Additive Partitioning of Species Diversity across Multiple Spatial Scales: Implications for Regional Conservation of Biodiversity

JON C. GERING,* THOMAS O. CRIST, AND JOSEPH A. VEECH
Department of Zoology, Miami University, Oxford, OH 45056, U.S.A.

Abstract: Ecologists and conservation biologists are keenly interested in how patterns of species diversity change across spatial scales. We examined how additive partitioning can be used to statistically evaluate spatial patterns of species diversity and develop conservation strategies. We applied additive partitioning to data on arboreal beetle diversity (richness, Shannon, Simpson) collected from a nested design consisting of four hierarchical levels—trees, forest stands, sites, and ecoregions—that corresponded to increasingly broader spatial scales within the eastern deciduous forest of Ohio and Indiana (U.S.A.). A significant percentage (relative to that of randomization tests) of total species richness and Shannon and Simpson diversity was attributed to beta diversity between ecoregions and, to a lesser extent, among sites (parks and nature preserves) within ecoregions. Hierarchical cluster analysis corroborated these findings. We also found differences between rare species (<0.05% of total abundance) and common species (>0.5% of total abundance) in the overall percentage of richness explained by each spatial scale. Rare species accounted for the majority (45%) of the 583 total beetle species in our study and were strongly influenced by broad spatial scales (i.e., ecoregions), whereas the richness of common species was significantly greater than expected across the range of spatial scales (from trees to ecoregions). Our results suggest that the most effective way to preserve beetle diversity in the eastern deciduous forest of the United States is to acquire and protect multiple sites within different ecoregions. More generally, we advocate the use of diversity partitioning because it complements existing models in conservation biology and provides a unique approach to understanding species diversity across spatial scales.

División Aditiva de la Diversidad de Especies en Escalas Espaciales Múltiples: Implicaciones para la Conservación de Biodiversidad Regional

Resumen: Los ecólogos y biólogos de la conservación están muy interesados en la manera en que cambian los patrones de diversidad de especies a través de escalas espaciales. Examinamos como se puede utilizar la división aditiva para evaluar patrones espaciales estadísticamente y desarrollar estrategias de conservación. Aplicamos la división aditiva a datos de diversidad de escarabajos arbóreos (riqueza, Shannon, Simpson) recolectados con un diseño anidado que consiste de cuatro niveles jerárquicos—árboles, bosques, sitios y ecoregiones—que correspondían a escalas espaciales progresivamente mayores en el bosque deciduo de Ohio e Indiana (E.U.A.) Un porcentaje significativo (relativo a pruebas al azar) del total de la riqueza de especies y la diversidad de Shannon y Simpson se debe a la diversidad beta entre ecoregiones y, en menor extensión, entre sitios (parques y reservas naturales) dentro de las ecoregiones. Análisis de cluster jerárquicos corroboraron estos hallazgos. También encontramos diferencias entre especies raras (<0.05% de la abundancia total) y comunes (>0.5% de la abundancia total) en el porcentaje total de riqueza explicada por cada escala espacial. Las especies raras fueron la mayoría (45%) del total de 583 especies de escarabajos en nuestro estudio y estuvieron fuertemente influidas por escalas espaciales amplias (es decir, ecoregiones), mientras que la riqueza de especies comunes fue significativamente mayor que lo esperado en todas las escalas espaciales (desde árboles a ecoregiones). Nuestros resultados sugieren que la manera más efectiva de preservar la diversidad de escarabajos en el bosque deciduo oriental de Estados Unidos es adquirir y proteger múltiples sitios dentro de...
Introduction

Conservation biologists and land managers frequently use ecological models to determine strategies for conservation. The most popular models are the species-area relationship (MacArthur & Wilson 1967), metapopulation models (Levins 1969; Hanski & Gilpin 1991), source-sink models (Pulliam 1988), and population viability models (Shaffer 1991). Collectively, these models have had a profound effect. For example, metapopulation and source-sink models have illustrated the importance of managing landscapes and networks of habitat, whereas population viability analyses have identified the importance of demographic and environmental stochasticity on the long-term persistence of populations. Despite their growing use and importance in conservation biology (Hunter 1996; Gaona et al. 1998), these models are not very applicable to the conservation of biodiversity because they emphasize processes (movement, population growth) more than patterns (diversity), single species more than communities, and the effects of landscape design on a single spatial scale (e.g., arrangement of patches with a reserve) more than effects over multiple spatial scales. In essence, the models convey little information about how species diversity is affected by spatial scale. Yet it is clear that ecologists and conservation biologists have been striving to understand how spatial scale influences biodiversity (Shmida & Wilson 1985; Peltonen et al. 1998; Peterson & Parker 1998; Wagner et al. 2000). Palmer and White (1994), for example, used a nested series of sampling plots to assess how the species-area relationship—a model critical for the design of nature preserves (Diamond and May 1981)—was affected by the spatial scale of sampling.

