

Does butterfly diversity predict moth diversity? Testing a popular indicator taxon at local scales

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Abstract

Indicator taxa are often proposed as efficient ways of identifying conservation priorities, but the correlation between putative indicators and other taxa has not been adequately tested. We examined whether a popular indicator taxon, the butterflies, could provide a useful surrogate measure of diversity in a closely related but relatively poorly known group, the moths, at a local scale relevant to many conservation decisions (10^0 – 10^1 km²). We sampled butterflies and moths at 19 sites representing the three major terrestrial habitats in sub-alpine Colorado: meadows, aspen forests, and conifer forests. We found no correlation between moth and butterfly diversity across the 19 sites, using any of five different diversity measures. Correlations across only meadow sites (to test for correlation within a single, species-rich habitat) were also not significant. Butterflies were restricted largely to meadows, where their host plants occur and thermal environment is favorable. In contrast, all three habitats contained substantial moth diversity, and several moth species were restricted to each habitat. These findings suggest that (1) butterflies are unlikely to be useful indicators of moth diversity at a local scale; (2) phylogenetic relatedness is not a reliable criterion for selecting appropriate indicator taxa; and (3) a habitat-based approach would more effectively conserve moth diversity in this landscape and may be preferable in many situations where indicator taxa relationships are untested. © 2001 Elsevier Science Ltd. All rights reserved.

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1. Introduction

The diversity of natural systems, coupled with the pace at which human societies are altering them, prevents biologists from cataloging the identities and distributions of all species before conservation decisions must be made (Ehrlich and Wilson, 1991; Ehrlich, 1992; Williams and Gaston, 1994). In setting geographic priorities for conservation, for example, obvious targets are biodiversity “hotspots” containing high levels of species richness and/or endemism (Myers, 1988; Reid, 1998). But how does one identify a hotspot of overall diversity if taxonomic descriptions, let alone distribution data, are available for perhaps only 10–15% of all species (Heywood, 1995)?

In response to this question, many authors propose using indicator taxa, groups of species whose distributions and taxonomies are well known and whose diversity patterns can be used as a surrogate measure of

patterns in other taxa or of diversity overall (Caro and O’Doherty, 1999). For example, Myers et al. (2000) use data on non-fish vertebrates and plants to identify 25 global hotspots of biodiversity, which the authors recommend as conservation priorities. The United States Gap Analysis Program (Scott et al., 1993a) relies on distribution data for vertebrates and butterflies to identify gaps in existing reserve networks. Common to these studies and many others (Rebelo and Siegfried, 1992; Sisk et al., 1994; Balmford and Long, 1995; Freitag et al., 1997) is an assumption, either implicit or explicit, that diversity patterns of the indicator taxa are correlated with those of other taxonomic groups. Using indicator taxa to guide conservation efforts therefore involves “bold extrapolations, which need to be supported with good evidence for their reliability” (Williams and Gaston, 1994).

To evaluate the reliability of such extrapolations, ecologists have begun to investigate the strength of correlations in diversity patterns among taxa. For example, Prendergast et al. (1993) examined richness pattern of birds, butterflies, dragonflies, liverworts, and aquatic

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angiosperms in 100 km² squares covering Britain and found little coincidence of richness hotspots among taxa. Pearson and Carroll (1998) found that species richness of tiger beetles is significantly related to that of butterflies, but not of birds, in North America. As evidenced by these examples, the building body of literature on indicator taxa has yielded few generalizations. In addition, the majority of such studies has been carried out over large areas and at coarse resolution (e.g. Williams and Gaston, 1994; Beccaloni and Gaston, 1995; Dobson et al., 1997; Kerr, 1997; Ricketts et al., 1999) and thus applies to a limited set of conservation issues (e.g. identifying megadiverse countries or continental biodiversity hotspots).

