Conservation of Insect Diversity: A Habitat Approach

Jennifer B. Hughes; Gretchen C. Daily; Paul R. Ehrlich

Conservation Biology, Vol. 14, No. 6 (Dec., 2000), 1788-1797.

Conservation of Insect Diversity: a Habitat Approach

JENNIFER B. HUGHES, GRETCHEN C. DAILY, AND PAUL R. EHRLICH

Center for Conservation Biology, Department of Biological Sciences, Stanford University,
Stanford, CA 94305-5020 U.S.A.

Abstract: *Neither time nor resources exist to design conservation plans for every species, particularly for little-studied, noncharismatic, but ecologically important taxa that make up most of biodiversity. To explore the feasibility of basing conservation action on community-level biogeography, we sampled a montane insect community. We addressed three issues: (1) the appropriate scale for sampling insect communities; (2) the association of habitat specialization—perhaps a measure of extinction vulnerability—with other ecological or physical traits; and (3) the correlation of diversity across major insect groups. Using malaise traps in Gunnison County, Colorado, we captured 8847 Diptera (identified to family and morphospecies), 1822 Hymenoptera (identified to morphospecies), and 2107 other insects (identified to order). We sampled in three habitat types—meadow, aspen, and conifer—defined on the basis of the dominant vegetation at the scale of hundreds of meters. Dipteran communities were clearly differentiated by habitat type rather than geographic proximity. This result also holds true for hymenopteran communities. Body size and feeding habits were associated with habitat specialization at the family level. In particular, habitat generalists at the family level—taxa perhaps more likely to survive anthropogenic habitat alteration—tended to be trophic generalists. Dipteran species richness was marginally correlated with hymenopteran species richness and was significantly correlated with the total number of insect orders sampled by site. Because these correlations result from differences in richness among habitat types, insect taxa may be reasonable surrogates for one another when sampling is done across habitat types. In sum, community-wide studies appear to offer a practical way to gather information about the diversity and distribution of little-known taxa.*

Conservación de la Diversidad de Insectos: una Estrategia a Nivel de Hábitat

Resumen: *No existe ni el tiempo ni los recursos para diseñar planes de conservación para cada especie, particularmente para los taxones poco estudiados, no carismáticas, pero ecológicamente importantes que componen la mayoría de la biodiversidad. Para explorar la factibilidad de basar acciones de conservación en biogegrafía a nivel comunitario, muestreamos una comunidad de insectos de montaña. Evaluamos tres aspectos: (1) la escala adecuada para el muestreo de comunidades de insectos; (2) la asociación de especialización de hábitat—quizá una medida de vulnerabilidad de extinción—con otras características ecológicas o físicas; y (3) la correlación de la diversidad a lo largo de los grupos principales de insectos. Mediante el uso de trampas en el condado Gunnison, en Colorado, capturamos 8847 dípteros (identificados a nivel de familia y morfoespecies), 1822 himenópteros (identificadas hasta morfoespecies) y 2107 otros insectos (identificados a nivel de orden). Muestreamos tres tipos de hábitats—vega, álamos temblones y coníferas—definidos en base a la vegetación dominante a escala de cientos de metros. Las comunidades de dípteros estuvieron claramente diferenciadas por tipos de hábitat y no por la proximidad geográfica. Este resultado también se mantiene para las comunidades de himenópteros. El tamaño del cuerpo y los hábitos alimenticios estuvieron asociados con la especialización del hábitat a nivel de familia. En particular, los generalistas de hábitat a nivel de familia—los taxones que posiblemente tengan mayor probabilidad de sobrevivir alteraciones antropogénicas del hábitat—tendieron a ser generalistas tróficos. La riqueza de las especies de dípteros estuvo marginalmente correlacionada con la riqueza de especies de himenópteros y estuvo significativamente correlacionada con el número total de órdenes de insectos muestreadas por sitio. Debido a que estas correlaciones resultaron de diferencias en la riqueza de especies entre tipos de hábitats, los taxones de insectos podrían ser substitutos mutuos razonables cuando se muestrea entre diferentes tipos de hábitats. En resumen, los estudios a lo largo de comunidades parecen ofrecer una forma práctica de recolectar información sobre la diversidad y distribución de los taxones poco estudiados.*

Paper submitted April 12, 1999; revised manuscript accepted February 23, 2000.

Introduction

Many authors have advocated community-level conservation approaches for noncharismatic, little-known taxa (e.g., Pearson & Cassola 1992; Pimm & Gittleman 1992; Scott et al. 1993; Meffe & Carroll 1997; Oliver et al. 1998), and insects certainly qualify for this category. The majority of insect species are undescribed (Hammond 1992), and the identification of those that have been described often requires a trained specialist.

Diptera constitute the third most diverse order of insects, with an estimated 120,000 species, and are often the most abundant animals in temperate habitats. They are involved in various ecological functions, including decomposition, pollination, and pest control (Kearns 1992; Berenbaum 1995). Despite their ecological importance, however, relatively little is known about their biology, distribution, or diversity.

We used a habitat-based approach to investigate the community patterns of a montane insect community that is extraordinarily rich in Diptera. We focused on three questions central to biodiversity conservation: (1) What is a biologically meaningful scale at which to sample and manage dipteran diversity? (2) Are Diptera that are locally rare or habitat specialists—and therefore perhaps more vulnerable to extinction from habitat loss—associated with other traits? (3) Is dipteran diversity correlated with that of other insect orders?

Biodiversity at a Habitat Scale

Perhaps the most useful information that basic distribution data can provide is an appropriate scale for sampling and, ultimately, managing a taxon's diversity. Changes in species composition across a landscape can be classified into two extremes: (1) gradual changes along spatially autocorrelated gradients of environmental factors and (2) abrupt changes between discrete habitat types. To maximize the number of species included in a reserve, the reserve area should encompass species turnover caused by both kinds of changes. In general, the larger the area of a reserve, the more gradual changes will be included (Kunin 1997). For a particular reserve size, however, many habitat types should be incorporated to capture the species turnover caused by habitat discontinuities. The challenge, then, is to identify habitats with distinct species assemblages for the taxon in question.

