
Spatial Variation in Species Diversity and Composition of Forest Lepidoptera in Eastern Deciduous Forests of North America

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Abstract: *The primary emphasis of conservation biology has moved away from attempting to manage single species within a given habitat to the preservation of entire communities within ecoregions, requiring that greater attention be paid to how biodiversity and species composition vary across spatial scales. Using a nested sampling design, we examined spatial variation in the biodiversity of forest Lepidoptera across three hierarchical levels: 20 forest stands, five sites, and three ecoregions. We used blacklight traps to sample the moth communities of each forest stand every week in June and August of 2000. Lepidopteran community composition was most significantly influenced by ecoregional differences, whereas patterns of α and β diversity across scales differed depending on how diversity was measured. Diversity partitioning models demonstrated that turnover in species richness occurred equally across all spatial scales because numerically rare species were continually encountered. In contrast, within-stand effects disproportionately influenced Simpson and Shannon diversity (relative to outcomes from randomization tests), suggesting that local factors determined species dominance. Because most Lepidoptera in forests appear to be rare (>50%), it will be impossible for conservation biologists to design management plans to account for every species. We suggest that a more meaningful strategy would be to identify species that attain a reasonable abundance within a community (5-10% of all the individuals in a sample) and that are unique to particular spatial levels. This strategy should produce two desirable outcomes: the conservation of species that render ecoregions distinct and the maintenance of functionally dominant species within forests.*

Variación Espacial de la Diversidad y Composición de Especies de Lepidópteros en Bosques Deciduos Orientales de Norte América

Resumen: *El enfoque principal de la biología de la conservación ha pasado del manejo de especies individuales en un hábitat determinado a la conservación de comunidades enteras en ecoregiones determinadas, para lo cual se requiere prestar mayor atención a variaciones de biodiversidad y composición de especies a distintas escalas espaciales. Utilizando un muestreo anidado, examinamos la variación espacial de la biodiversidad de lepidópteros de bosque a tres niveles jerárquicos: 20 áreas forestales, cinco sitios y tres ecoregiones. Utilizamos trampas de luz negra para muestrear semanalmente las comunidades de mariposas nocturnas de cada área forestal entre junio y agosto del 2000. La composición de la comunidad de lepidópteros varió significativamente con diferencias ecoregionales, mientras que los patrones de diversidad α y β en cada escala difirieron dependiendo de como se midió la diversidad. Los modelos de partición de diversidad demostraron que en todas las escalas espaciales hubo la misma renovación de la riqueza de especies porque continuamente se encontraban especies numéricamente raras. En contraste, los efectos dentro del área forestal tuvieron una influencia desproporcional sobre los índices de diversidad de Simpson y de Shannon (en relación a pruebas aleatorias), lo cual sugiere que la dominancia de especies depende de factores locales. Debido a que la mayoría de los lepidópteros en bosques parecen ser raros (>50%), será imposible para biólogos*

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de la conservación diseñar planes de manejo que tengan en cuenta todas las especies. Sugerimos que una estrategia más significativa sería identificar las especies que alcancen una abundancia razonable dentro de una comunidad determinada (5–10% de todos los individuos de una muestra) y que correspondan a una única escala espacial. Esta estrategia produciría dos resultados deseables: la conservación de especies que caracterizan las ecoregiones y el mantenimiento de especies funcionalmente dominantes dentro de los bosques.

Introduction

In recent years, the field of conservation biology has matured, its emphasis shifting from the management of individual species within habitats to the preservation of entire communities within ecoregions (The Nature Conservancy 1999; Gaston et al. 2001). This paradigm shift has required greater attention to how patterns of biodiversity vary across spatial scales. In response, a growing body of literature has mandated that successful conservation planning must account for the effects of spatial scaling of species diversity (e.g., Margules et al. 1988; Gaston et al. 2001). Our understanding of scale-dependent patterns of biodiversity, however, is incomplete. Even in well-studied temperate-forest ecosystems, our insufficient knowledge of spatial variation in species diversity and composition is a major impediment to the conservation of biodiversity and sustainable resource management (Ehrlich 1996; Summerville et al. 2001). Furthermore, because most temperate-forest ecosystems are poorly protected in reserves or are managed for timber production (e.g., Norton 1996), the selection of additional sites for conservation should be guided by an understanding of what scales are most critical for determining species composition and persistence.

Insects are one of the most hyperdiverse and critical components of forest ecosystems (Stork 1988) and thus should be of particular interest for understanding the effects of spatial scale on temperate-forest diversity (New 1999). Lepidoptera are among the most speciose and taxonomically tractable groups of insects and have important functional roles in forests as selective herbivores, pollinators, detritivores, and prey for migratorial passerines (Holmes et al. 1979; Schowalter et al. 1986). Furthermore, the Lepidoptera show promise as indicators of forest health (Kitching et al. 2000) and as surrogates for the diversity of other insect groups such as the Hymenoptera (Kerr et al. 2000). Thus, the Lepidoptera comprise a critical fauna for answering questions concerning spatial scale and biodiversity in forests.

In their attempts to understand how lepidopteran species diversity is influenced by spatial variation, previous researchers either used an intensive sampling protocol within a single spatial domain (Barbosa et al. 2000; Butler et al. 2001) or sampled extensively across a limited number of spatial scales with little replication (e.g., Rob-

inson & Tuck 1993; Hammond & Miller 1998; Summerville et al. 2001). Empirical data from these studies suggest several hypotheses for how spatial scale might influence lepidopteran community composition. At fine spatial scales (i.e., within-forest stands, approximately 1 ha), host-tree effects significantly influence diversity within individual hosts (Ostaff & Quiring 2000) and among tree genera (Neuvonen & Niemelä 1981; Barbosa et al. 2000). In contrast, processes at intermediate scales (among sites within ecoregions, approximately 10 km²) such as turnover in floristic communities, differences in management history, and isolation of forest stands become more important to species diversity and composition than host-tree effects (e.g., Usher & Keiller 1998; Summerville & Crist 2002). Finally, at broader spatial scales (e.g., ecoregions, approximately 100 km²), biogeographic history, contingency, and landscape heterogeneity all contribute to the formation of unique species assemblages and differing levels of species diversity (Hammond & Miller 1998; Aauri & de Lucio 2001; Summerville et al. 2001). All these observations suggest that species aggregation within habitats, landscapes, and regions is important in structuring lepidopteran communities, but patterns of species aggregation may differ among scales.