Many critical conservation decisions are made at smaller scales, however, such as locating reserves within a local landscape or identifying important habitats within an established reserve (Noss, 1999). Although indicator taxa would be equally useful in these local conservation decisions, there are fewer reasons to expect that diversity patterns will be concordant at these scales. Macro variables that correlate well with species richness, such as latitude, potential evapotranspiration (i.e. available energy), climate stability, and rainfall (Currie, 1991; Lawton et al., 1993), do not vary so widely on smaller scales. Instead, more taxon- and species-specific factors are likely to dominate, such as resource specificity and availability, vagility, and species interactions (Weaver, 1995; Böhning-Gaese, 1997; Pearson and Carroll, 1999). Indeed, existing studies show only occasional support for the local-scale utility of indicator taxa (Murphy and Wilcox, 1986; Daily and Ehrlich, 1996; Duelli and Obrist, 1998; Lawton et al., 1998; Blair, 1999). Therefore, there is a particular need to investigate putative indicator taxa at these smaller scales, where concordance is less expected and is likely to be idiosyncratic to the taxa being compared (Flather et al., 1997; Prendergast and Eversham, 1997).

Ironically, the same factors that make indicator taxa potentially useful conservation tools also render them difficult to evaluate; if distributions of other taxa were known well enough to allow rigorous comparisons, indicators would no longer be needed. As a result, putative indicator taxa tend to be tested against other well-known groups that in fact are used themselves as biodiversity indicators (e.g. Carroll and Pearson, 1998; Blair, 1999; Swengel and Swengel, 1999), instead of groups they are actually meant to indicate: poorly known taxa whose diversity patterns cannot easily be determined directly (but see Duelli and Obrist, 1998; Pharo et al., 1999).

In this study we examine whether diversity of a popular indicator taxon, the butterflies, is a useful surrogate measure of diversity in a closely related but relatively poorly known group, the moths. We perform these tests at a local landscape scale (10⁰–10¹ km²) that is relevant

to many kinds of local management and conservation decisions (Noss, 1990; Prendergast and Eversham, 1997). In addition, we examine patterns of community composition, habitat associations, and host plant use in both taxa. Understanding these patterns will help to illuminate factors that contribute to correlations (or lack thereof) in diversity across the landscape, and may thus improve a priori selection and use of indicator taxa in the future.

The butterflies (here defined as the Papilionoidea, or true butterflies) fulfill most of the important criteria for choosing a practical indicator taxon. Their diversity and distributions are well-described, they are relatively easy to sample, accessible field guides exist for identification, their taxonomy is relatively stable, and they are abundant and diverse in many ecosystems (Scott, 1986; Scoble, 1992; Caro and O'Doherty, 1999). Butterflies are perhaps the only insect group that meets these criteria worldwide (but see Pearson and Carroll, 1998). In addition, lepidopteran species are relatively host-specific (Janzen, 1988), so they may serve as biodiversity indicators of plants and thus other phytophagous insect taxa (Luff and Woiwod, 1995). Butterflies therefore have been a popular choice as an indicator taxon and are often included in biodiversity assessments as the lone representative of the class Insecta (Scott et al., 1993b; Sisk et al., 1994).

In contrast, the moths, which comprise the vast majority of Lepidopteran diversity, do not enjoy the same enthusiastic interest of taxonomists and amateurs (Scoble, 1992). Many species of moths have yet to be described, some even in North America (J. Powell, personal communication). For the species that are described, distribution and host plant data are generally poor (Janzen, 1988; Harp et al., 1999). Diversity patterns in moths are thus likely to remain poorly understood in many areas for at least the short term, during which many conservation decisions will be made.

Because of the taxonomic and ecological similarities between these two groups, butterflies are an intuitive choice as indicators of moth diversity. By testing this relationship, we present a case study that examines whether phylogenetic relatedness is a useful criterion for selecting indicator taxa. Examining a series of such case studies may better illuminate the factors determining correlations in diversity among taxa and thus allow conservationists to select the most appropriate indicators for each situation (Flather et al., 1997).

2. Methods

2.1. Study sites

We sampled moth and butterfly diversity in 19 sites near the Rocky Mountain Biological Laboratory in

Gunnison County, Colorado (Table 1). The sites represented the three major terrestrial vegetation types in this region of subalpine Colorado: meadows, aspen forests, and conifer forests (hereafter we refer to these vegetation types as “habitats”). Meadow habitats are characterized by diverse communities of herbaceous plants and by substantial proportions (10–30%) of bare ground. Aspen habitats are dominated by groves of *Populus tremuloides* and support dense understories of herbaceous vegetation. Conifer habitats are dominated by *Picea engelmanni* and support only sparse understories of shade-tolerant plant species. We also sampled one mixed habitat, termed “aspen/meadow”, characterized by widely-spaced (5–10 m) aspen trees with a diverse and well-lit meadow understory.