Whittaker (1960) first acknowledged the link between spatial scale and diversity when he popularized alpha, beta, and gamma diversity. MacArthur (1965) later equated within-habitat diversity to Whittaker's alpha diversity and between-habitat diversity to beta diversity (Magurran 1988). Although their terminology continues to pervade ecological literature and is described in conservation biology texts (e.g., Hunter 1996), there have been few attempts to apply the conceptual framework of diversity components to determining how species diversity is generated over spatial scales (but see Wagner et al. 2000). This is because Whittaker used a multiplicative relationship to relate alpha and beta diversity to regional diversity (i.e., gamma diversity; regional = alpha × beta). The practical disadvantage of this relationship—and the reason it is not used more often by ecologists and conservation biologists—is that diversity components are not weighted equally when they are partitioned across more than one spatial scale (Lande 1996). However, an additive relationship between diversity components (i.e., regional = alpha + beta) makes it possible to calculate the relative contributions of alpha and beta diversity to overall diversity across a range of spatial scales (Allan 1975a; Lande 1996). Wagner et al. (2000) used additive partitioning and concluded that beta diversity among land-use types is more critical than beta diversity between patches of the same land-use type in generating plant species richness in agricultural landscapes. Other researchers have used additive partitioning to examine how the species diversity of fruit-feeding butterflies is distributed among and within habitats of tropical forests (DeVries et al. 1997; 1999).

We build on these studies in three ways. First, we conduct statistical tests on additive partitioning of diversity by using a randomization approach. To date, additive partitioning has been used primarily as a descriptive tool to quantify how diversity is partitioned among spatial (Wagner et al. 2000), temporal (DeVries & Walla 2001), or vertical (DeVries et al. 1997) dimensions. Second, we used the results of the statistical analyses to consider the sampling designs and conservation strategies that will be most effective in maintaining the regional diversity of insect communities. Our study organisms—beetles in tree crowns—are the most diverse animal taxa in the world (Erwin 1982, 1983, 1998; Hammond 1992) and have functional roles as defoliators, predators, xylophages (i.e., wood feeders), and detritivores in forest ecosystems (Dajoz 2000). It is critical that we understand which spatial scales most strongly influence the diversity of beetles and other organisms with important functional roles so that we can improve management strategies and maintain the health of forest ecosystems. Finally, we discuss how additive partitioning can be used to strengthen conservation strategies for biotic communities.

We tested the null hypothesis (that our observed alpha and beta diversity are obtained by a random distribution of individuals among samples at all hierarchical levels) against three alternative hypotheses by analyzing species-richness data collected across nested spatial scales—trees, forest stands, sites, and ecoregions—in the eastern deciduous forest of the United States. The first alternative hypothesis was that diversity is generated on fine spatial scales (e.g., individual trees within a forest stand) because of host-tree differences in community
composition (Mawdsley & Stork 1997; Wagner 1997; Gering & Crist 2000). A second alternative was that intermediate spatial scales (i.e., forest stands and sites) have stronger effects on beetle diversity because of diversity in tree communities and differences in management history. For example, sites separated by <20 km may result in beetle communities being <10% similar (Davies et al. 1997). The third alternative was that the broad-scale effects of ecoregions have the strongest influence on beetle richness because biogeographical processes and historical factors may be most important in determining community structure (Ricklefs & Schluter 1993; Lawes et al. 2000; Smith 2001).