In reality, processes operating over a range of scales likely influence the structure of forest moth communities. Nonetheless, mechanisms at some spatial scales might have larger relative effects on community structure than others (Shmida & Wilson 1985; Wagner et al. 2000; Summerville & Crist 2002). The identification of such critical scales will be of great importance for the successful conservation of forest biodiversity (Ehrlich 1996). For example, if local processes such as host tree effects are the most important factors determining moth species diversity, then management and conservation initiatives should be directed toward maintaining floristic heterogeneity within forest stands. In contrast, if broad-scale ecoregional effects are predominate, then the successful conservation of biodiversity will ultimately depend on creating a regionally stratified set of natural areas, with preservation effort spread across as many ecoregions as possible.

We addressed the question of how the species diversity and composition of forest Lepidoptera vary across a hierarchy of spatial scales, from individual forest stands

to whole ecoregions. First, we tested the hypothesis that broad-scale differences between ecoregions were more important in influencing lepidopteran community composition than were local differences among sites within ecoregions. Second, we tested several contrasting hypotheses of how spatial scale would affect lepidopteran species diversity, each hypothesis predicting a different critical scale at which species diversity was determined. Our null hypothesis was that the observed diversity across hierarchical levels is no different than expected from random distributions of individuals among forest stands, stands among sites, and sites among ecoregions. Our alternative hypotheses predicted significant departures of diversity estimates from random expectation at (1) fine spatial scales because of differences in species composition and abundance among stands, (2) at intermediate spatial scales because of differences among sites within ecoregions, or (3) at broad spatial scales because of differences between ecoregions. Finally, we examined the contrasting roles of common, rare, and unique species in contributing to the scaling of species diversity and composition to identify how differences in abundance or incidence affect lepidopteran community structure.

Methods

Study Sites and Sampling Design

We used a nested design to sample Lepidoptera from forest stands in southern Ohio. Three hierarchical levels comprised the nested design: forest stands, sites, and ecoregions (Fig. 1). The ecoregions differed in glacial history, topographic heterogeneity, soil types, and floristic composition (McNab & Avers 1994; subdivided by The Nature Conservancy 1999). The forests of the North-Central Tillplain (NCT) are dominated by American beech (*Fagus grandifolia*) and sugar maple (*Acer saccharum*) (Braun 1961). Species such as white oak (*Quercus alba*), red oak (*Quercus rubra*), slippery elm (*Ulmus rubra*), and several ashes (*Fraxinus* spp.) are also important canopy species (Greller 1988). Land use

in the NCT is predominantly agricultural as a result of the flat topography and productive soils created by glacial scouring (ridges are separated by shallow, sloping floodplains). In contrast, the Western Allegheny Plateau (WAP) and the Interior Low Plateau (ILP) largely escaped Pleistocene glaciation. The WAP is characterized by acidic, less productive soils and a topography of steep ridges and long, narrow drainages. In the WAP, xeric aspects are dominated by chestnut oak (*Quercus montana*) and hickories (*Carya* spp.), whereas mesic areas contain a more diverse assemblage of trees, including American beech, tulip poplar (*Liriodendron tulipifera*), basswood (*Tilia americana*), and eastern hemlock (*Tsuga canadensis*) (Greller 1988). The portion of the ILP in Ohio occurs on dolomitic soils that are more alkaline and tend to support a greater diversity of vegetation. Ridges in the ILP tend to be dominated by white oak (*Q. alba*), and bottomlands tend to support similar tree species as the mesic valleys of the WAP (Braun 1961).

Our experimental design nested two sites within the NCT and the WAP (Fig. 1). Hueston Woods State Park (HWSP; Preble County, Ohio) and Caesar Creek State Park (CACR; Warren County, Ohio) occur in the glaciated NCT, whereas Clear Creek MetroPark (CLCR; Hocking County, Ohio) and Vastine Wilderness Area (VAST; Scioto County, Ohio) occur in the unglaciated WAP ecoregion. We included a fifth site in the study, the Edge of Appalachia Nature Preserve (EDGE; Adams County, Ohio), which falls within the ILP. Within each site, we selected four forest stands (of approximately 1 ha) that represented typical mesic and xeric aspects and were separated by a minimum distance of 250 m from other stands as well as other ecotones. We selected stands within sites by visual surveys and preliminary observations of differences in tree communities between mesic and xeric topographic positions. Because the EDGE falls near the transition zone between the WAP and the ILP, we selected stands for sampling at the EDGE that occurred on geologic formations more characteristic of the WAP. Thus, xeric stands at the EDGE occurred on acidic, sandstone-derived soils and were dominated by *Q. montana*, *Q. velutina*, and *C. glabra*. Mesic stands contained woody and herbaceous flora similar to bot-

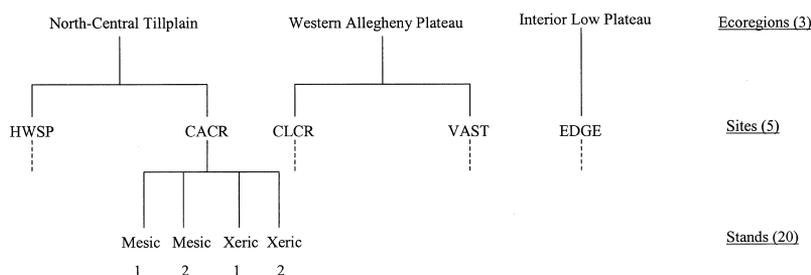


Figure 1. Hierarchical sampling design used to sample moths from five forest sites in three ecoregions. The five sites were nested within the three ecoregions, and 20 stands were nested within the five sites (HWSP, Hueston Woods State Park; CACR, Caesar Creek State Park; CLCR, Clear Creek Metropark; VAST, Vastine Wilderness Area; EDGE, Edge of Appalachia Nature Preserve).

tomlands at Shawnee State Forest (K.S.S., unpublished data).