We located 15 of the 19 sites along four transects crossing boundaries between meadow and forest (either conifer or aspen, Table 1). Three of these transects consisted of four sites: an interior and an edge site of both meadow and forest. In the remaining transect (No. 3), no interior meadow site was available (Table 1). These transects allowed us to examine edge effects by sampling interior and edge locations of adjacent habitats simultaneously.

Table 1
Richness and abundance of butterflies and moths in the 19 sample sites

Site ^a	Butterflies		Moths	
	Richness	Abundance	Richness	Abundance
1M	15	95	36	201
1ME	8	20	33	249
1AE	5	12	45	320
1A	2	13	51	583
2M	13	53	27	109
2ME	7	30	33	164
2AE	2	10	34	233
2A	3	17	42	379
3ME	4	20	24	77
3CE	2	11	28	121
3C	3	15	35	256
4M	17	68	32	201
4ME	12	47	32	229
4CE	3	20	30	128
4C	1	33	34	122
5M	16	35	29	139
6M	16	75	39	262
7AM	15	68	49	740
8AM	17	74	40	448
M mean (S.D.)	12.0 (4.6)	49.2 (26.0)	31.7 (4.5)	181.2 (63.6)
C mean (S.D.)	2.3 (1.0)	20.0 (10.0)	31.8 (3.3)	156.8 (66.2)
A mean (S.D.)	3.0 (1.4)	13.0 (2.9)	43.0 (7.1)	378.8 (148.8)
AM mean (S.D.)	16.0 (1.4)	71.0 (4.2)	44.5 (6.4)	594.0 (206.5)

^a Numbers in site codes correspond to trap transects crossing meadow/forest boundaries. Letters in site codes denote the habitat: M(E) is meadow (edge); A(E) is aspen (edge); C(E) is conifer (edge); and AM is aspen/meadow. Means are taken over both interior and edge sites.

2.2. Moth sampling

To sample moths we used bucket traps with 1-A fluorescent black lights (Bioquip No. 2851A + U), powered by 12-V batteries. Moths are attracted to the light, strike transparent baffles surrounding the lamp, and fall through a funnel into a bucket below. The traps turned on automatically when night fell (approximately 21:00 h) and operated for approximately 6.25 h before the battery discharged. We put solid insecticide strip (2.2 Dichlorovinyl dimethyl phosphate) inside each bucket to kill the trapped moths.

We sampled sites in rotation between mid-June and mid-August 1997, with six–eight traps in operation each night. Each site was sampled 8–10 times, spread as evenly as possible through two full lunar cycles. We reassigned batteries and traps to sites arbitrarily to control for differences in lamp brightness and battery capacity (although both were similar in tests at the beginning and end of the season).

Edge traps were placed 20 m from the edge of the habitat, and were masked with black plastic sheeting to illuminate only the 90° arc facing the edge. This allowed sampling of only the edge of the habitat, in a roughly triangular area. Interior traps were not masked and were placed at least 50 m from any other habitat. (A single exception is site 2M, where a narrow strip of coniferous forest reaches a point 20 m from the trap. The forest occupied less than 20° of the circle of radius 50 m around the trap). All traps were placed on the ground, and a 2-m radius around each trap was kept free of tall vegetation.

We sorted moth samples to morphospecies and retained a reference collection of up to four individuals from each morphospecies. Individuals with wing lengths less than 12 mm were excluded to avoid the high rate of sorting errors among microlepidoptera. Morphospecies were later identified by Jerry Powell (E. O. Essig Museum, University of California at Berkeley), Paul Opler (Colorado State University), and J. Don LaFontaine (Agriculture Canada, Ottawa). All morphospecies found to represent more than one recognized species (8% of original number) were eliminated from analysis. Morphospecies representing distinct but unidentified species were included. Some of these species may be undescribed (P. Opler, personal communication). Hereafter we refer to morphospecies as “species.”

2.3. Butterfly sampling

We sampled butterfly diversity in the same 19 sites using time-constrained searches, netting each observed butterfly or identifying them on the wing if possible. Butterfly sampling occurred between 10:00 and 12:00 h, typically the morning after a moth sample in the same site to keep the timing and accumulation of sampling as

closely matched as possible. We sampled each site 8–10 times through the season and searched between 15 and 45 person-minutes per sample, accumulating 210 person-minutes of searching effort per site. At interior sites, we searched for butterflies within an approximately 40-m radius of the moth trap location. At edge sites, we concentrated our searching effort within the triangular region illuminated by the moth trap. We recorded the number of individuals of each species observed (in addition to simply species presence/absence) and took care to avoid double counting individuals to the degree possible. With rare exceptions, the three of us searched together, to minimize observer bias.