**Methods**

**Sampling Design and Study Sites**

We used a hierarchically nested design to sample insects from tree crowns in the forests of southern Ohio and southeastern Indiana. Four hierarchical levels (corresponding to spatial scales) were represented in this design: ecoregions, sites, stands, and trees. The highest level (broadest spatial scale) was represented by two ecoregions (Bailey 1998) that differ in their glacial history and present-day forest composition, topography, and soil types (Fig. 1). The forests of the north-central Tillplain ecoregion (NCT) correspond to the beech-maple designation of Braun (1950) and are dominated by American beech (Fagus grandifolia) and sugar maple (Acer saccharum) and to a lesser extent by red oak (Quercus rubra), white oak (Quercus alba), elms (Ulmus spp.), and ash (Fraxinus spp.) (Ray & Vankat 1982; Delcourt & Delcourt 2000). The ecoregion is dominated by agriculture and is relatively flat as a result of glacial scouring. The topography is characterized by ridges with shallow (10–15 m), sloping drainages. The forests of the Western Allegheny Plateau ecoregion (WAP) are typical of the mixed mesophytic designation of Braun (1950) and are dominated by oaks (Quercus spp.) and hickory (Carya spp.) in xeric areas and American beech, tulip poplar (Liriodendron tulipifera), and hemlock (Tsuga spp.) in mesic areas (Delcourt & Delcourt 2000). Maples (Acer spp.) occur in both mesic and xeric areas. The ecoregion is unglaciated and has variable soils and a topography characterized by steep ridges and long, narrow drainages.

Three sites were nested within each of the ecoregions (Fig. 1). Hueston Woods State Park (HWSP; Preble County, Ohio), Brookville Reservoir (BROK; Franklin County, Indiana), and Caesar Creek State Park (CACR; Warren County, Ohio) were located in the NCT, and Clear Creek Metro Park (CLCR; Fairfield County, Ohio), Shawnee State Forest (SFFO; Scioto County, Ohio), and Edge-of-Appalachia Nature Preserve (EOAP; Adams County, Ohio) were located in the WAP (Fig. 1). We selected these parks and nature preserves as representative of the forest types in each ecoregion and because they have considerable conservation importance. The HWSP contains approximately 100 ha of Ohio’s oldest (>200 years old) beech-maple forest, SFFO is the largest (24,300 ha) of Ohio’s 20 state forests, and EOAP (486 ha) contains 50 rare plant and animal species and three plant communities that are globally rare. Within each site, we selected four stands (0.5–1 ha) that represented typical mesic and xeric areas. From those stands, we selected four individual trees to represent the lowest hierarchical level (i.e., finest spatial scale) in the study. The selected trees were representative of the dominant tree genera within the stand, as determined by our surveys. Quercus, Acer, Fagus, and Carya were common, whereas Liriodendron, Celtis, and Fraxinus were encountered less frequently.

**Insect Sampling**

We sampled the insect communities from each tree during two sampling periods in the summer of 2000: 22 May–20 June (early) and 2–25 August (late). We sampled twice during the summer because temporal change has a significant effect on beetle community composition (Gering & Crist 2000). Hence, there are two separ
rate estimates of richness for each individual tree, for a total of 192 records (96 trees × 2 sampling periods). We used the insecticide fogging technique to sample each tree because it is relatively unselective, does not depend on arthropod activity, and effectively samples adult beetles (cf. Basset et al. 1997; Stork & Hammond 1997). At dawn on windless mornings, the crown of each tree was inundated for 3 minutes with 0.5 L of a 0.5% pyrethrin-based insecticide (Pyrenone 50, AgrEvo Products, Berlin, Germany) emitted from a radio-controlled Curtis Dyna-Fogger. During the following 2 hours, insects fell into a ground-based array of 12, 0.5-m² collecting funnels. The funnels were located beneath each tree crown so that insects from neighboring tree crowns were unlikely to be collected. Our sampling protocol was based on previous studies (e.g., Davies et al. 1997; Harada & Adis 1997; Wagner 1997; Gering & Crist 2000) and the detailed evaluation of drop time, insecticide concentration, and recovery time provided by Stork and Hammond (1997). An important aspect of our protocol was that collecting effort was standardized (6 m²) for each tree. This enabled us to make valid statistical comparisons of beetle diversity across trees, stands, sites, and ecoregions, although it did not ensure an equal number of individuals in each sample.

Insect Processing

We sorted beetle specimens and identified them to families and recognizable taxonomic units (RTUs or morphospecies; Oliver & Beattie 1993, 1996). Species grouped by coarse morphological features often correspond closely to expert morphological identification (Longino & Colwell 1997), although this may vary among taxa. To validate our morphospecies designations, we sent 126 morphospecies to a Coleopteran systematist (D. K. Young, University of Wisconsin-Madison), who identified 140 actual species. Therefore, our estimates of species richness were conservative. Most of the lumping within this subset of morphospecies occurred in one weevil genus (Curculionidae: Curculio) and one darkling beetle genus (Tenebrionidae: Platydema). Family and subfamily designations follow the systematic relationships of Lawrence and Newton (1995), which differ somewhat from the familial relationships of Downie and Arnett (1996).