Lepidoptera Sampling

Within each forest stand, we used a single 12-W universal blacklight trap (BioQuip Products, Gardena, California) powered by a 12-V (26 Amp) gel battery to sample Lepidoptera. Blacklight traps are widely recognized as the standard tool for sampling moth communities, although the method is biased toward collecting phototactic species. Thus, species whose activity is primarily diurnal and species whose adults are only encountered at sap flows or pheromone traps were not sampled by this method. To avoid disruption of the UV light by seedlings and shrubs in the understory, we positioned UV traps on platforms approximately 1.5 m above the ground (Summerville & Crist 2002). Moths attracted to the UV lights were sacrificed inside the traps with ethyl acetate and Dichlorvos killing agents.

We sampled the moth communities of each forest stand during two sampling periods over the summer of 2000: 15 May–1 June (“early”) and 29 July–8 August (“late”). Sampling was seasonally stratified because temporal variation has significant effects on lepidopteran community structure, and our early and late sampling intervals roughly correspond to the peaks in species richness for moths in temperate forest systems (Thomas & Thomas 1994). We operated traps within each stand for two non-consecutive nights from 1930 to 0600 hours during both early and late seasons (four nights total per stand). Therefore, trapping accumulated 80 samples in the early and late seasons combined. On a given sampling night, we placed traps in all four stands at one randomly chosen site. Weather has a significant effect on moth flight behavior and light-trap efficiency, so we sampled only on nights when the minimum temperature was 15.5–17.5°C, there was no precipitation, and ambient moonlight was low (i.e., half to new moon phases), as recommended by Yela & Holyoak (1997). Despite these restrictions on our sampling protocol, we obtained a complete sampling rotation (all five sites sampled once) in 7–9 days.

Collected specimens were frozen after trap processing to facilitate curation and identification. We identified individuals to species when possible, based on available taxonomic keys and vouchered specimens in museum collections. Recognized taxonomic experts performed or verified determinations of Tortricidae, Pyralidoidea, and Gelechioidea. For several poorly known taxa (e.g., Gracillariidae; Tortricidae: Cochylini), we sorted individuals into morphospecies, as suggested by Robinson and Tuck (1993). Unnamed morphospecies comprised <20% of our species total, and we verified the majority of our morphospecies rankings with recognized taxonomic experts to reduce error due to splitting or lumping of superficially similar taxa.

Analysis of Community Composition across Scales

We tested for differences in moth community composition among forest stands differing in topographic position, site location, and ecoregion by using nonparametric multidimensional scaling (NMS). As with many other ordination techniques, NMS seeks to reduce complex multispecies responses to environmental variation to a smaller set of summary variables contained in ordination axes. In contrast to parametric ordination, however, NMS differentiates among sampling units by ranking them according to their pair-wise dissimilarity (McCune & Mefford 1999). Thus, NMS is well suited for data sets that are suspected to deviate from normality or are collected by sampling across spatial scales. A detailed treatment of NMS ordination has been given by Clarke (1993). Briefly, each ordination axis contains information termed “stress,” which indicates the difference in distance between the placement of sampling units in ordination space and their ranked dissimilarity in species composition. The algorithm for NMS provides different stress solutions depending on the number of ordination axes considered. McCune and Mefford (1999) recommend running an initial six-dimension solution and testing each axis against Monte Carlo simulations to assess the appropriate number of dimensions (n) for the final ordination. An ordination axis is considered significant if it reduces the total stress in the data by $\geq 10\%$ (Clarke 1993). The significance of the n -dimensional solution is tested against a Monte Carlo simulation to assess whether the ordination axes explained more variance in the data than could be explained by chance.

We performed NMS ordination with PC-ORD (version 4; McCune & Mefford 1999). Moth community data consisted of log-transformed species abundance data for each forest stand (total of 20 stands) in early and late sampling seasons. We used the Bray-Curtis statistic as the measure of ordination distance among moth communities because it is one of the most robust statistics for multivariate ecological analysis and is little affected by the presence of rare species (Jongman et al. 1995). In addition, we followed the recommendation of McCune and Mefford (1999) and used multiple runs of the NMS ordination (100 total runs) with our real data to avoid local stress minima, a problem that prevents the NMS algorithm from converging on the lowest possible stress solution. We used 1000 Monte Carlo simulation runs to evaluate the significance of our final ordination axes.

Analysis through Additive Partitioning of Species Diversity across Scales

Traditionally, tests to determine scale-dependent effects on insect biodiversity use techniques such as nested analysis of variance (ANOVA), in which the null hypothesis of interest is that there is no difference among mean

diversities across several spatial levels. One potential limitation of this analytical technique is that ANOVA cannot be used to detect changes in diversity and composition across scales (for additional limitations of ANOVA in diversity analyses, see Gotelli & Colwell 2001). To answer this question, we need an analysis tool such as diversity partitioning, by which total diversity is partitioned among spatial levels and the observed α and β diversity at each level in a sampling design are compared with expected values obtained through a randomization technique (e.g., Gering et al. 2002; Crist et al., unpublished). Thus, ANOVA may be useful for detecting differences in diversity among samples within a level and across sampling levels, but diversity partitioning is the method of choice for determining whether the observed species diversity at a given spatial level is greater than (or less than) expected by chance alone. This latter hypothesis may be of greatest current interest for conservation biologists and land managers interested in identifying diversity hotspots in which to focus their efforts (Gering et al. 2002)

Lande (1996) demonstrated that regional species diversity (γ diversity) can be calculated as the sum of α and β diversity, where α is the average within-sample diversity and β is the among-sample diversity, or the average diversity not found in a single, randomly chosen sample. Within the context of our experimental design (Fig. 1), α and β diversity are defined relative to a given level of observation. Thus, α_1 represents the mean diversity of moths within a forest stand, and β_1 represents the diversity among the 20 forest stands. Because α diversity at any given scale is simply the sum of the α and β diversity at the next lowest scale (Wagner et al. 2000), the overall diversity of moth species within the five sites in our study can be expanded by the following formula: $\alpha_{2(\text{sites})} = \alpha_{1(\text{stands})} + \beta_{1(\text{stands})}$. Similarly, $\alpha_{3(\text{regions})} = \alpha_{2(\text{sites})} + \beta_{2(\text{sites})}$, and, at the highest level, the total diversity $\gamma = \alpha_{3(\text{regions})} + \beta_{3(\text{regions})}$. By substitution, the additive partition for our study is $\gamma = \alpha_{1(\text{stands})} + \beta_{1(\text{stands})} + \beta_{2(\text{sites})} + \beta_{3(\text{regions})}$. Total diversity can therefore be expressed as the proportional contributions of diversity due to each level in the hierarchical sampling design. In practice, an additive partition of diversity is most easily obtained by first calculating the α diversity at each level. This is then followed by obtaining β diversity at a given level as the difference between α diversity at that level and α diversity at the next highest level. Note that α diversity is always an average of the samples at a given level regardless of how they are nested within samples at the next highest level. Therefore, additive partitioning is robust to unbalanced sampling designs, such as in our study. Thus, it is possible to identify scales that contribute most significantly to the overall moth species diversity.