2.4. Analyses

We calculated five measures of moth and butterfly diversity in each of the 19 sites. First, we counted the total number of species sampled (hereafter “raw richness”). Second, we excluded from each site species that were sampled there only once and recalculated raw richness (“nonsingleton richness”). Excluding singletons reduces the influence of inadequately sampled species or vagrant individuals on measures of site diversity. Third, we generated an average species accumulation curve, based on 100 randomizations, and calculated rarefied species richness at equal sampling effort (number of samples) among sites (“rarefied richness”; Gotelli and Graves, 1996). Fourth, we used the same curves to estimate the extrapolated total species richness, using a Michaelis–Menten equation (“extrapolated richness”; Colwell and Coddington, 1994). Finally, we computed the Shannon diversity index (“Shannon index”; Hayek and Buzas, 1997). We calculated the last three measures using the richness estimation program EstimateS (Colwell, 1997). Correlations between moth and butterfly diversity were tested with Spearman rank correlations (Sokal and Rohlf, 1995) because data were not normally distributed.

To investigate the influence of host plant availability on distribution patterns, we compared the habitat associations of butterfly and moth species with the habitat associations of their larval host plants. Here we define habitat association as the set of local habitats (i.e. mea-

dow, aspen, and/or conifer) in which a given moth species, butterfly species, or host plant occurred. For butterfly species, host plant species were compiled from Scott (1986) and Opler (1995), and locally occurring species were identified using the RMBL herbarium. For moth species, Paul Opler compiled for us all available published and unpublished information on known host plant taxa (often genera). With the assistance of Barbara Frase, we assigned host plant taxa to the habitat(s) in which they occur. This allowed us to determine the habitat associations of host plants for each butterfly and moth species and to compare them with the habitat associations of the species themselves.

Finally, we used our sampling design to test the radius of attraction of our moth traps. There is much uncertainty about the radius over which light traps effectively sample moths. Published estimates range from 3 m to over 700 m, but estimates based on field tests are generally less than 50 m (Dufay, 1964; Baker and Sadovy, 1978; Muirhead-Thomson, 1991; McGeachie, 1997; Leps et al., 1998). If our traps sampled moths over radii substantially greater than 20 m, edge sites facing each other across a habitat boundary would have sampled heavily overlapping areas and should have produced highly similar samples. To test this, we analyzed community similarity among sites using the Bray–Curtis index (Bray and Curtis, 1957), which incorporates both presence and abundances of species shared between sites. We compared Bray–Curtis coefficients between pairs of edge sites to the coefficients between edge sites and their respective interior sites, using Mann–Whitney tests (Sokal and Rohlf, 1995). For this analysis we used only the three full trap transects of four traps (i.e. transects 1, 2, and 4; Table 1).

3. Results

We observed 716 butterfly individuals representing 29 species and collected 4961 moth individuals representing 91 species (Appendices A and B). We found no correlation between moth and butterfly diversity across the 19 sites, using any of the five measures of diversity (Fig. 1,

Table 2
Spearman rank correlation coefficients between butterfly and moth diversity

Diversity measure	All sites ($n = 19$)		Meadow sites ($n = 9$)		Interior sites ($n = 11$)	
Raw richness ^a	−0.011	($P > 0.50$)	0.464	($P > 0.20$)	−0.183	($P > 0.50$)
Nonsingleton richness ^b	0.159	($P > 0.50$)	0.486	($P > 0.10$)	0.197	($P > 0.50$)
Rarefied richness ^c	0.051	($P > 0.50$)	0.477	($P > 0.20$)	0.045	($P > 0.50$)
Extrapolated richness ^d	−0.079	($P > 0.50$)	−0.320	($P > 0.20$)	−0.318	($P > 0.20$)
Shannon index	−0.025	($P > 0.50$)	0.437	($P > 0.20$)	−0.223	($P > 0.50$)

^a Total number of species observed in each site.

^b Number of species represented by at least two individuals in each site.

^c Richness estimates rarefied to standardize the number of samples among sites.

^d Extrapolated richness estimates using asymptotes of species accumulation curves.