Data Analysis

GENERAL COMMUNITY PATTERNS

We tallied species richness and abundance for the entire study and separately for ecoregions and sites within sampling periods. We also subdivided the entire richness into family-specific richness and identified the most abundant beetle species (by number of individuals).

SPECIES-ACCUMULATION CURVES

We constructed species-accumulation curves to assess the adequacy of our sampling. Species-accumulation curves relate sampling effort (e.g., number of trees) to the cumulative number of species to evaluate sampling effectiveness (e.g., Longino & Colwell 1997; Wagner 1997). We constructed accumulation curves with PCORD (McCune & Mefford 1999), which subsamples the entire sample (the community of each tree) 500 times to determine the number of species as a function of subsample size. Five separate accumulation curves were used to evaluate the effects of sampling across space and time: one for each ecoregion across both sampling periods, one for each sampling period across both ecoregions, and one for the entire study.

ADDITIONAL PARTITIONING OF DIVERSITY

Allan (1975a) and Lande (1996) demonstrated that regional diversity is the sum of alpha and beta diversity when alpha is the average diversity within the sampling units in the region and beta is diversity among sampling units. This differs from Whittaker’s (1960, 1977) multiplicative relationship and allows researchers to additively partition the total diversity in a region into scale-specific diversity components (Fig. 2). Within the context of our study, alpha and beta diversity maintain their traditional interpretations as within-unit diversity and between-unit diversity on a given scale, respectively. For example, \( \alpha_2 \) represents the mean number of beetle species among the 24 stands, whereas \( \beta_2 \) represents diversity in species among the 24 stands and \( \beta_1 \) represents diversity in species among the six sites. Because alpha diversity at a given scale is the sum of the alpha and beta diversity at the next lowest scale (i.e., \( \alpha_1 = \alpha_2 + \beta_2 \); Allan 1975a; Lande 1996), the overall beetle diversity in our study can be described by the following formula: \( \alpha_0 = \alpha_1 + \beta_1 + \beta_2 + \beta_3 + \beta_4 \) (Fig. 2).

Lande (1996) demonstrated that any metric can be partitioned into its components provided that it exhibits strict concavity, which means that the overall value of that metric for a pooled set of communities equals or exceeds the average diversity within communities. Species richness, Simpson diversity, and Shannon diversity are all strictly concave. We used all three metrics in our study to account for the pure effects of species (species richness) and the combined effects of richness and abundance (Shannon and Simpson diversity). An important difference between the Shannon and Simpson indexes is their relative sensitivity to rare species. The Simpson index is a dominance measure weighted toward common species, whereas the Shannon index is an information statistic weighted equally toward rare and common species (Magurran 1988). The Shannon index generally varies from 1 (low diversity) to 5 (high diversity), whereas
Figure 2. Relationships among hierarchical levels in our additive partitioning model (alpha Subscript 1,5 and beta Subscript 1,4). Whittaker’s (1960) terminology (in parentheses), and MacArthur’s (1965) designations (in brackets) of diversity. Because of the additive relationship between levels (e.g., point + pattern = alpha, alpha + beta = gamma), we can use substitution among levels to arrive at the following equation (illustrated by arrows and mathematical operators) to describe the total (i.e., regional or alpha Subscript 5) diversity: alpha Subscript 1 + beta Subscript 1 + beta Subscript 2 + beta Subscript 3 + beta Subscript 4

the Simpson index is always <1 because it is the probability that two individuals drawn from the sample belong to the same species. Both indices are calculated from the proportional abundance, P_i, of all species in the sample. The Shannon index is -[\sum P_i(lnP_i)] for species i = 1 to S_n, where S_n equals the number of species in the sample. The Simpson index is 1 - \sum P_i^2, which is also known as the Gini coefficient (Peet 1974; Lande 1996). Using these diversity indices, we conducted additive partitions for the entire community in both sampling periods for a total of six partitions (3 metrics × 2 sampling periods) by using a computer program, PARTITION.