We defined three habitat types by dominant vegetation—aspen, meadow, and spruce—in a subalpine region of Colorado. These habitats were easily categorized in the field and from aerial photographs. To test whether the habitat classifications reflect changes in the dipteran community, we asked whether habitat type or geographic proximity between sites is a better predictor of dipteran community composition. If the species composition sampled at a site is more similar to that at nearby sites than to sites within the same habitat classification, then most of the difference between sites can be attributed to spatially autocorrelated factors. Conversely, if species composition is more similar to that at other sites in the same habitat regardless of distance between the sites, then most of the differences can be attributed to habitat type. In this case, regions with greater diversity of the defined habitat types should support a higher species diversity of the taxon under consideration.

Extinction Vulnerability and Habitat Specialization

Local distribution data can also be used to identify species or family traits associated with habitat specialization. By knowing the characteristics associated with habitat specialization, one can predict not only which taxa might be vulnerable to extinction from habitat loss, but also some of the consequences of their loss for community composition and ecosystem function (e.g., Thomas 1991; Kremen et al. 1993; Bond 1995).

We asked whether habitat specialization of dipteran species is related to body size or larval trophic guild. One might expect that larger species could disperse farther and so would be better at colonizing and maintaining populations in different habitats. Similarly, families that include a variety of trophic guilds may be better able to occupy more habitat types than families that include few trophic guilds.

Insect Indicators

Because resources and time for the conservation of biodiversity are limited, rapid methods for assessing biogeographic patterns are needed. One proposed method is using well-known groups, such as butterflies, birds, and mammals, as indicators of overall species richness in an area (e.g., Kremen 1992; Pearson & Cassola 1992; Prendergast et al. 1993; Lawton et al. 1998; Ricketts et al. 1999). This method assumes that the species richness of well-known groups correlates with that of lesser-known groups. Likewise, it is useful to know whether taxa within diverse but poorly known insect groups share similar diversity patterns, appropriate sampling scales, and characteristics associated with habitat specialization. Thus, we examined whether dipteran diversity is correlated with wasp diversity (order Hymenoptera) or the diversity of all insect orders.

Methods

We sampled insects in the vicinity of the Rocky Mountain Biological Laboratory, Gunnison County, Colorado, from mid-June to mid-August of 1996. The major vegetation types in the region are meadow, aspen (*Populus tremuloides*) grove, and conifer forest. The conifer habitat is dominated by Engelman spruce (*Picea engelmanni*), except at one sampling location (Almont Summit) where lodgepole pine (*Pinus contorta*) dominates. The next most abundant habitat type is willow thicket, which occurs along the rivers and streams.

Meadow and aspen habitats support a diverse community of herbaceous plants, whereas conifer habitat has a sparse understory of shade-tolerant species. We selected sampling locations—Almont Summit, East River, Washington Gulch, and Kebler Pass—in four valleys. Within each location, we placed one malaise trap in each habitat type (meadow, aspen, and conifer) within 3 km of one another. We refer to the traps as "sites." Each location therefore included three sites, for a total of four locations and 12 sites. The locations were separated by at least 4 km, and the elevations ranged from 2800 to 3350 m. Almont Summit is 37 km south of the other locations, and although roughly the same elevation, it is much drier. The traps were surrounded by more than 100 m of uniform habitat in every direction. Each trap was open for 2 days every other week, for a total of four 2-day samples at each site.

Samples were sorted to insect order, and the Diptera and Hymenoptera were then sorted to morphospecies or recognizable taxonomic units (RTUs; Oliver & Beattie 1993). Hereafter we refer to morphospecies as species. The dipteran species were identified to family by the authors. D. M. Wood (Agriculture Canada) verified these identifications.

Habitat specialization was defined as the number of habitats from which we sampled a species. Thus, a species found in three habitats is a habitat generalist. This measure underestimates a species' degree of habitat specialization because it assumes that a species can complete its entire life cycle in any habitat in which it is found.

Five individuals (or fewer if fewer were collected) of each dipteran species and two individuals of each hymenopteran species were measured to the nearest 0.5 mm for length (head to tip of abdomen), width (of thorax), and height (of thorax). The species' "biovolume" (Siemann et al. 1996) was calculated by multiplying the three measurements and averaging across the specimens.

The dipteran families were placed in trophic guilds based on information given in the *Manual of Nearctic Diptera* (McAlpine et al. 1981). Each family was assigned to one or more of the following guilds: phytophagous, mycetophilous, saprophagous, and predaceous. The guild classifications are based on studies of the larval habitats and food resources of species in the family. Each fly species probably belongs to only one larval guild, so the number of guilds in a family represents the variability among species' trophic strategies (and not trophic generality within species).

We used two analyses to test whether insect communities were more closely related by geographic proximity (i.e., influenced mostly by spatially autocorrelated factors) or habitat types (i.e., influenced mostly by abrupt differences associated with the dominant vegetation). We used Kruskal-Wallis tests to detect differences in species richness, total insect abundance, and evenness among geographic locations and habitat types. Evenness (E) was calculated as Shannon's diversity index scaled by the total number of species (S) at a site:

$$E = -(\sum p_i \ln p_i)/\ln S,$$

where p_i is the proportional abundance of species i (Pielou 1975). We used additive similarity trees (Systat 7.0) to examine whether community composition was more similar by habitat type or geographic location. We calculated the similarity between sites j and k with S species as

$$2W/(A+B) \times 100, \text{ where } W = \sum_{i=1}^{S} [\min(X_{ij}, X_{ik})], A = \sum_{i=1}^{S} X_{ij}, \text{ and } B = \sum_{i=1}^{S} X_{ik}$$

(Bray & Curtis 1957). The X_i is the abundance of species i, and S is the number of species collected at a site. This similarity measure incorporates species' abundances and the number of species shared between sites. For correlation tests, we report Spearman's rank coefficient (r_s) when the data were not normally distributed. Otherwise, we report Pearson's correlation coefficient (r) (Zar 1984).