Table 2). Correlations using only interior sites (to remove any edge effects) and only meadow sites (to test for correlation within a single habitat) also were not significant (Table 2).

Butterflies (excluding singletons) were restricted largely to meadows, with only two species found in any non-meadow site (Fig. 2). For moths, on the other hand, diversity was more equivalent among the three habitats. Meadow, aspen, and conifer each contained a substantial number of nonsingleton species found only in that habitat, and many species were shared between two habitats or among all three (Fig. 2).

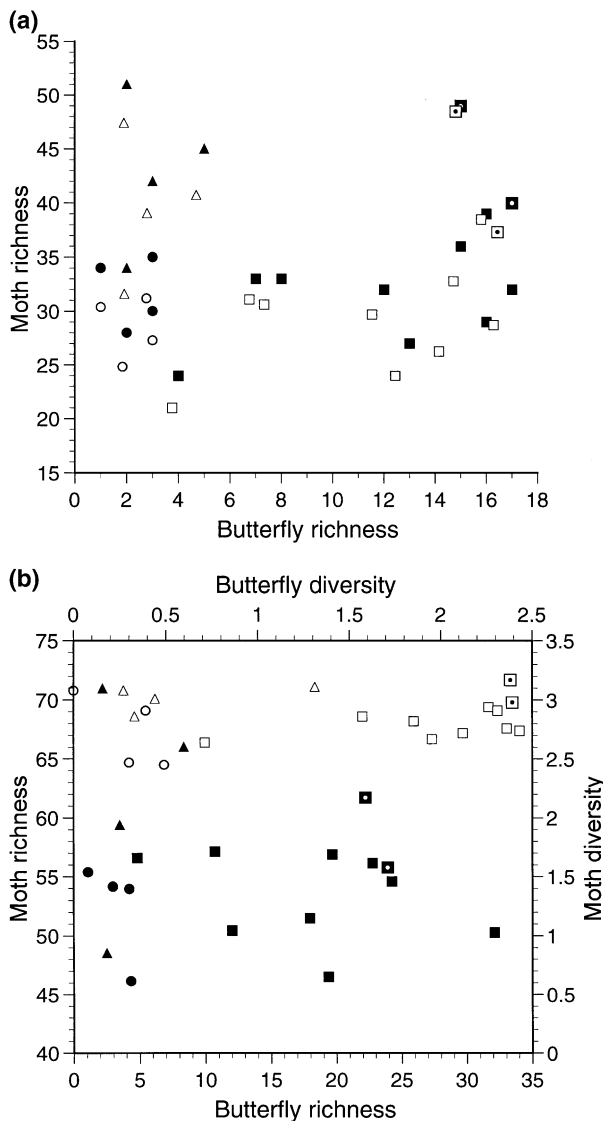


Fig. 1. Relationship between butterfly and moth diversity, using four different measures of diversity: (a) raw richness (filled symbols) and rarefied richness (open symbols); (b) extrapolated species richness (filled symbols) and Shannon diversity index (open symbols and separate scale). Squares are meadow sites, triangles are aspen sites, circles are conifer sites, and squares with dots are aspen/meadow sites. Completely overlapping points are shifted slightly to show both symbols. Correlation results presented in Table 2.

As expected (e.g. Sharp et al., 1974), host plants for butterflies were restricted almost entirely to meadows, with several plants also occurring in aspen but none in conifer (data not shown). In contrast, all three habitats contained host plants for moth species. Host plant data were available for only 50 of the 97 moth species we collected, and 15 of these 50 moth species were only observed as singletons and were thus excluded. Of the remaining 35 moth species, 19 occurred only in habitats that contained their host plants (Fig. 3, bold entries). On the other hand, 13 moth species occurred in at least one habitat in addition to those containing their host plants (italicized entries). Finally, for three species, habitat associations for moths and their known host plants did not overlap at all (entries in parentheses).

Pairs of edge sites were significantly less similar to each other in species composition than they were to their respective interior sites (Mann–Whitney test, $U = 18$, $n = 6.3$, $P < 0.025$). This result suggests that the areas sampled by edge traps did not extend substantially beyond a 20-m radius.

