PCA is not generally used on a species × site matrix of presence/absence data. Correspondence analysis (CA) or detrended correspondence analysis (DCA) are often advocated (Hill and Gauch 1980). However, CA has problems with distortions at the ends of the axes, and detrending techniques have been criticized (Wartenberg et al. 1987). The "arch effect" seen in PCA is an accurate representation of the data. PCA can be performed on binary data, provided that association tests based on assumptions of normality are avoided (Green 1979).

(2) Chi-square analysis was conducted to determine which species, if any, exhibited a tendency to be associated with a particular habitat type. Each site was coded with respect to habitat type (hydric, mesic, xeric,

TABLE 1. Total numbers of species of butterflies observed at census sites, by year, in Glacier National Park, Montana, USA. ··· = site not sampled.

Site*	N†	No. species per site 1987	1988	1989	1989‡
Spot Mountain	10	···	31	20	20
Christensen Meadow	9	27	30	24	23
Hidden Lake	10	11	20	17	17
Preston Park	12	4	19	5	5
Belly River Campground, Canada	4	···	19	19	19
Baring Creek	6	···	18	17	16
Sullivan Meadow	8	18	18	20	18
Lone Pine Prairie	5	13	17	22	18
Stony Indian Pass	6	7	17	8	8
Granite Park	7	···	17	14	14
Hidden Meadow	4	···	16	20	17
Wilbur Creek	5	···	16	16	16
Two Dog Flats	3	11	15	20	20
Big Prairie	4	3	14	15	15
McGee Meadow	6	3	13	19	14
Middle Fork of Flathead River, West Glacier	2	···	13	···	···
Scenic Point	4	8	12	16	16
Flattop Mountain	3	7	12	4	4
Rocky Knob	5	···	12	16	16
Desantos	5	···	11	18	18
Fifty Mountain	6	4	10	4	4
Route 8 burnscar	3	···	10	16	16
Saint Mary Lake	3	4	9	22	14
Round Prairie	4	5	7	18	16
Mud Creek		···	···	9	9

* Listed in declining order of species richness in 1988.
† N = the total number of census replicates in 1988.
‡ The species richness standardized by using only two temporal replicates (the first two censuses) of three plots each (six total replicates).

or alpine meadow for butterflies and interior forest, forest/meadow edge, forest/riparian edge, or alpine for birds) and east–west orientation relative to the continental divide.

(3) Analysis of site-specific species richness (S) was tested for correlations with topographic diversity using a variety of habitat measures. GNP's Geographic Information System characterizes each 50 × 50 m plot of land across the entire park using 99 spectral classes (based upon ultraviolet reflectance from satellite photography [C. H. Key, *personal communication*]), aspect, slope, and elevation. Thus, each 1-km^2 plot is characterized by 400 50 × 50 m subplots, and each subplot is described by 102 variables. Separate Shannon–Wiener habitat diversity (H') indices [$H' = -\text{sum}(p_i \log p_i)$] were calculated for spectral class diversity, elevation diversity, slope diversity, and aspect diversity using the 400 subplots within each of the sites. Elevation was subdivided by 60-m (200 ft), slope by 10°, and aspect by 45° increments. These habitat diversity indices were tested for correlation with S among sites.

Monitoring.—Because the data on species diversity were recorded as presence/absence, the significance of changes in species occurrences between 1988 and 1989 were tested using contingency tables and G tests (Sokal and Rohlf 1981).

RESULTS

Species observed

Species lists.—Historically, a total of 89 butterfly species were recorded in the park after standardization using Scott (1986). There were 125 species of passerines and woodpeckers. All but three of the butterfly species had been seen previously within the last decade, most within the past few years. *Colias pelidne* and *Everes comyntas* have not been seen since 1935, and *Papilio bairdii* has not been seen since 1950. For details regarding the butterfly species list see Debinski (1993).