We also examined two methodological issues. First, many Diptera swarm, so a sample from a malaise trap may not be representative of the actual proportions of flying insects in the immediate habitat. To test whether we were collecting representative samples, we sampled three times with a second trap in the East River meadow. The second malaise trap was located 25 m away from the primary trap and was open for 2 days at a time, overlapping with the primary trap sampling by 1 day.

Second, we wanted to test the assumption that the flies used resources in the habitat where they were collected. To get an idea of how far an insect might fly into unsuitable habitat, we placed a malaise trap on a talus slope (rock fragments) that was 80 m from any vegetation. Thus, we could be sure that most of the flies caught in this trap were not using resources in the area, but rather were just passing through.

Results

Diptera

A total of 12,776 insects from 14 orders was collected. Of these, 8847 individuals were Diptera, and 328 dipteran species from 46 families were identified (Appendix). The meadow sites were the most diverse (243 species), followed by aspen (232) and conifer (159). Thirty-four percent of the individuals were sampled in meadow, 38% in aspen, and 28% in conifer.

HABITAT TYPE VERSUS GEOGRAPHIC LOCATION

Dipteran species richness was significantly different among habitat types (Kruskal-Wallis $H = 7.7308$, df = 2, $p = 0.0210$), but there was no difference in species richness among geographic locations ($H = 0.8462$, df = 3, $p = 0.8384$). Similarly, evenness differed by habitat type ($H = 6.3395$, df = 3, $p = 0.0420$), not by location ($H = 1.5310$, df = 3, $p = 0.6751$). In all locations, species richness and evenness was lower in conifer than aspen or meadow sites (Table 1). Number of individuals captured did not differ significantly among habitats ($H = 1.8846$, df = 2, $p = 0.3897$) or location ($H = 6.8974$, df = 3, $p = 0.0752$), although average abundance at the East River sites was almost twice that of the other three locations.

Community composition was also more similar within habitat types than within geographic location (Fig. 1). Only Almont Summit aspen was clustered outside of its habitat type in the similarity tree, and it was grouped most closely with Almont Summit conifer.

ABUNDANCE AND HABITAT SPECIALIZATION

For the habitat specialization analyses, we excluded 12 species (3.7% of all species) that D. M. Wood thought included more than one actual species (i.e., more than one species was assigned the same morphospecies number). Of the 316 remaining species, 129 were found in one habitat type, 96 in two, and 91 in three. Seventy-eight species were represented by only one individual, accounting for 59% of the 129 species found in only one habitat. Even when we removed the species represented by one individual, the number of individuals of each species was highly correlated with the number of habitats in which the species was found (Spearman rank $r_s = 0.621$, $n = 238$, $p < 0.001$). Although many rare species were found in all three habitats, the most abundant species were almost never found in just one habitat type (Fig. 2).

The number of habitats in which a family was found was also positively correlated with the average number of indi-

Table 1. Number of individuals, number of species, and evenness (E) of Diptera collected at each location and the habitats within the locations.

Location and habitat	*No. of individuals*	*No. of species*	E
Almont Summit	1535	185	0.811
meadow	641	120	0.821
aspen	521	93	0.824
conifer	373	71	0.740
Kepler Pass	1939	197	0.804
meadow	720	123	0.774
aspen	886	131	0.803
conifer	333	63	0.731
East River	3479	211	0.785
meadow	982	128	0.810
aspen	1235	126	0.770
conifer	1262	92	0.724
Washington Gulch	1894	197	0.787
meadow	684	132	0.868
aspen	694	103	0.731
conifer	516	66	0.733
All locations	8847	328	

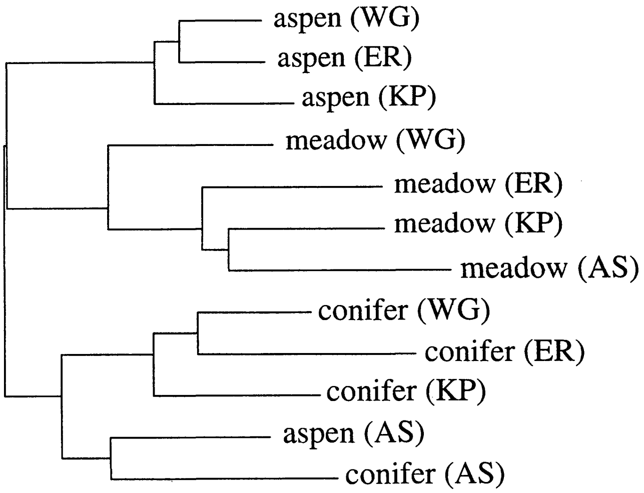

Figure 1. Additive similarity tree of dipteran communities from 12 sites in Colorado (AS, Almont Summit; ER, East River; KP, Kepler Pass; WG, Washington Gulch).

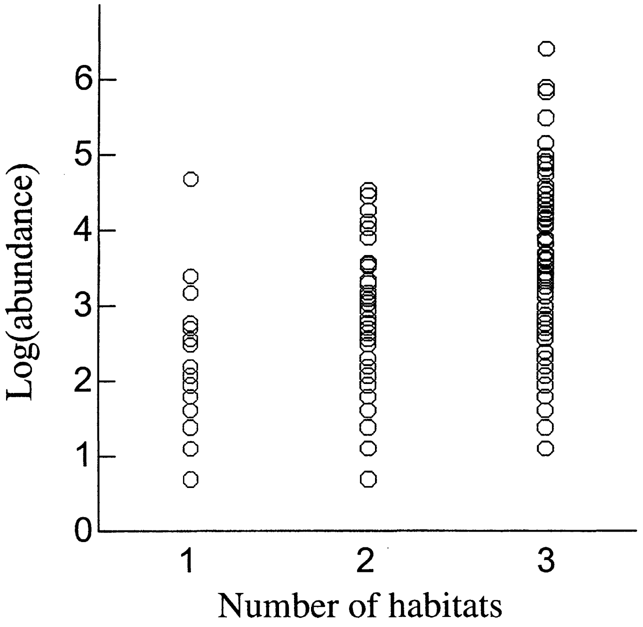

Figure 2. Log abundance versus the number of habitats in which each dipteran species (abundance >1) was found.

viduals per species caught in the family ($r_s = 0.377$, $n = 44$, $p < 0.02$) and even more so with the number of species caught in the family ($r_s = 0.546$, $n = 44$, $p < 0.001$).