There is a multitude of ways to describe species diversity (reviewed by Magurran 1988), but diversity metrics

can only be partitioned into their alpha and beta components provided that they exhibit what Lande (1996) termed strict concavity. A diversity metric displays strict concavity when the overall value of the metric for a pooled set of communities is greater than or equal to the average diversity within communities ($\gamma \geq \alpha$). Lande (1996) demonstrated that species richness and the Simpson and Shannon diversity indices are all strictly concave. We used all three metrics in our study so that we could account for the effects of pure species richness and the combined effects of species richness and relative abundances (Simpson and Shannon indices). One major difference between the Simpson and Shannon indices is their relative emphasis on the contribution of rare species. The Simpson index is a measure of dominance within a community (weighted toward common species), whereas the Shannon index is more equally weighted toward rare and common species (a measure of evenness) (Magurran 1988). Using these diversity indices, we additively partitioned the entire data set of each sampling period into components representing $\alpha_{1(\text{stands})}$, $\beta_{1(\text{stands})}$, $\beta_{2(\text{sites})}$, and $\beta_{3(\text{regions})}$. This gave a total of six partitions (three diversity metrics \times two sampling seasons). We used a self-contained computer program, Partition (Gering et al. 2002; Crist et al., unpublished), to calculate the diversity components and to test their statistical significance.

The program Partition assesses the statistical significance of observed diversity components by testing, for each component, the null hypothesis that the observed component could have been obtained by a random distribution of sampling units at the next lowest level. More specifically, Partition gives the probability that a component greater than or equal to the observed component could have been obtained by chance alone. A probability defined in this way is equivalent to a p value from traditional significance test (Manly 1997). The probabilities associated with the observed components are obtained by repeatedly randomizing the data and then conducting a partition on each randomized version of the data. The p value is simply the proportion of randomized data sets with a diversity component greater than (or less than for a two-tailed test) the observed diversity component.

The randomization for a hierarchical design with three levels proceeds as follows: individual moths are randomly distributed to samples at level 1 (e.g., stands) that belong to the same sampling unit at level 2 (e.g., a site); this produces random samples at level 1 that are still nested within the appropriate sampling unit at level 2. In a separate randomization, random samples at level 2 are obtained by randomly distributing level 1 samples to any of the level 2 samples that belong to the same sampling unit at level 3 (e.g., an ecoregion). In a separate randomization, random samples at the highest level (level 3, ecoregions) are obtained by randomly distributing

level 2 samples to any level 3 sample. This type of restricted randomization preserves the nested structure of the data (whether balanced or unbalanced) but requires three separate randomization events. It is also important to note that Partition preserves the original species-abundance and sample-size distributions (Gering et al. 2002). Thus, each randomization may produce different numbers of species among samples, although the actual abundance of each species and size of each sample (at all levels) remains identical to the observed data. Rarefaction of samples is not necessary because diversity partitioning is generally robust to differences in the number of individuals contained in different samples (T.O.C. et al., unpublished), particularly for the minor differences of this study. In addition, if sampling effort (e.g., trap size and/or time spent sampling) is equal among all samples, as in this study, then differences in the number of individuals in samples may be representative of real ecological differences among the forest stands.

The series of three randomization events described in the previous paragraph can be repeated any number of times to form null distributions for each diversity component. We repeated these randomizations 10,000 times to form a null distribution of each α and β estimate (species richness, Shannon diversity, and Simpson diversity) at each level of analysis. Each of the level-specific estimates is then compared to the appropriate null distribution. Statistical significance is assessed by determining the proportion of null values that are greater than or less than our observed estimate (that is, our significance test was two-tailed). For example, if 3 out of 10,000 null values are greater than the observed estimate, then the probability of obtaining (by chance) an estimate greater than the observed value is 0.0003.

Analysis of the Influence of Rare and Common Species

To assess how differences in species abundance might influence the partitioning of species diversity (and thus community structure), we examined how the numbers of rare and common species varied among forest stands. We interpreted rarity in two different ways: (1) species were considered rare if they were unique to particular levels of sampling (i.e., present in a single replicate of a sampling level regardless of abundance) or (2) species were considered rare if they occurred as singletons (abundance = 1) or doubletons (abundance = 2) within any particular sampling level. An important distinction between singletons and unique species is that singletons (or doubletons) can occur multiple times at a given same spatial scale if the abundance of a species is 1 (or 2) within replicates at any particular sampling level. For example, *Tripudia flavofasciata* (Noctuidae) was represented by a single individual at both the HWSP and CACR sites within the NCT. This species was considered a singleton at both sites, but was only unique to the NCT ecoregion. Thus, we interpreted rarity based on both species incidence and abundance.

Additionally, we constructed a three-level nested analysis of variance (ANOVA) model to test for variation in the log-abundance of four of the most common moth species sampled across the spatial scales used in this study (PROC GLM; SAS Institute 2000). In contrast to the rare species, common species were defined purely based on their relative abundance. We calculated F tests for the significance of the ANOVA model effects for each level by treating the level below it as a random effect (Sokal & Rohlf 1995).

Results

Differences in Community Composition across Scales

We sampled a total of 28,017 individuals comprising 636 moth species from the five forest sites in Ohio. Four families represented a disproportionate number of species. The Noctuidae, Geometridae, Tortricidae, and Pyralidae comprised >50% of the total species richness recorded. The abundance of moths within families was similarly skewed, with the Pyralidae, Noctuidae, Geometridae, and Arctiidae providing nearly 67% of the individuals sampled. In terms of abundance, the four dominant species from this study were the eastern tent caterpillar, *Malacosoma americanum* (Lasiocampidae); *Herculia olinalis* (Pyralidae); the slowpoke, *Anorthodes tarda* (Noctuidae); and the hickory tussock moth, *Lophocampa caryae* (Arctiidae).