Fifty-seven of the 89 butterfly species were found during the 1987 censusing. Because of a late field season (starting 30 June), several of the early species were missed in 1987. Two species (*Lyceana hyllus* and *Nymphalis californica*), found in 1987, had not been recorded previously in the park, four species (*Callophrys sheridanii, Vannessa carye annabella, Satyrium saepium,* and *Neophasia menapia*) were first found in 1988, and three additional species were found in 1989 (*Callophrys polios, Speyeria aphrodite,* and *Danaus plexippus*). Due to taxonomic changes, some taxa previously recognized as species are now recognized as subspecies. Thus the total number of taxa observed during the 3-yr censusing was 84 and the new total for the Park is 97 taxa (see Debinski 1993 for more details).

Ninety-two of the 125 bird species were observed in

TABLE 2. Total number of bird species observed at census sites, by year. ··· = site not sampled.

Site*	Number of species 1987	1988	1989
Hidden Meadow	···	25	38
Desantos	···	20	32
Route 8 burnscar	11	19	30
Flathead Ranger Station	5	17	21
Middle Fork of Flathead River, West Glacier	23	17	27
Granite Park	···	17	9
Belly River Campground, Canada	21	16	···
Lone Pine Prairie	12	16	39
Saint Mary's Lake at Visitor Center	13	16	25
Sullivan Meadow	8	16	33
Lake McDonald	5	14	29
Dry Fork	···	14	···
Swan Lake	···	14	···
Quarter Circle Bridge	8	13	27
Logan Pass	6	13	12
Belly River Ranger Station	6	12	···
McGee Meadow	···	12	24
Christensen Meadow	14	12	28
Mud Lake	11	12	30
Apgar Lookout	9	12	19
Sperry Trail	11	11	19
Moose Flat	···	11	···
Ponderosa Pine Route 7	···	11	17
Packer's Roost	8	11	20
Sacred Dancing Cascade	15	10	18
Isaac Walton Ranger Station	11	10	34
Baring Creek	···	9	14
Rocky Knob, Flathead ranger station road	···	8	23
Anaconda Meadow	8	8	31
Avalanche Lake	···	8	17
Belly River near Cosley Lake trail	7	8	21
Mud Creek Meadow	···	7	32
Fish Lake	9	4	···
Two Dog Flats	···	···	32
Scenic Point	3	···	17
Round Prairie	5	···	···

* Listed in declining order of species richness in 1988.

the 3 yr of our biodiversity sampling. Eighty-seven of these species were seen in sampling sites; some were seen outside of the sampling region.

Analysis of rarity.—Some species are only found in a few habitats within the park. For example, birds such as Brown Creepers and Northern Waterthrushes showed rigid habitat requirements. Furthermore, butterflies such as *Euphydryas gillettii, Colias nastes, Vanessa atalanta,* and *L. hyllus* were only noted once in all of the 1987 sampling. Later seasons (1988, 1989) revealed a similar level of rarity. *E. gillettii* is habitat specific, while *C. nastes* is on the edge of its range.

Lone Pine Prairie, Sullivan Meadow, Hidden Lake, and Scenic Point (two meadows and two alpine sites) supported numerous rare butterflies in 1989 (rare defined as occurring in <3 (13%) of the 24 total sites) and also had a high species richness. No rare species were found in sites that had fewer than 14 total species.

Sites supporting rare bird species (occurring in ≤13% of the sites) included Desantos (8 rare species), Spot Mountain (3), Lone Pine Prairie (2), Hidden Meadow (2), Two Dog Flats (2), Logan Pass (2), and Saint Mary Campground (2). As in the butterfly data, sites that supported rare species also tended to have high species richness. Desantos was an outlier with respect to the number of rare species. This may be explained by the fact that it was the most northern site, and this aspen parkland habitat was not similar to any of the other sites.

Diversity hot spots.—The 1987–1989 sites were ranked with respect to species richness in 1988 (Tables 1 and 2). Three of the low-elevation sites were diversity hot spots for both butterflies and birds (Lone Pine Prairie, Sullivan Meadow, and Hidden Meadow). In some cases the same site ranked high in species richness for two consecutive years (Christensen Meadow for butterflies, Hidden Meadow for birds).