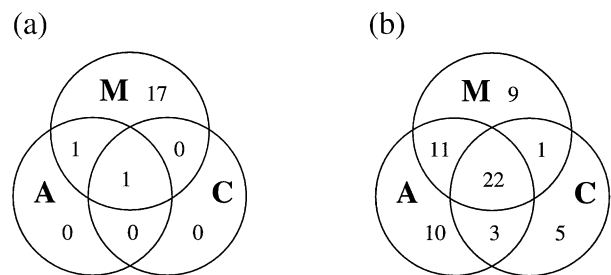


Fig. 2. Venn diagram of species distributions among the three major habitats for (a) butterflies and (b) moths. Each circle represents a habitat: M is meadow, A is aspen, and C is conifer. Numbers indicate the number of species found exclusively in each habitat, in each combination of two habitats, or in all three. This analysis excluded singletons (species found only once in a site), to reduce the influence of poorly sampled or vagrant species.

Host plants	Moths						
	M only	A only	C only	M+A	M+C	A+C	M+A+C
M only	0	(2)	-	2	0	(1)	2
A only	-	0	-	0	-	0	0
C only	-	-	1	-	0	0	2
M+A	1	2*	-	3	0	1	2
M+C	1	-	1	0	0	0	4
A+C	-	0	0	0	0	0	0
M+A+C	3	1	0	2	1	0	3
Total	5	5	2	7	1	2	13

Fig. 3. Comparison of the habitat associations of moth species (excluding singletons) and their host plants. M, A, and C represent meadow, aspen, and conifer, respectively. Each moth species is placed in a column according to its habitat association, and in a row according to the habitat association of its known host plants. (For example, the entry marked with a “*” represents two moth species that were found only in aspen habitat while their host plants occur in both meadow and aspen habitats). Entries in bold: moth species only found in habitats containing their host plants. Entries in italics: moth species found in at least one habitat in addition to those containing their host plants. Entries in parentheses or dashes: no overlap in observed moth and host habitat associations.

4. Discussion

4.1. Patterns of butterfly and moth diversity

We found no correlation in diversity patterns between butterflies and moths in this landscape, regardless of diversity measure used (Fig. 1). The lack of correlation across all sites is primarily because butterflies were almost entirely restricted to meadows, while our moth samples yielded more equivalent diversity levels among all three habitats (Fig. 2; Table 1). Even across only meadow sites, however, butterfly and moth diversity were not correlated (Table 2). These findings suggest that the two taxa have substantially different distribution patterns on a local scale, and that butterflies are unlikely to be a useful local indicator taxon even for this closely related group.

The restriction of butterflies to meadows is not surprising, as larval host plants, adult nectar sources, and favorable thermal environments for the majority of these species are found only in meadows (Sharp et al., 1974; Scott, 1986). The only two butterfly species found more than once outside of meadows (Fig. 2) are *Pieris napi*, whose host plants are found in all habitats (Scott, 1986, C. Boggs, personal communication), and *Papilio zelicaon*, a large and extraordinarily vagile species, which we observed twice moving swiftly through aspen stands.

For moths, in contrast, each habitat appears to support a substantial number of species in somewhat distinct communities (Kitching et al., 2000). Meadow, aspen, and conifer habitats each contained several moth species that were restricted to that habitat (Fig. 2). Many moth species, however, were more widespread; we found 22 moth species (36% of nonsingletons) in all three habitats, and 15 more (24%) were shared between two habitats. These widespread species either (1) are associated with widespread plant resources (because they utilize a broad array of plants or because the plants themselves are found in more than one habitat), or (2) depend on a single habitat but move frequently among habitat patches and were merely sampled en route (Woiwod and Stewart, 1990; Daily and Ehrlich, 1996).

Comparisons between habitat associations of moths and their hosts can help to illuminate the relative importance of these two possibilities (Fig. 3). Nineteen of the 35 moth species analyzed were only found in habitats containing their known host plants, suggesting that these species tend to stay where their larval resources are. On the other hand, we found 16 moth species in at least one habitat containing none of their known host plants, indicating that these species were sampled outside of their required habitat, perhaps while moving among patches. These equivocal results suggest that both factors may be important: some local moth species are widespread because their host plants are, while others have more restricted habitat requirements, but

appear widespread due to inter-patch movement. It deserves note, however, that since available host plant data for many moth species are incomplete, the number of moth species that appear more widespread than their hosts is probably inflated, and the prevalence of habitat generality in moths is thus greater than this analysis indicates.