The utility of PARTITION is that the statistical significance of level-specific alpha and beta estimates can be tested through a randomization procedure. This process is called complete randomization because the numbers of individuals and species in samples at all hierarchical levels are determined by the random placement of individuals into any of the samples at the lowest level (i.e., the randomization is unrestricted) (T.O.C. et al., unpublished data). Briefly, the species abundances from all samples at a given level were combined to create a single species-abundance distribution (Solow 1993; Wiens et al. 1996). The distribution is then used to randomly assign individuals (without replacement) to samples such that the initial size (number of individuals) of the sample is maintained. As with the actual data, the randomized data (samples) were partitioned and the diversity estimates obtained. This process was repeated 10,000 times to form a null distribution of each alpha and beta estimate (for species richness or for Shannon or Simpson diversity) at each level of analysis. Each of the level-specific estimates was then compared with the appropriate null distribution and used to test the null hypothesis that the observed alpha and beta diversity are obtained by a random distribution of individuals among samples at all hierarchical levels.

Statistical significance was assessed by the proportion of null values that are greater than (or less than) the actual estimate. For instance, if 30 out of 10,000 null values were greater than or equal to an observed estimate, then the probability of obtaining (by chance) an estimate as great or greater than the observed value was 0.003. In such a case, the actual estimate was significantly large. The probabilities obtained from randomization tests can be interpreted as p values in traditional significance tests (Manly 1997). The randomization test conserves the size of each sample and the overall abundance of each species. This approach, together with the equal sampling effort, negates the need for adjusting for unequal sample size by rarefaction, but it does not remove differential bias in species richness caused by different sizes among samples.

In addition to overall richness and diversity, we were also interested in how spatial scale affected the richness of rare and common species. Thus, we subdivided the entire community into rare and common species, where rare species were those with an abundance of <0.05% of the total community abundance within a sampling period and common species were those with an abundance of >0.5% of the total community abundance within a sampling period. Only species richness was used in the partitioning of groups of rare and common species, for a total of four partitions (2 groups × 2 sampling periods).

The complete randomization approach is relevant to testing theory and mechanisms (e.g., patterns of aggregation, species distribution, and abundance) that influence observed partitions of diversity (T.O.C. et al., unpublished data). An alternative approach—restricted randomization—can be performed by PARTITION to conduct statistical tests on observed components of diversity against a null hypothesis that the observed alpha and beta diversity at each level k are obtained from a random distribution of k - 1 sample units among k samples that form a k + 1 sample. In essence, restricted randomization determines whether an observed component of diversity at a level is greater or less than expected by random draws from the samples at the next lowest level. Restricted randomization is appropriate for testing some null hypotheses, but it generally has less statistical power than complete randomization. On the regional level, for example, we found that restricted randomization had limited power to detect departures from the null hypothesis because fewer samples were randomized than with complete randomization (results not shown).
cause we were interested in comparing patterns of significance for the partitions of rare and common species, we used the more powerful complete randomization approach.

**SITE CLASSIFICATION**

To examine the similarity of beetle communities between sampling periods and among sites and ecoregions, we used hierarchical cluster analysis with the Jaccard index of similarity (Magurran 1988). The Jaccard index compares samples based on the presence or absence of species. We selected this similarity index to emphasize species composition and because it does not dilute the importance of rare species, which can be numerous in canopy beetle communities (e.g., Gering & Crist 2000). We combined the four stands from within each site to arrive at a composite community for that site. We performed the cluster analysis using the average linkage method in PC-ORD (McCune & Mefford 1999).

**Results**

**General Community Patterns**

We recorded 15,907 individuals representing 583 species. Richness was not distributed evenly in time or space. It was higher in the early than in the late sampling period and slightly higher in the NCT than in the WAP (Table 1). The species-abundance distribution was characterized by a high percentage of singletons (i.e., species represented by one individual) and a few dominant species; approximately one-third (185) of the 583 total species were singletons. A similar percentage (37–46%) of species was found as singletons within ecoregions and sampling periods (Table 1).

The dominant families in terms of species richness were weevils (Curculionidae), long-horned beetles (Cerambycidae), leaf beetles (Chrysomelidae), and click beetles (Elateridae) (Table 2). There was considerable variation in the percentage of singletons represented within each family (e.g., 10% for Scarabaeidae to 47% for Cerambycidae). The dominant species (in terms of abundance) included two exotic species, the Asiatic oak weevil \( \text{Cyrtepistomus castaneus} \) (Roleofs) and the Asian ladybird beetle \( \text{Harmonia axyridis} \) (Pallas). Together, they accounted for more than one-third of all individuals in the late sampling period and approximately 20% of all individuals across both sampling periods. Other dominant species included a tenebrionid, a minute brown scavenger beetle (Latridiidae), and a carabid.