Direct interpretation of the butterfly species richness data is constrained, however, by differential sampling replication between some of the sites. Weather did not always permit three samples per season at each site. To correct for an effect of differential replication between sites, the butterfly data were reanalyzed, using

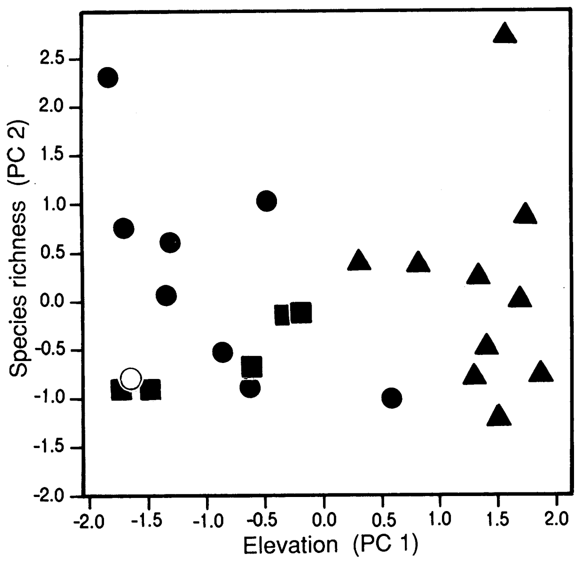

FIG. 1. Principal components analysis of sites in Glacier National Park, Montana, using presence/absence data for butterflies in 1988 (PC 1 vs. PC 2). Species frequencies are based upon repeated sampling at each site during the summer months. ● = mesic meadow, ▲ = alpine meadow, ■ = xeric meadow, ○ = hydric meadow.

data from only the first two censuses (Table 1: Column 1989‡).

Species–habitat relationships

PCA of species assemblages.—For butterflies in 1988, when plotting PC scatter plots (Figs. 1 and 2), the following descriptions were applied to PC axes 1–3: axis 1 = elevation of sites, axis 2 = species richness of sites, and axis 3 = moisture of site. Elevation was used to describe PC axis 1 because sites with high elevations had high scores while low-elevation meadows had low scores. Species richness was used to describe axis 2 because Christensen Meadow and Spot Mountain (the two sites with highest scores on axis 2) had high species richness, while sites with lower scores on axis 2 had low species richness. Moisture was used to describe axis 3 because xeric sites had high scores, while mesic and hydric sites had low scores. Tests for correlation revealed that axis 1 was significantly correlated with elevation ($r = 0.83$, $P < 0.01$) and axis 2 was significantly correlated with species richness ($r = 0.88$, $P < 0.01$). Axis 3 was not tested for correlation because moisture was not measured.

Because the first four PC axes explained a high percentage of the variance in the 1988 butterfly data (17.75, 10.46, 9.42, and 8.30 for axes 1 through 4, respectively), PC scores 1, 3, and 4 were used in cluster analysis to form dendrograms (Fig. 3). The two major clusters are separated into alpine and low-elevation sites. When PC 2 is included, Spot Mountain and Christensen Meadow are outliers due to the high species richness of the sites. By removing PC 2 from the analysis, these two outliers are incorporated into the two main clusters. McGee Meadow, Rocky Knob, and Route 8 burnscar are also outliers in Fig. 3, potentially distinguished due to their extremes of moisture level; McGee Meadow is very wet while Rocky Knob and Route 8 burnscar are very dry.

The first three PCs explained 60% of the variation in butterflies for 1989 (29.1, 18.0, and 12.7 for axes 1–3, respectively). Elevation was correlated with PC 2 ($r = 0.30$), but the correlation was not significant. Characterization of PC 1 as moisture is based upon the array of sites, with moister areas on the lower end of the scale. PC 3 separates some sites into east and west sides relative to the continental divide, but the fit is not entirely consistent. Cluster analysis revealed high- and low-elevation grouping similar to that of 1988.