A potential problem in our sampling design is that, if the attraction radius of our traps were large, the traps may have sampled not only the habitat in which they were placed, but also those around it. A large attraction radius thus would tend to homogenize moth samples, resulting in many apparently widespread species and relatively even diversity among sites, as we observed (Fig. 2). If the radius of attraction is substantially greater than 20 m, however, pairs of facing edge traps would sample heavily overlapping areas and should produce highly similar samples. In fact, we found that community composition of edge sites is significantly more similar to their corresponding interior sites than to the edge sites facing them across the habitat boundary. Thus the patterns we find are not likely due to sampling design alone.

4.2. Conservation implications

Because patterns of diversity appear to differ fundamentally between butterflies and moths in this landscape, conservation strategies that maximize the diversity of these two taxa should differ as well. For butterflies, meadows are the most important habitat to target for conservation, while for moths, landscape mosaics comprising all three habitats are probably important. Relying on butterflies as indicators of diversity in other taxa, therefore, may mislead conservation efforts if those taxa do not share similar patterns of habitat specificity.

These results suggest that phylogenetic relatedness, although intuitive, is not a reliable criterion for selecting appropriate indicator taxa (Holl, 1996). Other studies have found strong correlations in diversity pattern between distantly related and ecologically dissimilar taxa (e.g. Blair, 1999; Ricketts et al., 1999). Certain ecological traits [in our study, perhaps nocturnality (Daily and Ehrlich, 1996)] may overwhelm phylogeny and other ecological similarities in determining the degree of correlation in diversity. Traits that are likely to be important are difficult to predict and may be idiosyncratic to each pair of taxa tested, making it difficult to choose indicators wisely.

Certainly, however, some “shortcut” will continue to be necessary in making conservation decisions, because diversity patterns of many taxa, and the factors determining them, will remain unknown in many areas. Given the potential of indicator taxa to mislead efforts to conserve poorly known taxa, a habitat-based

approach may be a preferable strategy in many situations (Faith and Walker, 1996; Panzer and Schwartz, 1998; Hughes et al., 2001). The goal of habitat-based approaches is to conserve the diversity of habitats in a landscape or region, with the assumption that species diversity in many taxa will be conserved as well. Although defining relevant habitats in some cases may be complex and subtle, the three habitats used in this study were based on readily observable vegetation communities and were distinguishable from aerial photographs. A conservation strategy based even on this crude definition of habitat would likely be effective in conserving local diversity of moths, and probably other poorly known taxa, in this landscape (Hughes et al., 2001). The representation of all habitats in conservation plans is a basic tenet of global and regional conservation strategies (Noss and Peters, 1995; Olson and Dinerstein, 1998), where enormous spatial scales make coarse resolution necessary. Taking a similar approach at more local scales, perhaps in combination with carefully chosen indicator taxa, may afford the best opportunity to conserve biodiversity efficiently in the face of accelerating anthropogenic habitat destruction.

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Appendix A. Butterfly species recorded during this study

Family	Species	Abundance
Nymphalidae	<i>Cercyonis sthenele</i>	26
	<i>Coenonympha tullia</i>	27
	<i>Erebia epipsodea</i>	9
	<i>Oeneis chryxus</i>	39
	<i>Chlosyne palla</i>	11
	<i>Nymphalis milberti</i>	1
	<i>Phyciodes campestris</i>	1
	<i>Polygonia zephyrus</i>	4
	<i>Vanessa atalanta</i>	1
	<i>Vanessa cardui</i>	5
	<i>Euptoieta claudia</i>	16
	<i>Speyeria atlantis</i>	4
	<i>Speyeria mormonia</i>	116
Lycaenidae	<i>Lycaena heteronea</i>	40
	<i>Lycaena nivalis</i>	27
	<i>Lycaena helloides</i>	1
	<i>Everes amyntula</i>	27
	<i>Glaucopsyche lygdamus</i>	8
	<i>Plebejus saepiolus</i>	4
	<i>Agriades glandon</i>	2
Pieridae	<i>Colias alexandra</i>	23
	<i>Colias eurytheme</i>	1
	<i>Euchloe ausonides</i>	53
	<i>Pieris napi</i>	199
	<i>Pieris occidentalis</i>	30
	<i>Pieris protodice</i>	18
Papilionidae	<i>Papilio rutulus</i>	1
	<i>Papilio zelicaon</i>	21
	<i>Parnassius phoebus</i>	1
Total abundance		716
Total species		29