**Species-Accumulation Curves**

The accumulation curves showed little evidence of approaching an asymptote (Fig. 3), suggesting that we did not sample total species richness in any of the communities despite the spatial and temporal extent of our sampling design.

**Additive Partitioning**

The most noticeable result from the additive partitioning was that the highest beta component (\( \beta_4 \)) in the model was always greater than expected by chance, whereas the

<table>
<thead>
<tr>
<th>Ecoregion and site*</th>
<th>Richness</th>
<th>Singletons</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>early</td>
<td>late</td>
</tr>
<tr>
<td></td>
<td>early</td>
<td>late</td>
</tr>
<tr>
<td></td>
<td>early</td>
<td>late</td>
</tr>
<tr>
<td>North-central Tillplain</td>
<td>336</td>
<td>243</td>
</tr>
<tr>
<td>HWSP</td>
<td>194</td>
<td>148</td>
</tr>
<tr>
<td>BROK</td>
<td>190</td>
<td>108</td>
</tr>
<tr>
<td>CACR</td>
<td>176</td>
<td>146</td>
</tr>
<tr>
<td>Western Allegheny Plateau</td>
<td>324</td>
<td>229</td>
</tr>
<tr>
<td>EOAP</td>
<td>178</td>
<td>128</td>
</tr>
<tr>
<td>SSFO</td>
<td>218</td>
<td>116</td>
</tr>
<tr>
<td>CLCR</td>
<td>182</td>
<td>120</td>
</tr>
</tbody>
</table>

*Abbreviations: HWSP, Hueston Woods State Park; BROK, Brookville Reservoir; CACR, Caesar Creek State Park; EOAP, Edge-of-Appalachia Nature Preserve; SSFO, Shawnee State Forest; CLCR, Clear Creek Metropark.

<table>
<thead>
<tr>
<th>Family</th>
<th>No. of species*</th>
<th>No. of singletons</th>
</tr>
</thead>
<tbody>
<tr>
<td>Curculionidae (snout beetles and weevils)</td>
<td>70</td>
<td>19</td>
</tr>
<tr>
<td>Cerambycidae (long-horned beetles)</td>
<td>51</td>
<td>24</td>
</tr>
<tr>
<td>Chrysomelidae (leaf beetles)</td>
<td>47</td>
<td>5</td>
</tr>
<tr>
<td>Elateridae (click beetles)</td>
<td>47</td>
<td>13</td>
</tr>
<tr>
<td>Anobiidae (death-watch beetles)</td>
<td>25</td>
<td>4</td>
</tr>
<tr>
<td>Coccinellidae (ladybird beetles)</td>
<td>21</td>
<td>4</td>
</tr>
<tr>
<td>Tenebrionidae (darkling beetles)</td>
<td>21</td>
<td>5</td>
</tr>
<tr>
<td>Mordellidae (tumbling flower beetles)</td>
<td>20</td>
<td>3</td>
</tr>
<tr>
<td>Cleridae (checkered beetles)</td>
<td>20</td>
<td>7</td>
</tr>
<tr>
<td>Staphylinidae (rove beetles)</td>
<td>20</td>
<td>7</td>
</tr>
<tr>
<td>Buprestidae (metallic wood boring beetles)</td>
<td>14</td>
<td>3</td>
</tr>
<tr>
<td>Carabidae (ground beetles)</td>
<td>14</td>
<td>6</td>
</tr>
<tr>
<td>Cantharidae (soldier beetles)</td>
<td>15</td>
<td>4</td>
</tr>
<tr>
<td>Nitidulidae (sap-feeding beetles)</td>
<td>11</td>
<td>5</td>
</tr>
<tr>
<td>Scarabaeidae (scarab beetles)</td>
<td>10</td>
<td>1</td>
</tr>
</tbody>
</table>

*Cumulative value for sampling conducted during early (22 May–20 June) and late (20 August–5 September) sampling periods.
alpha component was always lower than expected (Table 3). This was evident across all combinations of group, index, and sampling period, despite the fact that the alpha component accounted for a substantial proportion of the richness of common species (Fig. 4) and a large proportion of the Shannon and Simpson diversity for the entire community (Fig. 5). There were also differences between Shannon and Simpson diversity in the percentage of total diversity accounted for by alpha, which was greater for Simpson diversity than for Shannon diversity (Fig. 5).