PCA results for the 1988 bird data revealed somewhat less obvious PC classifications upon initial inspection. However, the habitat characteristics were revealed by investigating habitat preferences of prominent species at the extremes of the PC values. The following descriptions were assigned using Figs. 4 and 5: PC 1 = structural diversity of habitat, PC 2 = elevation of site, and PC 3 = moisture level of site. Structural diversity (the horizontal and vertical occupation of space by plants) was used to describe PC 1 because meadows had low scores, sites with some trees had intermediate scores, and forested sites had high scores. Elevation was used to describe PC 2 because high-elevation sites had high scores while low-elevation sites had low scores. Moisture was used to describe PC 3 because xeric-to-

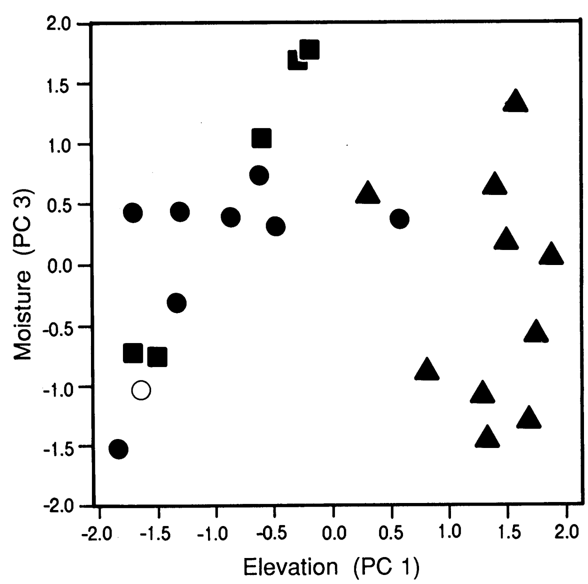

FIG. 2. Principal components analysis of sites using presence/absence data for butterflies in 1988 (PC 1 vs. PC 3). Species frequencies are based upon repeated sampling at each site during the summer months. ● = mesic meadow, ▲ = alpine meadow, ■ = xeric meadow, ○ = hydric meadow.

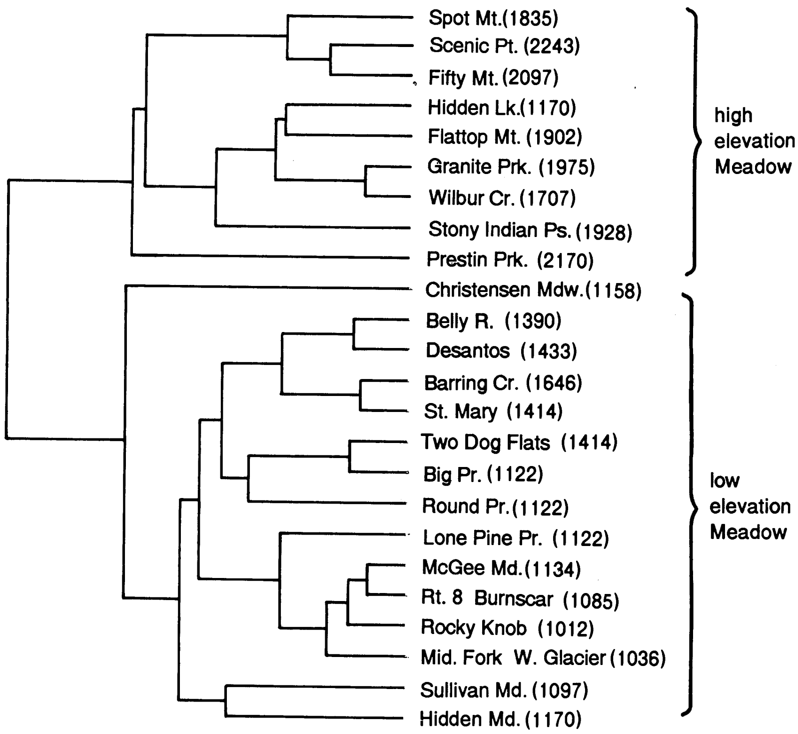

FIG. 3. Cluster analysis using principal components scores for butterflies in 1988 (PC 1, PC 3, and PC 4). The number in parentheses after each site name is the elevation of the site in metres.

mesic sites had high scores and hydric sites, or sites near water, had low scores.