Temporal and broad-scale ecoregional effects most significantly influenced moth community composition (Fig. 2). Preliminary runs of the NMS algorithm indicated that a two-dimensional ordination was optimal, and our final ordination accounted for 90% of the variance in species abundances among moth communities. Forest stands grouped into early and late-season moth communities along axis 1 (mean stress = 52.42, $p < 0.001$) and clustered into ecoregional associations along axis 2 (mean stress = 26.54, $p < 0.001$). We found little evidence for differentiation among sites within ecoregions, and moth communities did not differ between mesic and xeric stands within sites (Fig. 2). Interestingly, EDGE clustered tightly with other sites in the Western Allegheny Plateau, perhaps because it is located on the periphery of the Interior Low Plateau ecoregion very near to the WAP (Fig. 2). Thus, for the diversity partitioning analyses, we included the EDGE site with the two original sites from the WAP to test the null hypothesis that the distribution of moth diversity between the NCT and the WAP+ILP was no different than expected from a random distribution.

Partitioning of Species Diversity across Spatial Scales

Moth communities in the glaciated NCT were generally less species-rich than moth communities in the unglaciated WAP (Table 1). In terms of Shannon or Simpson di-

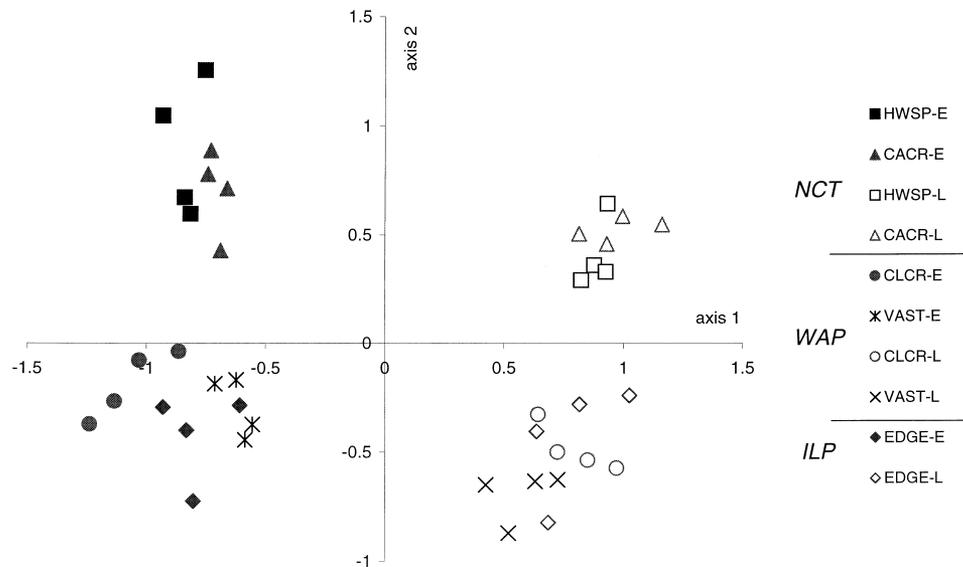


Figure 2. Nonmetric multidimensional scaling ordination of five forest sites sampled in early (E) and late (L) sampling seasons. Abbreviations: HWSP, Hueston Woods State Park; CACR, Caesar Creek State Park; CLCR, Clear Creek MetroPark; VAST, Vastine Hollow; EDGE, Edge of Appalachia Nature Preserve.

iversity, however, forest sites in the WAP and the ILP were less diverse than sites in the NCT, suggesting that moth communities in the WAP were dominated by a few highly abundant species (Table 1). Three general results emerged from our additive partitioning models. First, the observed β diversity among sites (β_2) was greater than expected by chance, except for Simpson and Shannon diversity in the early season (Table 2). Second, for the Shannon and Simpson indices, β diversity among stands was always less than expected by chance. Finally, the observed α diversity at the lowest level (within stands) was always greater than expected by chance, a single exception being species richness in the early season.

This pattern emerged despite the fact that α diversity accounted for low levels of the total species richness observed within stands (approximately 20%) but high levels (>75%) of the Shannon or Simpson diversity for the entire moth assemblage (Fig. 3). The contribution of α diversity to Simpson diversity was slightly greater than that for Shannon diversity, suggesting that patterns of species dominance occur at fine spatial scales. Each spatial scale in our sampling hierarchy, however, made relatively equal, though occasionally nonsignificant (Table 2), contributions to total species richness in both seasons (Fig. 3). Interestingly, the observed β diversity components between ecoregions (β_3) were never significantly different than expected from a random distribution of sites within ecoregions. This may be the consequence of low statistical power because we have only five sites to randomize between the two ecoregional groups (NCT and WAP+ILP) in testing the null hypothesis: observed $\beta_{3(\text{regions})} - \text{expected } \beta_{3(\text{regions})} = 0$.

Influence of Rare and Common Species on Scaling of Diversity and Composition

Rare species were a substantial component of the moth communities within each forest site (Table 3). Because many singletons also represent species unique to a given sampling level, turnover in rare species appeared to influence the equal partitioning of species richness across spatial scales (Table 3; Fig. 3). Although singletons and doubletons were present in roughly equal numbers among sites within ecoregions and between ecoregions, the unglaciated WAP contained nearly 50 more unique

Table 1. Diversity statistics for Lepidoptera sampled in five forest sites nested within three Ohio ecoregions.

| Ecoregion | Site ^a | Species richness | Shannon index ^b | Simpson index ^b |
|------------------------------|-------------------|------------------|----------------------------|----------------------------|
| North Central Tillplain | | 431 | 4.91 | 0.983 |
| | HWSP | 327 | 4.57 | 0.982 |
| | CACR | 348 | 4.57 | 0.981 |
| Western Allegheny Plateau | | 452 | 4.01 | 0.901 |
| | CLCR | 333 | 4.53 | 0.951 |
| | VAST | 363 | 4.13 | 0.885 |
| Interior Low Plateau | EDGE | 409 | 4.33 | 0.852 |

^aAbbreviations: HWSP, Hueston Woods State Park; CACR, Caesar Creek State Park; CLCR, Clear Creek MetroPark; VAST, Vastine Hollow; EDGE, Edge of Appalachia Nature Preserve.

^bCalculations for these diversity metrics are described in the Methods section.