BODY SIZE AND HABITAT SPECIALIZATION

There was a potential sampling artifact between body size, habitat occupancy, and number of individuals when we tested whether body size is related to the number of habitats a species or family occupies. First, the number of individuals captured was negatively correlated with the body size of a species, excluding species represented by only one individual ($r_s = -0.288$, $n = 235$, $p < 0.001$). Second, because there was a significant relationship between a species' local abundance and the number of habitats in which it was found, we expected to find a disproportionate number of smaller individuals in more habitats because of the underdetection of species with low local abundance and larger body size.

To minimize this bias, we regressed the biovolume of all fly species (abundance > 1) against their abundance and calculated the residuals ($F = 26.131$, df = 1,233, $p < 0.001$). We then tested whether the residuals were significantly different among species in two or three habitats. (We excluded species found in only one habitat because the sample sizes of these families were small. It is thus uncertain that they were really restricted to one habitat.) Body size did not appear related to a fly species' habitat specialization (Mann-Whitney $U = 4475.5$, $n = 93,91$, $p = 0.499$).

FAMILY BODY SIZE AND HABITAT SPECIALIZATION

Unlike in the species analyses, the average biovolume of dipteran families (each species equally weighted) was not correlated with family abundance, the sum of the individuals of all species in the family (log-transforming average family biovolume and family abundance: $r = -0.089$, $n = 44$, $p > 0.5$). Because of low sample sizes, we again excluded families found in only one habitat. Although there was no significant difference between body size of families found in two or three habitats (Mann-Whitney $U = 121$, $n = 10,29$, $p = 0.440$), 11 out of the 12 families with the largest average body size (>16 mm^3) were found in all three habitats (Fig. 3).

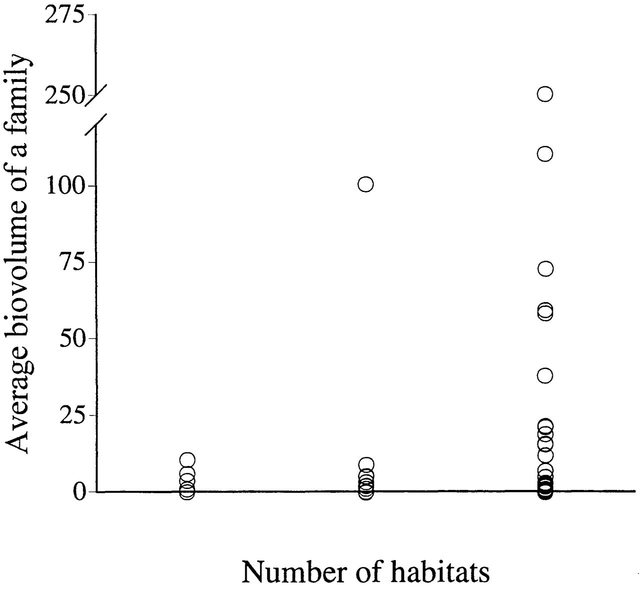

Figure 3. Number of habitats in which a family of Diptera was found versus the average biovolume of species in the family.

TROPHIC GUILDS AND HABITAT SPECIALIZATION

Of the 46 families, 27 were classified into one guild, 12 into two, 3 into three, and 4 into all four guilds (Appendix). The number of guilds a family included and its habitat specialization were not significantly correlated ($r_s = 0.260$, $n = 40$, $p > 0.10$). In this test, families that were represented by <5 individuals were excluded, and a habitat was considered occupied by a family only if more than one individual from the family was found in the habitat. Although the correlation was not significant, 6 out of 7 of the families with three or four guilds were found in all three habitats, and the seventh family was found in two habitats (Fig. 4). No families with three or four guilds were found in only one habitat. Furthermore, the tendency among families with many guilds did not appear to be a sampling artifact. Family abundance was

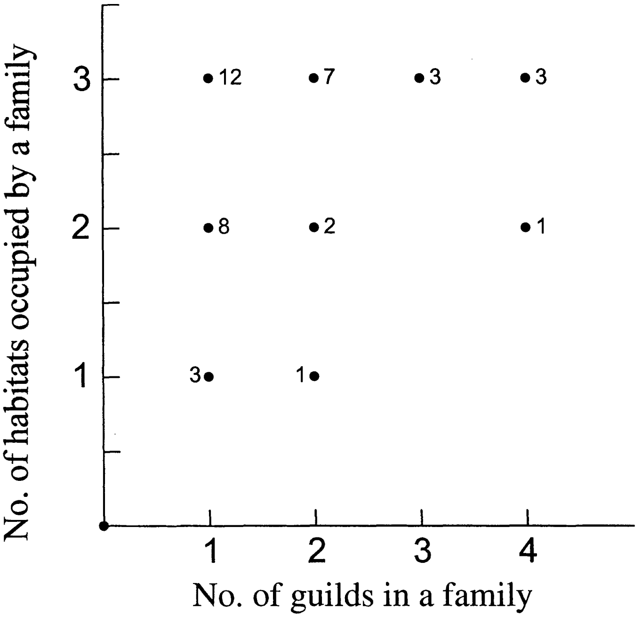

Figure 4. The number of guilds included in a dipteran family versus the number of habitats in which the family was found. The number by each point indicates how many families occurred at that point.

correlated with the number of habitats in which the family is found ($r_s = 0.597$, $n = 44$, $p < 0.001$) but not with the number of guilds in the family ($r_s = 0.236$, $n = 44$, $p > 0.10$).

To look for differences in habitat specialization among trophic guilds, we first examined families that included only one guild ($n = 25$). Predaceous families appeared to be present in all habitats more often than families from other guilds (Table 2), but the sample sizes were too small to test this statistically. Rather, we examined whether families that included predators (regardless of the other guilds in the family) were more likely to be in three habitats versus either one or two habitats and found that families that include predators are more likely to be found in all three habitats ($\chi^2 = 3.725$, df = 1, $p = 0.038$). Based on the results of the same test for each guild type, families including the mycetophilous guild were more likely to be found in three habitat types than one or two ($\chi^2 = 4.302$, df = 1, $p = 0.038$), whereas families including phytophagous and saprophagous larvae were not ($\chi^2 = 0.444$, df = 1, $p = 0.505$ and $\chi^2 = 0$; df = 1; $p = 1.0$, respectively).