Structural diversity of habitat and moisture level of the sites were not estimated in this analysis, so PC axes 1 and 3 could not be tested for correlation. However, PC 2 was tested for correlation with elevation. The correlation ($r = 0.39$) was lower than that for butterflies, but it was still significant ($P < 0.05$). The first few eigenvalues did not explain a high percentage of the variance for the bird data in 1988, and there was a comparatively gradual tapering of explained variance from axes 1–32 (axes 1–5 = 9.97, 8.00, 6.44, 6.14, and 5.92, respectively). Consequently, the PCs for the 1988 bird data are poorly defined.

The first three axes for birds in 1989 explained half of the variation in the data (21.1, 15.4, and 12.6 for axes 1–3 respectively). Interpretation of the axes (by examining the characteristics of sites and species with high loadings) yielded the following characterizations of PCs: PC 1 = moisture, PC 2 = elevation, and PC 3 = a gradient between sites with coniferous and deciduous vegetation. Elevation was significantly correlated with PC 2 ($r = 0.62$, $P < 0.01$). PC 1 and PC 3 were not as easily tested. Cluster analysis of these data did not reveal any easily distinguished groupings.

Chi-square for species–habitat associations.—In general, birds were more habitat-specific than butterflies. While six birds exhibited a significant east–west preference (Table 3) and three birds exhibited a significant habitat preference (Varied Thrush: interior forest, $\chi^2 = 10.58$, df = 3; Brownheaded Cowbird: forest/meadow edge, $\chi^2 = 9.80$, df = 3; and Cedar Waxwing: forest/meadow edge, $\chi^2 = 9.70$, df = 3), only one species of butterfly exhibited an east–west preference (*Euphydryas anicia*: west preference $\chi^2 = 4.05$, df = 1) and only one species exhibited a habitat preference (*Nymphalis antiopa*: hydric, $\chi^2 = 4.05$, df = 3).

Habitat diversity and species richness.—Spectral-class diversity, which is indicative of habitat-type diversity, had the expected positive correlation with species diversity; however, the relationship was much more marked in butterflies ($r = 0.46$) than in birds ($r = 0.22$). Aspect diversity (i.e., sites with a diversity of aspects) had a very slight negative correlation with species diversity in both butterflies ($r = -0.10$) and birds ($r = -0.12$). Elevation diversity exhibited a different correlation between taxa. The correlation was extremely marked and negative for butterfly species ($r = -0.45$), yet there was virtually no correlation for bird species diversity ($r = -0.05$). Slope diversity was slightly negatively associated with diversity in both cases ($r = -0.39$ for butterflies and $r = -0.23$ for birds). In no case was the relationship between species diversity and habitat diversity significant for butterflies or birds.

Changes between years.—Application of a G test to the 1988 and 1989 butterfly data revealed several significant differences. Twenty-four of the 100 species exhibited significant changes in frequency between the

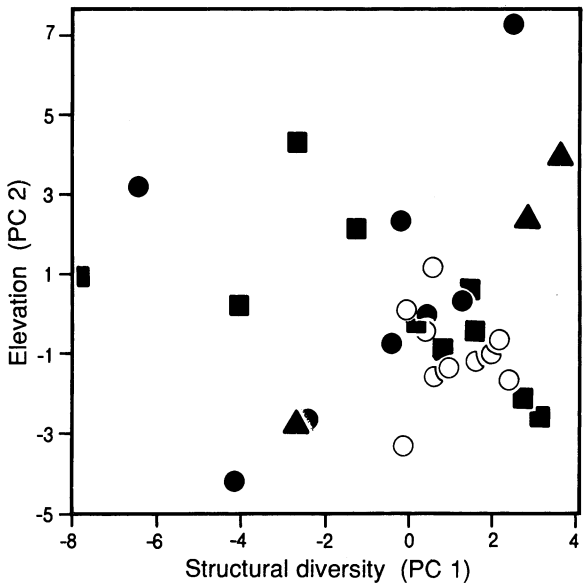

FIG. 4. Principal components analysis of sites using presence/absence data for birds in 1988 (PC 1 vs. PC 2). Species frequencies are based upon repeated sampling at each site during the summer months. ● = mesic meadow, ▲ = alpine meadow, ■ = riparian, ○ = woodland.

two years, 15 species higher in 1988 and 9 species higher in 1989. In contrast, a comparison of bird data between 1988 and 1989 revealed that for each species that had significantly different frequencies of occurrence between the two years, the frequencies were always higher in 1989. For details see Debinski (1991).