Table 2. Additive partition of α and β diversity components across a hierarchically scaled study of forest lepidopteran diversity.^a

| Source | No. samples | Species richness | | | Shannon index | | | Simpson index | | | | |
|---|----------------------------|------------------------------|-------|-------|---------------|-------|-------|---------------|-------|-------|-------|---|
| | | obs | exp | p^b | obs | exp | p^b | obs | exp | p^b | | |
| Moths, early regions (β_3) ^d | 2 | 90.8 | 111.7 | 0.643 | 0.21 | 0.333 | 0.559 | 0.026 | 0.080 | 0.632 | ns | |
| | 4 | 109.1 | 78.6 | 0.021 | 0.14 | 0.206 | 0.764 | 0.013 | 0.081 | 0.108 | ns | |
| | among stands (β_1) | 16 | 116.2 | 116.8 | 0.588 | 0.27 | 0.419 | 0.002 | 0.031 | 0.068 | 0.023 | - |
| | | within stands (α_1) | 130.9 | 121.5 | 0.214 | 2.97 | 2.715 | 0.060 | 0.799 | 0.727 | 0.048 | + |
| totals | 447 | 428.6 | | 3.59 | | | 0.869 | 0.956 | | | | |
| Moths, late regions (β_3) ^d | 2 | 114.6 | 125.0 | 0.606 | 0.22 | 0.131 | 0.365 | 0.004 | 0.002 | 0.231 | ns | |
| | 4 | 118.2 | 83.6 | 0.001 | 0.26 | 0.155 | 0.008 | 0.005 | 0.003 | 0.026 | + | |
| | among stands (β_1) | 16 | 123.3 | 125.2 | 0.603 | 0.42 | 0.597 | 0.001 | 0.007 | 0.022 | 0.002 | - |
| | | within stands (α_1) | 116.9 | 110.9 | 0.029 | 4.13 | 3.970 | 0.002 | 0.972 | 0.956 | 0.007 | + |
| totals | 473 | 445 | | 5.02 | 4.85 | | 0.988 | 0.983 | | | | |

^a Abbreviations: obs, observed; exp, expected. In total, 636 species and 28,017 individuals were sampled.

^b The p values were obtained by comparing the observed values to the distribution of values from the 1000 randomizations.

^c Observed partitions are compared to those expected from means of 1000 randomizations.

^d Expected values of α and β are not necessarily additive to the observed total diversity (γ) because the statistical significance of each component is tested with a separate set of randomizations (see Methods). A plus (+) indicates that the observed value is significantly higher than expected. Tests of regional β diversity are based on differences between moth assemblages from the North Central Tillplain and the Western Allegheny Plateau + Interior Low Plateau.

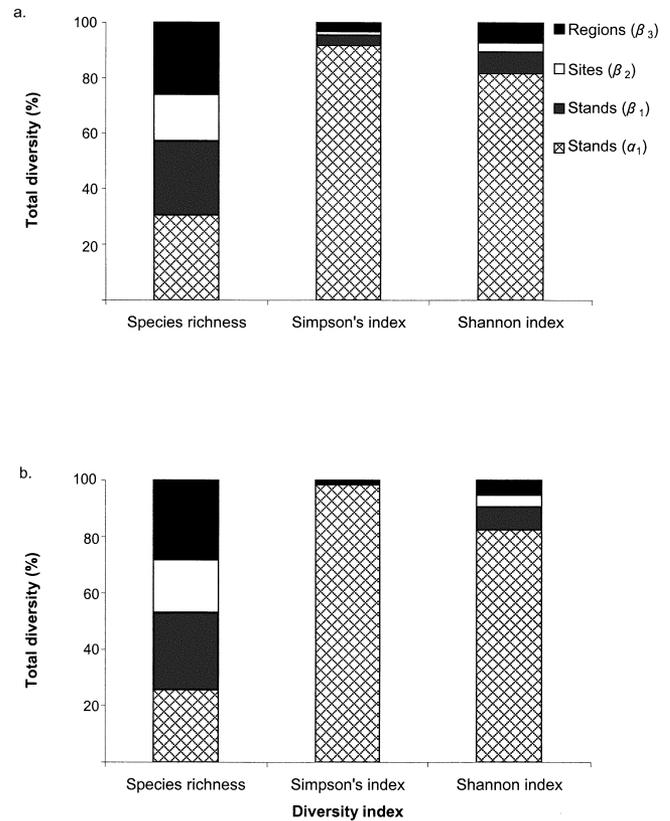


Figure 3. Percentage of total moth species richness, Simpson diversity, and Shannon diversity explained by α and β components of regional diversity: within and among forest stands (α_1 and β_1), among sites (β_2), and between ecoregions (β_3). Separate diversity partitioning analyses were performed in (a) early and (b) late seasons.

species than the glaciated NCT (Table 3). Therefore, rare species with restricted distributions were important for determining the observed β diversity estimates for species richness across sampling levels: the equal contribution of each spatial level in our hierarchy suggests that a proportional number of unique species are encountered as the spatial scale of an inventory is expanded (e.g., a species-area phenomena).

The nested ANOVA model demonstrated that the log-abundance of the four most common species sampled over the course of this study differed significantly between ecoregional groups and, for two species, between mesic and xeric stands (Table 4; Fig. 4). Forest stands in the WAP and the ILP were clearly dominated by two species of defoliators, *Malacosoma americanum* and *Herculia olinalis*, with their combined abundances approaching 30–40% of the individuals sampled within sites. The effect of these species on community structure was evident: forest stands in the WAP and ILP had low values of Shannon and Simpson diversity compared with the those in the NCT (Table 1). Regard-

Table 3. Contrasting forms of rarity for Lepidoptera sampled in five forest sites nested within three Ohio ecoregions.

| Ecoregion | Site ^a | Total species richness | Unique species ^b | Singletons ^c | Doubletons ^c |
|---------------------------|-------------------|------------------------|-----------------------------|-------------------------|-------------------------|
| North Central Tillplain | | 431 | 108 | 110 | 57 |
| | HWSP | 327 | 47 | 102 | 64 |
| | CACR | 348 | 37 | 112 | 60 |
| Western Allegheny Plateau | | 452 | 154 | 102 | 57 |
| | CLCR | 333 | 22 | 95 | 46 |
| | VAST | 363 | 38 | 89 | 56 |
| Interior Low Plateau | EDGE | 409 | 52 | 105 | 65 |
| Total | | 636 | | 127 | 73 |

^aAbbreviations: HWSP, Hueston Woods State Park; CACR, Caesar Creek State Park; CLCR, Clear Creek MetroPark; VAST, Vastine Hollow; EDGE, Edge of Appalachia Nature Preserve.