Appendix B. Moth species collected during this study

Family	Species	Abundance	Family	Species	Abundance
				<i>Lasionycta conjugata</i>	99
				<i>Lasionycta leucocycla</i>	2
				<i>coloradensis</i>	
				<i>Lasionycta perplexa</i>	558
				<i>Lasionycta subfuscata</i>	136
				<i>Leucania insueta</i>	243
				<i>Mamestra</i> sp.	1
				<i>Melanchra adjuncta</i>	24
				<i>Melanchra pulverulenta</i>	199
				<i>Mniotype</i> spp #1	22
				<i>Oncocnemis dayi</i>	2
				<i>Paradiarsia littoralis</i>	581
				<i>Polia purpurissata</i>	5
				<i>Protolampra rufipectis</i>	13
				<i>Scoliopteryx libatrix</i>	2
				<i>Spaelotis</i>	15
				<i>Syngrapha angulidens</i>	108
				<i>Syngrapha ignea</i>	1
				<i>Trichoplexia</i> sp.	22
				<i>Trichordestra beanii</i>	14
				<i>Xestia oblata</i>	323
				<i>Xestia perquiritata</i>	2
				<i>Xestia speciosa</i>	3
				??	1
				??	1
				??	105
				??	20
				??	1
				??	3
				??	9
				??	1
				??	30
				??	4
				??	3
				??	1
			Notodontidae	<i>Clostera albosigma</i>	3
				<i>Clostera brucei</i>	5
				<i>Furcula scolopendrina</i>	36
				<i>Gluphisia severa</i>	14
				<i>Pheosia rimosa</i>	10
			Sphingidae	<i>Hyles lineata</i>	3
				<i>Smerinthus cerisyi</i>	88
				<i>Sphinx vashti</i>	6
			Tortricidae	<i>Choristoneura conflictana</i>	94
			Total individuals		4961
			Total species		91
Arctiidae	<i>Grammia williamsi</i>	37			
Crambidae	<i>Loxostege commixtalis</i>	1			
Geometridae	<i>Dysstroma citrata</i>	2			
	<i>Ecliptopera silaceata</i>	19			
	<i>Enypia venata</i>	276			
	<i>Epirranthis substriataria</i>	2			
	<i>Eulithis xylina</i>	1			
	<i>Hydriomena morosata</i>	3			
	<i>Neoterpes trianguliferata</i>	6			
	<i>Pero behrensarius</i>	151			
	<i>Rheumaptera hastate</i>	26			
	<i>Scopula inductata</i>	40			
	<i>Scopula</i> sp.	11			
	<i>Semiothisa neptaria</i>	4			
	<i>Semiothisa subminiata</i>	3			
	<i>Spargania magnoliata</i>	140			
	<i>Xanthorhoe abrasaria</i>	1			
	<i>Xanthorhoe pontiaria</i>	44			
	??	1			
Lasiocampidae	<i>Malacosom californicum</i>	96			
	<i>Phyllodesma americana</i>	21			
Noctuidae	<i>Acrionicta impressa</i>	2			
	<i>Acrionicta lepusculina</i>	2			
	<i>Admetovis oxymorus</i>	90			
	<i>Agrotis venerabilis</i>	343			
	<i>Andropolia contacta</i>	1			
	<i>Anomogyna vernilis</i>	1			
	<i>Apamea alia</i>	27			
	<i>Apamea atosuffusa</i>	66			
	<i>Apamea inficita</i>	2			
	<i>Apamea infinita</i>	5			
	<i>Apamea lateritia</i>	5			
	<i>Aseptis binotata</i>	3			
	<i>Discestra farnhami</i>	29			
	<i>Drasteria hudsonica</i>	70			
	<i>Enargia decolor</i>	59			
	<i>Euplexia benesimilis</i>	8			
	<i>Euxoa divergens</i>	364			
	<i>Euxoa terrena</i>	8			
	<i>Euxoa tessellata</i>	1			
	<i>Hada sutrina</i>	6			
	<i>Hadena jola</i>	46			
	<i>Hadena variolata</i>	14			
	<i>Hyppa brunneicrista</i>	2			
	<i>Hyppa xylinoidea</i>	5			
	<i>Lacanobia nevadae</i>	32			
	<i>Lacinipolia olivacea</i>	70			
	<i>Lasiestra</i> sp.	2			

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