Among the families that included only one guild ($n = 25$), the average biovolume was significantly different between guilds (Kruskal-Wallis $H = 10.712$, df = 3, $p = 0.013$; Fig. 5). On average, predaceous families had larger bodies than other guilds ($\bar{x} = 68.0$ mm^3), saprophagous were intermediate in size (9.7 mm^3), and mycetophilous and phytophagous families were relatively small (3.1 and 3.6 mm^3, respectively). Although abundance was not significantly different among guilds (Kruskal-Wallis; $H = 5.668$, df = 3, $p = 0.129$), the two mycetophilous families were the families with the two highest abundances (Fig. 6).

CONTROLLING FOR PHYLOGENY

Spurious correlations (or noncorrelations) result when traits of species and families are not independent from one another (Harvey & Pagel 1991). To account for this problem, we examined the relationships within families. For seven of the eight families, the number of habitats occupied by a species was positively correlated with the number of individuals captured but was not correlated with species biovolume (Table 3). Biovolume and total abundance tend to be negatively related (although significantly only for Muscidae; Table 3). Only the Tachinidae does not follow the general trend: the largest tachinid species are the most abundant and are found in more habitat types.

Table 2. Number of dipteran families that were sampled in one, two, or three habitats by guild.

	Number of habitats		
Guild	*1*	*2*	*3*
Mycetophilous	0	0	2
Phytophagous	1	3	1
Predaceous	1	1	7
Saprophagous	1	4	4
Total	3	8	14

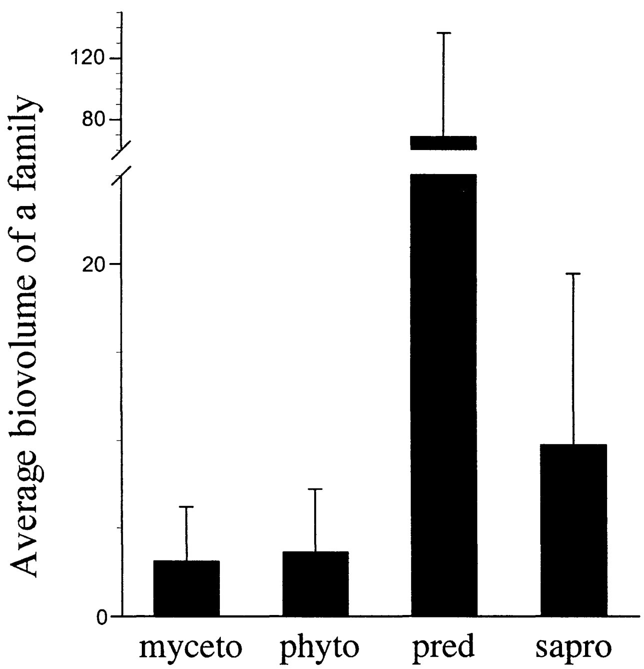

Figure 5. Average biovolume of dipteran families by guild (excludes families that include more than one guild). Error bars 1 SD. Myceto, mycetophilous; phyto, phytophagous; pred, predaceous; sapro, saprophagous.

METHODOLOGICAL TESTS

The samples in the extra East River meadow trap differed from those in the original trap by as much as 50% in dipteran abundance and 17% in species richness during the same sampling weeks. Despite this variation, the two traps in the East River meadow were more similar to each other than to any other trap from any sampling location. The similarity value between the two East River traps was 0.52, whereas the range of similarity values between the extra East River meadow trap and the 11 traps at the other sites was 0.16–0.42. Thus, within-site variation probably did not mask between-site biogeographic differences.

The abundance of Diptera trapped at the talus site was lower than that at all other sites for those 2 weeks (45 and 20 individuals collected at the talus site versus an average of 184 ± 105 SD individuals at the nontalus sites). In addition, there was no trend in the families or the size of the flies collected at the talus site (Kruskal-Wallis $H = 4.070$, df = 2, $p = 0.131$).

Other Insects

We sampled a total of 1822 individuals and 391 species of Hymenoptera. The meadow sites were the most di-

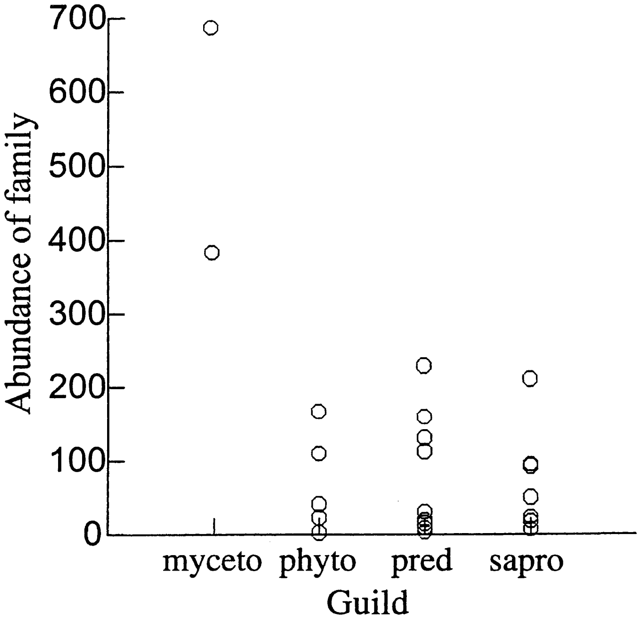

Figure 6. Total abundance of families by guild (excludes families that include more than one guild). See Fig. 5 legend for definition of guild abbreviations.

verse (203 species), followed by aspen (213) and conifer (137). Fourth-two percent of the individuals were sampled in meadow, 37% in aspen, and 22% in conifer. Of these 391 species, 259 were found in one habitat type, 99 in two, and 32 in three. Many of the species (164) were represented by only one individual, accounting for 64% of the species found in only one habitat.