^bUnique species are those found only once within a particular sampling level.

^cSingletons are species represented by only one individual, and doubletons are species represented by only two individuals within replicates at any particular sampling level.

less of absolute abundance, however, each of the four most common species remained a numerically dominant species within all forest stands relative to the other suite of species present (many of which were singletons; Table 3; Fig. 4) For example, *Malacosoma americanum* was significantly less abundant in forest stands of the glaciated NCT; however, relative to the other species in the NCT stands, *M. americanum* was ≥ 10 times as commonly encountered in our samples.

Discussion

As expected, lepidopteran species diversity and composition varied across spatial scales. Community composition, species dominance, and species richness, however, appeared to be differentially influenced by discrete levels within our sampling hierarchy. Thus, our results add to an emerging body of literature from temperate forests suggesting that (1) insect community composition varies most significantly over broader spatial scales, even when total species richness does not (Magurran 1985; Atauri & de Lucio 2001; Summerville et al. 2001); (2) species dominance and evenness within a community

are determined at finer spatial scales (DeVries et al. 1997; Spitzer et al. 1999; Wagner et al. 2000); and (3) changes in insect species richness occur across virtually all spatial scales as unique species are encountered within each sampling level (Summerville et al. 2001). In addition, our study expands on these generalizations by demonstrating the contrasting effects of scale on moth communities from a single data set collected by sampling simultaneously across a hierarchy of spatial scales. Furthermore, we show that the observed diversity at lower spatial scales is often significantly different from (either greater than or less than) what would be expected if species distributions were determined by chance alone.

Because the paradigm of conservation biology has shifted to include greater emphasis on multiscale approaches to the preservation of biodiversity, there will be some value in understanding what mechanisms operate at a given spatial scale to cause differences in community composition and species diversity. Diversity partitioning is emerging as a promising tool with which to identify the spatial scales at which species diversity is greater or less than that predicted by a random distribution of species in space.

Table 4. Three-level nested analysis of variance values for difference in the four of the most abundant moth species sampled in 2000 from forest preserves in the North Central Tillplain and the Western Allegheny Plateau + Interior Low Plateau.^d

| Source of variation | DF | Malacosoma americanum | | Herculia olinalis | | Anorthodes tarda | | Lophocampa caryae | |
|--|----|-----------------------|----------|-------------------|----------|------------------|-------|-------------------|---------|
| | | MS | F | MS | F | MS | F | MS | F |
| Ecoregion | 1 | 92.7 | 154.7*** | 120.3 | 17.08* | 0.16 | 0.47 | 14.2 | 32.57** |
| Sites (within ecoregions) ^b | 3 | 0.60 | 1.31 | 7.0 | 2.27 | 0.38 | 0.67 | 0.44 | 0.71 |
| Aspect (within sites) ^c | 5 | 0.46 | 1.45 | 3.1 | 10.41*** | 0.52 | 5.51* | 0.61 | 2.13 |
| Error | 10 | 0.32 | | 0.29 | | 0.09 | | 0.30 | |

^aAbundances for each species were log-transformed prior to analysis. Sources of variation used in the analysis of variance model were derived from the hierarchical sampling design illustrated in Fig. 1. Probability: *p < 0.05, **p < 0.01, ***p < 0.001.

^bUsed as error term for tests of the significance of the ecoregion effect.

^cUsed as the error term for tests of the significance of the sites (within ecoregions) effect.

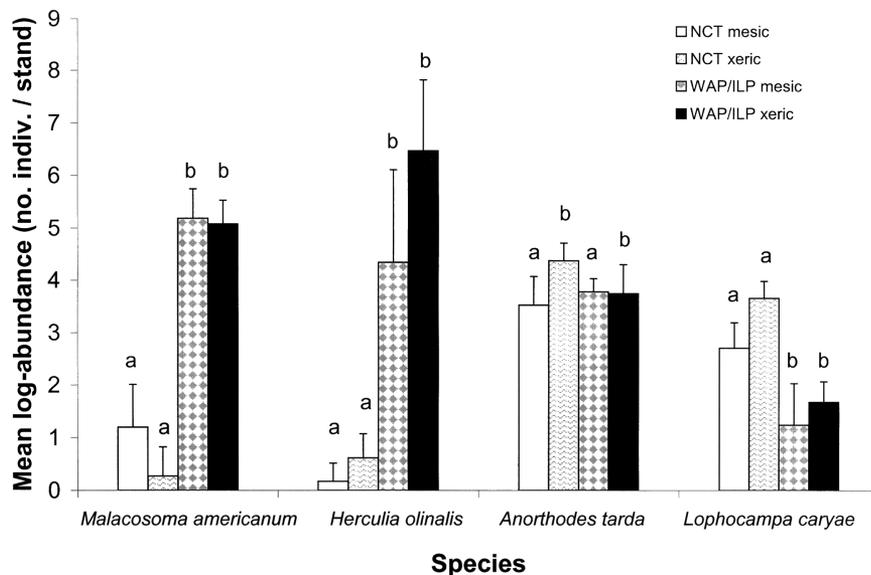


Figure 4. Variation in mean log abundance (± 1 SD) of four of the most common moth species sampled from forest stands in two ecoregional associations. Mean log abundance of the species differed between ecoregions and, in some cases, between mesic and xeric forest stands. Abbreviations are as follows: NCT, North Central Tillplain; WAP/ILP, Western Allegheny Plateau/Interior Low Plateau (see Methods section).

The composition of moth communities in forests appeared to be most significantly influenced by broad-scale, ecoregional effects. Indeed, the NCT, WAP, and ILP differ in their glacial exposure, topography, vegetation, and land-use history, all of which have been shown to play a role in structuring lepidopteran communities (Fleishman et al. 2000; Summerville et al. 2001; Summerville & Crist 2002). Little difference was found between the composition of the moth faunas of the WAP and the ILP, however, perhaps because we were careful to sample forest stands in the ILP that were geologically and floristically similar to those of the WAP.