Differences also occurred between rare and common species in the percentage of overall richness distributed among levels of the hierarchical model (Table 3; Fig. 4). Deviations from expected values were positive for rare species only at the highest level in the partition, whereas deviations from expected values were always positive for common species throughout the higher levels in the partition. The reverse was true at lower levels. Only beta was consistently greater than expected for rare species (Table 3).

Site Classification
As expected from previous studies, our cluster analysis identified strong differences in community composition between sampling periods (Fig. 6). Sites were grouped according to their ecoregions in both sampling periods. In general, there was a higher degree of similarity between ecoregions and among sites in the late sampling period than in the early sampling period.

Discussion
In principle, additive partitioning is simply a mathematical approach to describing the relative contributions of components to a sum total. It can be used on a variety of metrics and can quantify spatial and temporal patterns of diversity, size (e.g., basal area), abundance, and other ecological data. In practice, however, this approach has not been applied to many ecological phenomena. The exceptions include Wagner et al.’s (2000) study of plant species richness in agricultural landscapes, DeVries et al.’s studies (1997, 1999; see also DeVries & Walla 2001) of temporal and spatial patterns of butterfly diversity in rainforests, and Allan’s (1975b) study of benthic insect diversity in an alpine stream. Additive partitioning of diversity has also been used in other studies, but was clearly not the main emphasis of the research (e.g., Holland & Jain 1981; Barker et al. 1983). Even so, it has considerable potential because it allows conservation biologists to understand the contributions of alpha and beta diversity to total diversity over a range of user-defined spatial scales.

Our finding that broad-scale beta components of diversity were greater than expected supports the hypothesis that the effects of ecoregions structure the richness and composition of arboreal beetles in the eastern deciduous forest. This is supported by our cluster analysis,
Figure 4. Percentage of total beetle species richness explained by alpha and beta components of diversity on four spatial scales: trees, forest stands, sites, and ecoregions. The contributions to the total richness for each scale were determined by the additive partitioning of diversity. Total species richness for each of the three groups (denoted on the x-axis) is the number at the top of each bar. Early (22 May–20 June) and late (2–25 August) are sampling periods.

Figure 5. Percentage of total Shannon and Simpson diversity explained by alpha and beta components of diversity on four spatial scales: trees, forest stands, sites, and ecoregions. Contributions to total diversity for each scale were determined by an additive partitioning of diversity.
In addition to identifying the importance of broad-scale effects, additive partitioning also identified significant differences between rare and common species in the percentage of overall richness explained by levels in the hierarchical model. The richness of rare species was enhanced (i.e., greater than expected) only at the highest levels in the model, whereas significant enhancement of common species richness was evident throughout all levels (except tree-level alpha) in the models. We interpret this as evidence that the richness of rare species was strongly influenced by beta diversity between ecoregions and among sites. More important, the partitioning results for the entire community mirrored those of the rare species, indicating that rare species may be driving the patterns of the entire community. This is probable, because the rare species, as we have defined them, accounted for a high percentage (36–47%) of the species in the community. It is unclear whether the rare species in our study are sampling artifacts, biologically meaningful, or truly rare (Rabinowitz 1981; Gaston 1994), but the proportion of singletons we recorded is typical of other canopy insect communities. Despite working in different locations, Allison et al. (1997; Papua New Guinea) and Davies et al. (1997; Venezuela) recorded 40–50% singletons in their studies or found high diversity values that indicated a high proportion of singletons.

The consistent proportion of rare species in insecticide fogging studies (Erwin 1998) can be explained, in part, by our partitions of beetle diversity. For example, our finding that the species-accumulation curve did not reach an asymptote suggested that our sampling design—despite its spatial extent—was not sufficient to account for all the species present in the sampling area. The partitioning of richness for the rare species, and to a lesser extent for the entire community, provides an explanation for this well-documented pattern. As sampling designs incorporate a greater spatial extent, saturation of accumulation curves is less likely because rare species will be encountered more frequently at the broadest scales. For this reason, accumulation curves should not be expected to become saturated in spatially extensive studies of hyperdiverse communities (Palmer 1995; Novotny & Basset 2000; Summerville et al. 2001). The only way to force accumulation curves for hyperdiverse communities toward saturation is to sample intensively over a limited spatial area. Basset and Arthington (1992), for example, nearly flattened their cumulative saturation curves by sampling (using restricted canopy fogging) and resampling (eight times) the same individual trees in a 35-ha stand of warm subtropical forest.