Hymenopteran species richness did not differ between geographic locations (Kruskal-Wallis: $H = 5.051$, df = 3, $p = 0.168$) or habitat type ($H = 3.500$, df = 2, $p = 0.174$), but, like the Diptera, the conifer habitat had the lowest total species richness (203 species in meadow, 213 in aspen, and 137 in conifer). Hymenopteran evenness was not significantly different between sites ($H = 0.333$, df = 3, $p = 0.954$) or habitat types ($H = 4.192$, df = 2, $p = 0.123$). As with species richness, evenness was lowest in the conifer habitat ($E = 0.878$ in meadow, 0.872 in aspen, and 0.793 in conifer). Hymenopteran abundance also did not differ among locations ($H = 5.359$, df = 3, $p = 0.147$) or habitats ($H = 3.500$, df = 2, $p = 0.174$). The additive similarity tree groups the sites by habitat type rather than geographic location, suggesting that Hymenoptera, like Diptera, are distinguishing between habitat types (similarity tree not shown).

In addition to Diptera and Hymenoptera, 12 other insect orders were captured in the malaise traps: Coleoptera, Ephemeroptera, Hemiptera, Homoptera, Isoptera, Lepidoptera, Neuroptera, Orthoptera, Plecoptera, Psocoptera, Thysanoptera, and Trichoptera. The diversity and abundance of insect orders as a whole showed biogeographic patterns similar to those of species among the Diptera and Hymenoptera. For example, the difference in number of orders among habitat types was marginally significant (Kruskal-Wallis $H = 5.087$, df = 2, $p = 0.079$) but not significant among locations ($H = 1.453$, df = 3, $p = 0.693$). On average, the conifer habitat had the fewest orders ($\bar{x} = 6.50$), followed by aspen (7.75) and meadow (8.25). The mean number of insect individuals (excluding Diptera) was significantly different among habitat types ($H = 7.423$, df = 2, $p = 0.024$) and not significantly different among locations ($H = 0.744$, df = 3, $p = 0.863$).

The number of hymenopteran and dipteran species captured at a trap tended to be positively related, but not significantly so ($r_s = 0.545$, $n = 12$, $p < 0.10$). When we excluded the Almont Summit aspen site (an outlier in the dipteran similarity tree), the relationship became significant ($r_s = 0.709$, $n = 11$, $p = 0.02$). The number of insect orders collected in a trap was also highly correlated with the number of dipteran species ($r_s = 0.748$, $n = 12$, $p < 0.01$). These relationships appear to be driven by habitat differences. The meadow sites all had high numbers of dipteran species, hymenoptera species, and insect orders, whereas the conifer sites had low numbers of these groups.

Table 3. The relationships (reported as Spearman rank correlation coefficients) between the number of habitats in which a species is found, its abundance, and its biovolume for species in the eight most abundant dipteran families.[a]

Family	*No. species*	*No. habitats vs. abundance*[b]	*No. habitats vs. biovolume*[b]	*Biovolume vs. abundance*[b]
Anthomyiidae	23	0.669***	-0.013	-0.162
Chironomidae	20	0.621**	-0.160	-0.198
Dolichopodidae	12	0.758**	0.361	-0.152
Empididae	12	0.425	-0.031	-0.455
Muscidae	22	0.730***	-0.296	-0.679***
Mycetophilidae	21	0.660**	-0.130	-0.128
Syrphidae	13	0.609*	0.071	-0.383
Tachinidae	14	0.853***	0.584*	0.419

[a] *Only species with abundances of >1 are included in this analysis.*
[b] * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Discussion

Dipteran communities were more clearly differentiated by habitat as defined by dominant vegetation rather than geographic proximity between sites. This result does not mean that spatially autocorrelated factors do not influence these communities, however. In regions such as our study area that incorporate many habitat types, distance may not be as important as habitat type (e.g., Harrison et al. 1992). Yet at sampling scales that capture a different amount of habitat variation, distance might influence community composition. For instance, French (1999) found that the similarity of dipteran communities decreases with distance between sites in an Australian eucalypt forest. In a Finnish forest, however, the similarity of beetle and spider assemblages was not related to distance (Niemelä et al. 1996).

Classifying habitats in this region of Colorado was relatively straightforward, so management decisions aimed at maximizing local dipteran diversity could be made without knowing the habitat requirements for individual species. O'Neil et al. (1995) found that their vegetation classifications in Oregon also agree well with animal community composition. In areas of more complex vegetation such as tropical forests, however, habitat classification is not as simple (Condit 1996), although not impossible (Tuomisto et al. 1995).

Problems with Measuring Habitat Specialization

The most abundant dipteran species (the sum of all individuals of a species) and families (the sum of all individuals of all species in a family) were found in more habitat types. A positive abundance-distribution (here abundance-habitat occupancy) relationship appears ubiquitous in studies that sample in only a small part of a species' geographic range (e.g., Brown 1984). There has been much discussion about the extent to which this relationship results from "sampling artifact."

From our data, we cannot easily disentangle the contribution of sampling bias from the genuine relationship between abundance and habitat occupancy. The relationship we found is at least partially an artifact of detection; that is, the distribution of locally rare species is underestimated because they were less likely to be detected in any given sample. We tried to mitigate this bias by excluding rare species or all species found in only one habitat so that we might detect how habitat specialization—not low local abundance—is related to trophic specialization and body size.

Regardless of sampling bias, it is unclear how well the number of habitats in which adult flies were found reflects a species' true habitat specialization. Few Diptera were captured in the talus sites, which suggests that vagrants—individuals that cannot survive in the habitat in which they are collected—probably did not greatly modify our results. More problematic is that trapping adults ignores the larvae; adults and larvae may have different habitat requirements. For instance, Syrphidae are predaceous as larvae, but as adults they consume nectar and pollen. Delettre et al. (1998) found almost twice as many Diptera species flying above a 50 × 50 m area than they recorded emerging from the same area. We sampled much larger areas, however, so were less likely to capture adults that had developed elsewhere.