Diversity partitioning also demonstrated that a large number of species (i.e., between 90 and 115) were unique to each ecoregion. The β -diversity component between ecoregional groups (β_3), however, was not significant for each of the diversity metrics. Because our experimental design lacked substantial replication of sites within ecoregions, we believe the absence of significance for the difference between observed and expected values of β_3 may be the consequence of low statistical power. Two main conclusions emerge from a consideration of ecoregional β diversity. First, fairly large differences in lepidopteran species richness among sampling units should be expected simply as a result of random species distributions, although this does not necessarily mean that all species are randomly distributed. Second, many replicates must be compared to assess whether the β diversity in any given level is unusually high or low (i.e., nonrandom).

Each spatial level in our sampling hierarchy contributed a similar proportion of unique species to the community. The addition of unique species to inventories as scale is expanded is, at least in part, a species-area phenomena and, for moths, may result when rare species with restricted geographic ranges, specialized host-plant

requirements, or limited vagility are encountered as sampling extent is increased (e.g., Palmer & White 1994; T.O.C. et al., unpublished). Communities in which a large proportion of the total richness is composed of rare species will pose several challenges to conservation biologists. For example, because most of the unique diversity within forest stands was contributed by singleton and doubleton species (assumed to have genuinely low population densities), management of stands to control pest species may have unintended consequences for the majority of the moth species comprising the richness of a community. In our system, forest stands within the WAP contained a greater absolute abundance of outbreak species such as *M. americanum* and *H. olinalis* and were under immediate risk of infestation by the gypsy moth (*Lymantria dispar*), so reserve managers and foresters face an immediate dilemma in balancing the need to maintain productive forest resources and the desire to protect native biodiversity (Liebold et al. 1995). If non-selective insect control agents are used in forest reserves, then managers should be aware of the potential for extirpation of a large proportion of native moth biodiversity (e.g., Wagner et al. 1996; Butler et al. 1997).

Indeed, one of the most pressing questions emerging from studies of insect communities in temperate forest systems is why so many species appear to have tiny populations (Novotny & Basset 2000). Regardless of the explanation, it will be impossible for conservation biologists to design site management plans to account for species represented by a few individuals in a sample (New 1999), even if such species compose the majority (>50%) of the species in a community (also see Gaston et al. 2001).

We suggest that a more meaningful conservation approach will be first to identify species that attain a reasonable abundance within a community (perhaps each

species with a relative abundance of 5–10% of all the individuals in a given sample) and that are unique to particular spatial levels—a modification of a critical faunas approach (Ackery & Vane-Wright 1984). In the WAP, for example, such ecoregionally distinctive species might include *Metrea ostrionalis* (Pyrilidae), *Crambidia cephalica* (Arctiidae), *Semiothisa fassinotata* (Geometridae), and *Hemileuca maia* (Saturniidae). To conserve such distinctive faunal elements of the lepidopteran community in the WAP, site management plans could be designed with the purpose of maintaining viable host-plant populations for these species and encouraging periodic monitoring of their populations. Such a strategy should also prevent overemphasis on establishing new preserves on transition zones between ecoregions, where many species may occur at very low abundance at the edges of their range (Gaston et al. 2001) and may undergo very unstable population dynamics (Thomas et al. 1994). In contrast, land for additional preserves or conservation management would be prioritized according to its value as a diversity hotspot (i.e., less diversity than expected by chance) and its ability to sustain populations of unique or distinctive faunal elements (rather than simply focusing on the overall species richness of the site).

We found an apparent contradiction between the ecoregional influences on abundance demonstrated by the nested ANOVA models (Table 4) and the potential local control of observed Shannon and Simpson diversity at fine spatial scales. Understanding the mechanism behind these species aggregation patterns lies in different contributions of absolute and relative dominance to community structure (Fig. 3). Some common moth species may attain greater absolute abundance within forests sites of particular ecoregions due to factors such as differences in broad-scale forest structure and floristic composition (Hammond & Miller 1998; Butler & Straznec 2000). Shifts in the absolute dominance of common species among sites are possible explanations for the significantly high β diversity among sites in the late season (for Simpson and Shannon indices). In contrast, we would expect a significantly low β diversity among sites if a single species was very abundant and widespread across all communities. Such a pattern may be observed among stands invaded by the gypsy moth (*Lymantria dispar*) because population sizes may exceed those of native species by several orders of magnitude and *L. dispar* is not completely restricted to any single deciduous forest association (Butler et al. 2001). The overall effect of such species would be to homogenize communities as measured by species dominance.

In apparent contrast to the high β diversity among sites, β diversity among the stands within sites was significantly low in both early and late seasons. At the fine scale of stands within sites, the most common species were more evenly distributed; that is, there were no shifts in dominance from one stand to the next. Thus,

common species may affect the partition of species diversity in two ways, through an equitable distribution at fine spatial scales and through shifts in absolute dominance at broad spatial scales. In such cases, diversity partitioning is particularly useful because it can identify combinations of sites with β diversity that is higher than expected by chance. For example, when diversity is measured with Simpson's index and is greater than expected by chance, moth species composition is less determined by super-abundant species (evenness is greater than expected). If species richness is also greater than expected by chance, the site may contain a unique suite of species that attain reasonable abundance within the community. Such species assemblages should then be the focus of conservation efforts.

Communities may appear to be more or less diverse than expected by chance, depending on the scale of observation. Diversity partitioning can aid in this determination and thus assist in the selection of sites to include in a reserve system where ecological processes dictate, in large degree, moth community structure. For moth communities, a species survey at the scale of a few stands may indicate low species diversity within a given site, but if that same site contains a unique subset of dominant species compared with other sites in the region, it should be highly valued for conservation. Similar conclusions could also be obtained through existing complementarity analyses. What diversity partitioning adds is the identification of sites where ecological processes operate to produce significantly greater or lesser diversity than random species distributions would dictate. Identification of critical scales at which ecological processes influence species diversity will ultimately be crucial to ascertaining the appropriate scales at which habitat management or ecological restoration should be implemented. Finally, the results of our study suggest that conservation biologists and preserve managers should focus on the protection of regionally distinctive species assemblages and natural community dominance patterns. This strategy should produce two desirable outcomes: the conservation of species that render ecoregions distinct and the maintenance of functionally dominant species within forest stands.

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