The preponderance of rare species in spatially extensive sampling designs presents conservation biologists with a peculiar dilemma. In most cases, the first step in conservation programs is to produce a comprehensive species list within the region of interest. The best way to accomplish this is to sample intensively over a limited
spatial area, as indicated above. Yet our diversity partitioning suggests that a significant percentage of species richness is generated by diversity among sampling units (i.e., beta diversity) at relatively broad scales. Therefore, there is a trade-off between the spatial extent of sampling and the thoroughness of the species inventory. A spatially intensive sampling design will probably produce a thorough species list but miss many rare species that occupy neighboring habitats. Spatially extensive sampling designs, in contrast, produce unsaturated accumulation curves but provide a better assessment of the heterogeneity of species diversity. Palmer and White (1994) reject the idea of a "regional" species-area curve and point out, as we have, that scale-dependent processes (e.g., disproportionate accumulation of rare species at broad scales) can render accumulation curves ineffective for estimating the number of species in a given area. Additive partitioning was particularly helpful in arriving at this conclusion because it identified significantly large beta diversity as the reason for the unsaturated accumulation curves.

With a spatially intensive sampling design, we may have concluded that tree-crown beetle communities are overwhelmed by a few dominant and exotic species such as the Asiatic oak weevil. In fact, our partitioning of Simpson diversity indicated the extent to which fine spatial scales are dominated by common (and exotic) species. Shannon diversity reflected this pattern to a lesser extent because it gave equal weight to rare and common species. An important point, then, is that different types of diversity indices (e.g., dominance indices and evenness indices) should be used with species richness to gain a full understanding of how rare and common species contribute to overall regional diversity. For example, we were able to determine that rare species represent a critical component of the community and contribute to differences between ecoregions, whereas the richness of common species was explained by alpha diversity at the finest spatial scales.

These findings emphasize the need for programs of regional conservation planning. For example, the protection and acquisition of additional sites within an ecoregion will be more effective in conserving insect diversity than local-scale management approaches that strive to increase tree species diversity within stands. Our findings further suggest that management approaches for rare species will be sufficient to maintain common species because the important spatial scale for rare species (i.e., ecoregions) also encompasses the spatial scales that appear to be important for the richness and diversity of common species. This is noteworthy because such management accomplishes two goals: conservation of species richness, which is produced by rare species, and maintenance of the functional aspect of forest insect communities, which is driven by common species that have greater effects on host trees and food-web interactions. Thus, even the alpha diversity produced by common and exotic species has an important role in conservation strategies.

Finally, additive partitioning represents a contrast to source-sink and metapopulation approaches because it is a multispecies method of analyzing biodiversity. In some cases, the patterns of species richness and diversity—not the processes that determine them—will be more useful for determining conservation strategies. The species-area relationship, for example, simply describes species richness as a function of area without making assumptions about the processes that may be driving the relationship, even though it is clear that colonization, species coexistence, and numerous scale-specific processes can affect the shape of the curve (MacArthur & Wilson 1967; Shmida & Wilson 1985; Palmer & White 1994). Similarly, additive partitioning will be useful in situations where researchers wish to describe change in species richness or diversity over spatial or temporal scales without invoking specific processes. Source-sink and metapopulation models will continue to be more useful in single-species studies, in which processes such as dispersal and mortality are critical for determining conservation strategies. These differences suggest that additive partitioning is a valuable tool for conservation biologists because it complements existing approaches while providing a unique way to understand community diversity over space and time.

Acknowledgments

The Nature Conservancy’s Ecosystem Research Program, the Miami University Committee on Faculty Research, and the Ohio Board of Regents Research Challenge Program generously provided funding for this project. C. Yeager, N. Anderson, J. Kahn, J. Vecch, K. Summerville, and D. Golden helped with insect sampling. N. Anderson also contributed greatly to insect processing. D. Clausen, A. Rypstra, M. Vanni, J. Vankat, K. Summerville, and K. McGrath provided comments on the experimental design and the general format of the manuscript. R. Lande and P. DeVries also reviewed the manuscript; we thank them for their valuable and insightful comments. We are grateful to the landowners and managers of the state parks, metroparks, reservoirs, and nature preserves used in this study. Without their cooperation, it would not have been possible to conduct this study. This paper was written in partial fulfillment of the requirements for the doctoral degree of J. Gering.

Literature Cited