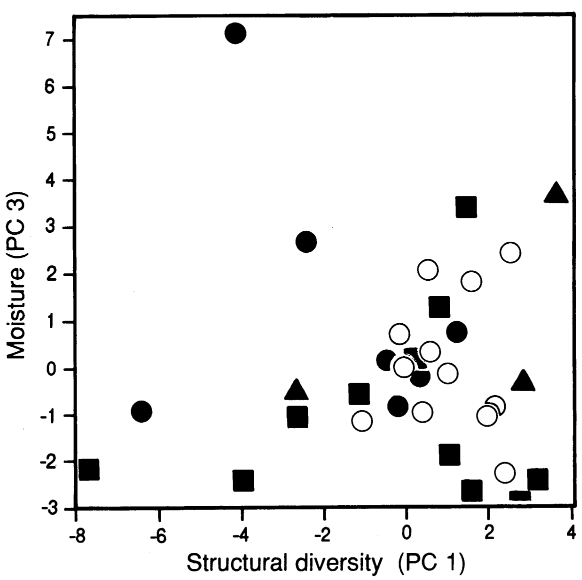

FIG. 5. Principal components analysis of sites using presence/absence data for birds in 1988 (PC 1 vs. PC 3). Species frequencies are based upon repeated sampling at each site during the summer months. ● = mesic meadow, ▲ = alpine meadow, ■ = riparian, ○ = woodland.

TABLE 3. Bird species showing significant ($P < 0.05$) differences in presence between east and west sites using chi-square test.

Species	χ^2	Habitat preference
American Redstart	5.96	West
Varied Thrush	4.13	West
Pileated Woodpecker	4.28	West
Orange-crowned Warbler	4.27	West
Clark's Nutcracker	4.13	East
White-crowned Sparrow	11.19	East

DISCUSSION

Species lists

The total number of new species observed increased each year for both birds and butterflies. Two butterfly species were added to park records in 1987, four in 1988, and three in 1989. Possible reasons for discrepancies between historic lists and present census results for both taxonomic groups include: (1) missed spring or early summer species—due to the late start of censusing season, (2) strays or accidentals (29 of 47 of the bird species that were not observed are noted as accidental or rare in the GNP Bird List [Glacier Natural History Association, West Glacier, Montana, USA]), (3) misidentifications of original list (e.g., two butterflies), (4) taxonomic changes (especially with butterflies), and (5) extinctions. Reasons 1–3 explained most of our discrepancies.

Biodiversity data must be scrutinized for reliability from two perspectives: (1) reliability of presence data and (2) reliability of absence data. In general, presence data is much more reliable than absence data; i.e., if a species is not present in a survey, how many times does one need to search for it to be certain that it is indeed absent? (e.g., Mangel 1981)?

The bird data from 1987 differ significantly from those of 1988 and 1989. The 1988 and 1989 data are more complete for two reasons: the censuses were longer in duration after the sampling methodology was standardized, and the observers became better at identification with each year of experience. As a result, comparisons between years should be interpreted conservatively. Butterfly data are much more reliable, as unrecognized species were collected and pinned, allowing for identification in the laboratory.

Analysis of commonness and rarity

Some of the birds were underrepresented in the biodiversity sites relative to their commonness on the park checklist. These groups include species specific to three habitat types: interior forest (e.g., Evening and Pine Grosbeaks, Cassin's Finch, Red Crossbill, and Brown Creeper); grassland (e.g., Vesper and Savannah Sparrows, Horned Larks); and mountain slopes (e.g., Townsend's Solitaires). Interior forest species (including the less observed woodpeckers) probably had lower detectability, relative to other birds, in a census. Several of the bird sites can be considered interior forest: Packer's Roost, Avalanche Lake, Belly River near Cosley Lake trail, Fish Creek, and others.