Habitat Specialization and Taxon Traits

Body size and guild type appear to be associated with the degree of dipteran habitat specialization. Our chi-square tests suggest that families that include predaceous and mycetophilous species occur in more habitats than those that include phytophagous and saprophagous species. The significance values of these analyses are suspect, however, because the number of guilds included in a family and the number of habitats in which the family was found are not independent (Fig. 4). For example, every family that includes four guilds also includes the guild being tested, and families with four guilds almost always occupied all three habitats.

Despite this bias, we conclude that predaceous and mycetophilous families are more likely to be habitat generalists than phytophagous and saprophagous families. The largest-bodied families are predaceous, and large-bodied families tend to be found in more habitats. Similarly, the two mycetophilous families are the most abundant, and abundant families are found in more habitats. Thus, large, predaceous families and abundant, mycetophilous families may be less vulnerable to extinction resulting from habitat loss. This result does not imply, however, that the species within these families are more likely to be habitat generalists. For instance, 5 out of the 12 dolichopodid species (a predaceous family) were found only in one habitat type, although the family was found in all habitats.

With the exception of the Drosophilidae (of which only seven individuals were sampled), families that include three or four guilds were found in all habitats. The opposite was not true, however; families that include only one or two guilds were found in any number of habitat types (Fig. 4). In other words, not all trophic specialists were habitat specialists, but habitat generalists were almost certainly trophic generalists. The number of guilds was not significantly correlated with the number of individuals or species in the family; therefore, the relationship between trophic specialization and habitat specialization does not appear to be an artifact of trophic generalists being more abundant.

Comparisons with Other Insects

The communities of Hymenoptera and insect orders as a whole were also better defined by habitat type than by geographic location. Thus, habitat type appears to be biologically meaningful to many insect groups.

In trying to find reliable indicators of overall biodiversity, researchers have searched for taxa whose richness positively correlates with that of many other taxa. In our study, dipteran species richness was correlated with the number of insect orders. The sampling points we used in these correlations were not independent, however. In fact, these relationships may result from richness differences among habitat types, whereas within habitat types, diversity of insect order may not correlate with dipteran diversity.

At the same time, insect order richness may be a reasonable surrogate of dipteran species richness across different habitat types. Fujisaka et al. (1998) report that plant species, genus, and family richness are positively correlated across different agricultural habitats in Brazil. In studies of larger geographic scales, families of birds, bats, butterflies, and plants are positively correlated with lower taxa (Williams & Gaston 1994; Balmford et al. 1996*a*, 1996*b*). Thus, higher-taxon richness may be a good indicator of species richness when sampling is done across a large geographic area or across habitat types where variation in higher-taxon richness is high. Assessing numbers of insect orders is certainly much easier and quicker than identifying insect morphospecies. Finally, because insects have a reputation for high interannual population variation (e.g., Davidson & Andrewartha 1948), it would be interesting to know if these relationships hold across multiple years.

Conclusions

Our study of the local biogeography of flies demonstrates how much can be gained from a community-wide survey of a little-studied major taxon. The general applicability of local biogeographic studies to conservation will be determined by how transferable the results are to other years, taxa, and geographic areas. If new taxon-specific information is going to contribute to conservation decisions, we suggest that community-wide approaches similar to this study should be developed and refined. For the majority of the world's biodiversity, broad-brush studies offer the only way to gather biological information faster than the subject itself disappears.

Acknowledgments

We thank S. Daily, C. Kokesh, and M. Lulow for many hours of sorting, M. Wood for checking dipteran identifications, D. Inouye for sharing his malaise trap samples, and D. Goehring and J. Pitluk for data entry. A. Beattie, J. Hellmann, and T. Ricketts provided valuable discussions and comments.

Literature Cited

Balmford, A., M. J. B. Green, and M. G. Murray. 1996*a*. Using higher-taxon richness as a surrogate for species richness. I. Regional tests. Proceedings of the Royal Society of London B **263:**1267–1274.

Balmford, A., A. H. M. Jayasuriya, and M. J. B. Green. 1996*b*. Using higher-taxon richness as a surrogate for species richness: II. Local applications. Proceedings of the Royal Society of London B **263:** 1571–1575.

Berenbaum, M. R. 1995. Bugs in the system: insects and their impact on human affairs. Addison-Wesley, Reading, Massachusetts.

Bond, W. J. 1995. Assessing the risk of plant extinction due to pollinator and disperser failure. Pages 131–146 in J. H. Lawton and R. M. May, editors. Extinction rates. Oxford University Press, Oxford, United Kingdom.

Bray, J., and J. T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecological Monographs **27:**325–349.

Brown, J. H. 1984. On the relationship between abundance and distribution of species. The American Naturalist **124:**255–279.

Condit, R. 1996. Defining and mapping vegetation types in mega-diversity tropical forests. Trends in Ecology and Evolution **11:**4–5.

Davidson, J., and H. G. Andrewartha. 1948. Annual trends in a natural population of *Thrips imaginis* (Thysanoptera). Journal of Animal Ecology **17:**193–199.

Delettre, Y. R., N. Morvan, and P. Tréhen. 1998. Local biodiversity and multi-habitat use in empidoid flies (Insecta: Diptera, Empidoidea). Biodiversity and Conservation **7:**9–25.

French, K. 1999. Spatial variability in species composition in birds and insects. Journal of Insect Conservation **3:**183–189.

Fujisaka, S., G. Escobar, and E. Veneklass. 1998. Plant community diversity relative to human land uses in an Amazon forest colony. Biodiversity and Conservation **7:**41–57.

Hammond, P. M. 1992. Species inventory. Pages 17–39 in B. Groombridge, editor. Global biodiversity, status of the Earth's living resources. Chapman and Hall, London.

Harrison, S., S. J. Ross, and J. H. Lawton. 1992. Beta-diversity on geographic gradients in Britain. Journal of Animal Ecology **61:**151–158.

Harvey, P. H., and M. D. Pagel. 1991. The comparative method in evolutionary biology. Oxford University, Oxford, United Kingdom.

Kearns, C. A. 1992. Anthophilous fly distribution across and elevation gradient. American Midland Naturalist **127:**172–182.