In two ways, the sampling method employed may have selected against these birds. First, while the majority of the park area is forest, this habitat was proportionately underrepresented in the sampling scheme in order to include some of the more rare habitat types. Second, many of the censuses include a proportion of edge habitat; specifically forest/meadow or forest/riparian edge; edge inhabitants are more easily detected than interior forest- (or grassland)-dwelling species. Third, sound does not travel through a dense forest as well as it does from the edge of a forest to a listener in a meadow.

The apparent absence of some species (e.g., Redpolls and Nighthawks), however, was not explained by the sampling. These discrepancies may be explained by temporal sampling problems. The Redpoll is less common during the summer months and the Nighthawk is much more active at dawn and dusk, both thus being less available for detection during this study.

Finally, categorization as "common" or "rare" may be confounded by the underrepresentation of human-inhabited areas. Some of the birds on the park list (e.g., Mourning Dove and Evening Grosbeak) may be classified as common because they are seen frequently around human dwellings. Thus, species considered common on the park list may in fact be uncommon or even rare in the larger ecosystem.

Rare species may be important to monitor, as they may be particularly vulnerable to environmental change. For example, the loss of specific habitat types (alpine, successional, etc.) may lead to the decline of a rare species dependent solely upon such habitat. Predictions of extirpations are contingent upon knowledge of both species natural history and future park management scenarios (e.g., plans to alter specific habitats).

Diversity hot spots

Three low-elevation meadows were diversity hot spots for both birds and butterflies, and two of these meadows ranked highest in species richness for two consecutive years. These meadows tended to have a diversity of trees at their border and supported a high diversity of flowers. They were both mesic meadows with riparian components. Another interesting finding was the relationship between sites that supported high species diversity and sites that supported rare species. Just because a site harbors high species diversity, it does not automatically follow that it also supports rare species. Because hot spots in GNP also supported rare species, they are extremely important to preserve.

Species–habitat relationships

Elevation was a common PC for both taxonomic groups during each of the two years. Structural diversity was an important PC for birds in 1988, but in 1989 there was more of distinction between coniferous and deciduous habitats. Commonness and rarity was a PC for butterflies in 1988. Moisture was a PC for butterflies in 1989, and for birds in both years. East–west orientation was a PC for the butterfly data of 1989. However, the percentage of explained variance never topped 60% for the first three axes, so interpretations must be viewed conservatively.

The bird data of 1988 demonstrate a continuous level of explained variation throughout the variables. Each eigenvalue explained a small percentage of the variance. In effect, the PCA results indicated that the bird data exist as a spherical data cloud. No major axis could be found to separate the sites because each site was characterized by a unique species assemblage. A larger sample of sites would be necessary before one would be capable of prioritizing preservation values of various sites based upon their distinctness.

In the butterfly results presented, general habitat groupings (e.g., low-elevation meadow or alpine meadow) can be discerned from the clusters, and therefore species assemblages could potentially be used as an indicator of habitat type (Fig. 3).

While six birds exhibited a significant east–west preference (Table 3) only one butterfly species exhibited any such preference. With respect to habitat types, only three species of birds and one butterfly species exhibited a preference. The difference between the taxonomic groups is of interest. The continental divide may be more of a significant barrier to birds than it is to butterflies.

Sites with higher habitat complexity would be expected to support higher species diversity, and thus a direct correlation was expected between habitat diversity and species diversity. The habitat diversity variable having the highest correlation with species richness was spectral-class diversity, but even this relationship was not significant. The habitat diversity parameter showing the most marked inverse relationship with species richness was elevation diversity. One would not intuitively expect a site with less elevational diversity to have higher species richness, as higher topographic diversity often provides more microhabitats and thus more different species. However, on a scale of 1 km^2, perhaps high topographic diversity is not conducive to supporting a diversity of species. Perhaps vegetation diversity is a more influential factor.

Monitoring and management

Twenty-four of the butterfly species found in 1988 and 1989 exhibited significant changes in frequency between the two years. Fifteen species were found in more sites in 1988 than in 1989; nine were found in more sites in 1989 than in 1988. Six of these species are biennial; thus, they would be expected to show large fluctuations in occurrence between years. The change in frequencies in two other species can perhaps be attributed to misidentification; the underlying reasons for the changes in the others are unknown.

There are several potential reasons for the increase in frequencies of occurrence of bird species between 1988 and 1989. A drought year occurred in 1988, and fires burned extensive areas during August and September. However, the fires may have created additional habitat favorable to certain species in 1989. Unfortunately, these data do not allow a test of these hypotheses with any degree of confidence. The birding skills of the observers increased between 1988 and 1989; extra effort was made to find rare species during 1989, and replication during 1989 was higher.

Regular monitoring of species occurrences in the plots is a necessary component of biodiversity monitoring. The data base increases in value with each subsequent monitoring event, and repeated censusing ensures that any changes in biological diversity can be detected. Although the status of rare species should be checked yearly, it will probably be necessary to completely resurvey each site for species diversity in all indicator groups only every 3–5 yr.

After several years of data have been collected, it may be possible to find answers to important questions. For example, if a frequency index has a high level of variance, a decline may be a false alarm, while some declines may not be detected in time for action. Trends in species occurrences can also be examined using linear regression analysis with census year as the independent variable and number of sampling plots occupied by a certain group of species as the dependent variable.

Sites of special importance could be identified based upon high species richness or because a certain species is restricted to it. The variety of habitats necessary to maximize the total park species diversity could also be determined. This value would be taxon specific, however, and assemblages of taxa would have to be considered in order to manage the entire ecosystem.

Many species were detected only in one or two sites. If the next year they are not detected, or if they continue to be detected in only one or two sites, should the park managers be concerned? Ironically, at the present intensity of sampling (24 butterfly sites, 35 bird sites of 1 km^2 described by presence/absence data), population trends can be detected best for common species.

A major goal of this research was to identify habitats that are important for preserving biodiversity. These types of habitats include sites of high biodiversity, sites supporting relatively rare species, successional habitats, and habitats that are range edges for rare species. Although the sampling was limited in both space and time, some examples of these habitats were identified. A few examples are listed below.

Christensen Meadow and Hidden Meadow are examples of important habitats because of their high bird and butterfly richness. Range edges are important because the loss of such an area may contract a species' range. For example, *Colias nastes* is an arctic species and Glacier National Park may be the southernmost extension of its range. It occurs only at high elevations within the park. Loss of habitats such as Siyeh Pass might result in the shrinkage of the total range of this species. The value of sites supporting rare species is widely accepted. Finally, successional habitats are important to monitor. Species such as *Euphydryas gillettii* depend on wet meadows where the larval host plant *Lonicera involucrata* is present. These types of meadows are often in the early stages of succession. If large trees begin to encroach, blocking the sun, the habitat may no longer be suitable for the species. Management that would preserve the meadow and prevent succession may be called for in this case.

Conclusions

Analysis of the GNP biodiversity data has allowed us to (1) obtain baseline data on species occurrences and map them in both topographic and ecological space so that long-term trends in species distribution and abundance can be tracked; (2) identify locations and habitats that are particularly species-rich for each indicator group (e.g., Christensen Meadow, Spot Mountain, Hidden Lake, Preston Park, Hidden Meadow, Desantos, and the Route 8 burnscar); (3) discriminate common, widely distributed species from uncommon, local ones; (4) reveal species assemblages that are indicative of specialized habitat types; and (5) reveal variables (elevation, moisture, structural diversity) that are influential in predicting the species composition of a site. Although specifically designed for Glacier National Park, these techniques should be adaptable, with minor modifications, to any other relatively large reserve.

This research emphasized a new approach that provides information on the dynamics of local extirpations and colonizations. Presence/absence data were used to assess patterns of species distribution and abundance and will prove valuable in the future by documenting changes in these patterns over time.

Acknowledgments

This research was supported by the National Park Service, Glacier National Park, Montana. We thank Tom Vawter, Craig Odegard, Steve Bracken, and Tom Jacobsen for their assistance in the fieldwork, and Daniel Goodman, Ward Watt, David Bradley, and James Pritchard for their comments on the written manuscript.

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