Kremen, C. 1992. Assessing the indicator properties of species assemblages for natural areas monitoring. Ecological Applications **2:**203–217.

Kremen, C., R. K. Colwell, T. L. Erwin, D. D. Murphy, R. F. Noss, and M. A. Sanjayan. 1993. Terrestrial arthropod assemblages: their use in conservation planning. Conservation Biology **7:**796–808.

Kunin, W. E. 1997. Sample shape, spatial scale and species counts: implications for reserve design. Biological Conservation **82:**369–377.

Lawton, J. H., D. E. Bignell, B. Bolton, G. F. Bloemers, P. Eggleton, P. M. Hammond, M. Hodda, R. D. Holt, T. B. Larsen, N. A. Mawdsley, N. E. Stork, D. S. Srivastava, and A. D. Watt. 1998. Biodiversity inventories, indicator taxa, and effects of habitat modification in tropical forest. Nature **391:**72–76.

McAlpine, J. F., B. V. Peterson, G. E. Shewell, H. J. Teskey, J. R. Vockeroth, and D. M. Wood. 1981. Manual of nearctic diptera. Canadian Government Publishing Centre, Hull, Quebec.

Meffe, G. K., C. R. Carroll, and contributors. 1997. Principles of conservation biology. 2nd edition. Sinauer Associates, Sunderland, Massachusetts.

Niemelä, J., Y. Haila, and P. Puntilla. 1996. The importance of small-scale heterogeneity in boreal forests: variation in diversity in forest-floor invertebrates across the succession gradient. Ecography **19:**352–368.

Oliver, I., and A. J. Beattie. 1993. A possible method for the rapid assessment of biodiversity. Conservation Biology **7:**562–568.

Oliver, I., A. J. Beattie, and A. York. 1998. Spatial fidelity of plant, vertebrate, and invertebrate assemblages in multiple-use forest in Eastern Australia. Conservation Biology **12:**822–835.

O'Neil, T. A., R. J. Steidl, W. D. Edge, and B. Csuti. 1995. Using wildlife communities to improve vegetation classification for conserving biodiversity. Conservation Biology **9**:1482-1491.

Pearson, D. L., and F. Cassola. 1992. World-wide species richness patterns of tiger beetles (Coleoptera: Cicindelidae): indicator taxon for biodiversity and conservation studies. Conservation Biology **6:** 376-391.

Pielou, E. C. 1975. Ecological diversity. Wiley, New York.

Pimm, S. L., and J. L. Gittleman. 1992. Biological diversity: where is it? Science **255**:940.

Prendergast, J. R., R. M. Quinn, J. H. Lawton, B. C. Eversham, and D. W. Gibbons. 1993. Rare species, the coincidence of diversity hotspots and conservation strategies. Nature **365**:335-337.

Ricketts, T., E. Dinerstein, D. Olson, C. Loucks, W. Eichbaum, K. Kavanagh, P. Hedao, P. Hurley, K. Carney, R. Abell, and S. Walters. 1999. Terrestrial ecoregions of North America: a conservation assessment. Island Press, Washington, D.C.

Scott, J. M., F. Davis, B. Csuti, R. Noss, B. Butterfield, C. Groves, H. Anderson, S. Caicco, F. D'erchia, T. C. Edwards Jr., J. Ulliman, and R. G. Wright. 1993. Gap analysis: a geographic approach to protection of biological diversity. Wildlife Monographs **123**.

Siemann, E., D. Tilman, and J. Haarstad. 1996. Insect species diversity, abundance and body size relationships. Science **380:**704-706.

Thomas, J. A. 1991. Rare species conservation: case studies of European butterflies. Pages 149-197 in I. F. Spellerberg, F. B. Goldsmith, and M. G. Morris, editors. The scientific management of temperate communities for conservation. Blackwell Scientific, Oxford, United Kingdom.

Tuomisto, H., K. Ruokolainen, R. Kalliola, A. Linna, W. Danjoy, and Z. Rodriguez. 1995. Dissecting Amazonian biodiversity. Science **269:** 63-66.

Williams, P. H., and K. J. Gaston. 1994. Measuring more of biodiversity: can higher-taxon richness predict wholesale species richness? Biological Conservation **67**:211-217.

Zar, J. H. 1984. Biostatistical analysis. Prentice Hall, Englewood Cliffs, New Jersey.

Appendix

The number of species collected and larval guild classification of the dipteran families found.

Family	*No. of species in family*	*Larval guild**
Agromyzidae	5	Y
Anthomyiidae	28	S,Y
Anthomyzidae	1	Y
Asilidae	4	P
Asteiidae	1	S
Bibionidae	2	S,Y
Calliphoridae[c]	3	S
Cecidomyidae	7	M,P,S,Y
Ceratopogonidae	6	M,S
Chironomidae	25	P,S,Y
Chloropidae	7	M,P,S,Y
Conopidae	1	P
Culicidae	2	P
Dolichopodidae	12	P,Y
Drosophilidae	2	M,P,S,Y
Dryomyzidae	1	S
Empididae	14	M
Heleomyzidae	6	M,S
Lauxaniidae	5	S
Lonchaeidae	3	S,Y
Milichidae	3	S
Muscidae	39	M,P,S,Y
Mycetophilidae	23	M
Opomyzidae	1	Y
Otitidae	2	S,Y
Pallopteridae	1	P
Phoridae	4	P,S
Piophilidae	1	S
Pipunculidae	4	P
Platypezidae	1	M
Psilidae	3	Y
Psychodidae	3	S
Rhagionidae	1	S,P
Sarcophagidae	6	P
Scatophagidae	12	P,S,Y
Sciaridae	3	M,S
Sciomyzidae	4	P
Sepsidae	4	S
Simuliidae	3	P,Y
Sphaeroceridae	1	S
Stratiomyiidae	1	P,S
Syrphidae	18	P
Tachinidae	20	P
Tephritidae	5	Y
Therevidae	1	P
Tipulidae	14	M,S,Y

**Larval guild abbreviations: M, mycetophilous; P, predaceous; S, saprophagous, Y, phytophagous.*