BIODIVERSITY RESEARCH

Do body size and diet breadth affect partitioning of species diversity? A test with forest Lepidoptera

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ABSTRACT

Two of the major themes resulting from recent macroecological research are the central roles that body size and niche breadth may play as determinants of species geographical distribution. Unanswered questions, however, linger regarding how similarities in body size or niche breadth affect the allocation of α- and β-diversity across spatial scales. Using data on moth diversity in the eastern deciduous forest of North America, we tested the predictions that smaller-bodied and diet-restricted species would have lower levels of α-diversity within forest stands and greater β-diversity at higher sampling scales compared to larger or more generalist species. Moths were sampled using a nested sampling design consisting of three hierarchical levels: 20 forest stands, 5 sites and 3 ecoregions. Body size for 492 species was estimated as mean forewing length, and diet breadth was assessed from the published literature. Moth species were then classified according to body size (small or large) or diet breadth (generalist or restricted), and partitioning was conducted on each group. Diversity partitions for large- and small-bodied species yielded similar patterns. When observed diversity components differed from those derived from our null model, a consistent pattern was observed: α-diversity was greater than expected, β-diversity among forest stands was less than expected, and β-diversity among sites and ecoregions was higher than expected. In contrast, diet-restricted moths contributed significantly less to stand-level α-diversity than generalist feeders. Furthermore, specialists contributed to a greater proportion of β-diversity across scales compared to generalist moths. Because absolute measures of β-diversity among stands were greater for generalists than for restricted feeders, we suggest that regional β-diversity of forest moths may be influenced by several possible factors: intraspecific aggregation of diet-restricted species, local fluctuations in population size of eruptive generalists and small geographical distributions of generalist moths than predicted by the geographical extent of putative host plants

Keywords

Additive diversity partition, β-diversity, macroecology, moths, regional diversity, species composition.

INTRODUCTION

Macroecology is primarily concerned with detecting emergent properties of ecological communities and finding parsimonious explanations for patterns of species distribution and abundance at broad spatial scales (Brown, 1995). Two of the major themes resulting from recent macroecological research are the central roles that both body size and niche breadth play as determinants of species bionomics and geographical distribution (e.g. Blackburn & Gaston, 2003). To more fully understand the organization of

ecological communities, it is necessary to test whether differences in species traits (e.g. body size, niche specialization) lead to non-random differences in the allocation of species diversity across spatial scales (e.g. Summerville *et al.*, 2003). Veech *et al.* (2003) offered a preliminary assessment of factors influencing diversity components in space by demonstrating that significant intra-specific aggregation is correlated with low local species diversity (α-diversity) and high species turnover (β-diversity) within a region. The recently derived analytical approach to diversity partitioning (see Crist *et al.*, 2003) may further provide a framework

to examine whether body size or niche breadth leads to similar patterns in the allocation of α- and β-diversity components in space described in Veech *et al.* (2003).

Body size is both easy to measure and is correlated with species dispersal ability (Gardezi & da Silva, 1999; Bowman *et al.*, 2002; Brändle *et al.*, 2002). The relationship between body size and geographical range size, however, is not necessarily linear. Brown (1995) and Blackburn and Gaston (2003) suggest that species with either large or very small body sizes tend to possess larger home ranges, but species with intermediate body sizes tend to show a positive correlation between body size and geographical range (the complete relationship this thus triangular). As postulated by Brändle *et al.* (2002), the body size–geographical range hypothesis states that when large-bodied, non-parasitic organisms are more vagile, they should be present at a larger number of sites within their geographical range or over a larger total area than smaller-bodied organisms (see also Swihart *et al.*, 2003). Given the potential positive correlations between body size and dispersal ability, body size may also affect the partitioning of α- and β-diversity components from a regional species pool (Gaston & Reavey, 1989). Larger-bodied species should have a relatively high α-diversity within ecological communities, while smaller-bodied species, which may be more limited in geographical distribution, should have significantly low α-diversity and greater β-diversity among communities within a region. In contrast, Gaston's (1988) study of local and regional patterns in moth population dynamics suggests that an opposite pattern may actually be observed: smaller-bodied species may be the most widely distributed although populations of such species can be highly variable and experience frequent local extinction (see also Blackburn & Gaston, 1996).

The potential effects of niche breadth on community organization have been studied most extensively using diet specialization, with studies demonstrating that species known to feed on a greater range of resources possess greater potential fecundity (Spitzer *et al.*, 1984; Hunter, 1991), larger geographical distribution (Gaston, 1988; Roy *et al.*, 1998), and perhaps greater susceptibility to environmental stochasticity (Rajmánek & Spitzer, 1982; Spitzer *et al.*, 1984; Hunter, 1991). These patterns remain somewhat equivocal, as other studies have found no relationship or even the opposite relationships between a species diet and the above variables (Redfearn & Pimm, 1988; Lepš *et al.*, 1998). It remains plausible, however, that dietary generalists have a greater likelihood of having their resource needs met in a greater number of habitats, whereas specialists should be highly restricted to a smaller subset of habitat patches within the greater landscape (Roy *et al.*, 1998; Summerville *et al.*, 2002; Swihart *et al.*, 2003). In terms of hierarchical patterns of species diversity, generalists should have higher levels of α-diversity within communities compared to specialists, which should have higher levels of β-diversity among communities (e.g. Tscharntke *et al.*, 2002).

The goal of this study was to determine if body size and diet breadth affect α- and β-diversity across a number of sampling scales. Diversity partitioning is increasingly being used to examine patterns in α- and β-diversity within a regional species pool (Veech *et al.*, 2002; Crist *et al.*, 2003). First, we tested the prediction that large-bodied moths would display greater levels of α-diversity

and lower levels of β-diversity within communities compared to smaller-bodied species. Second, we tested the prediction that moth species with a broader diet breadth would have higher α-diversity and lower β-diversity compared to specialists. Both tests were conducted using data on moth communities from the eastern deciduous forest in Ohio, USA. The Lepidoptera were well-suited to this study because data regarding both body size and diet breadth are well-documented in the literature (e.g. Summerville & Crist, 2002).

METHODS

Study sites and sampling design

We used a nested design to sample Lepidoptera from stands of eastern deciduous forest in Ohio, USA. Three hierarchical levels comprised the design, listed from broadest to smallest: ecoregions, forest sites and forest stands (see Summerville *et al.*, 2003). Ecoregions differed in their glacial history, topographical heterogeneity, soil types and floristic composition (Fig. 1). The forests of the North Central Tillplain (NCT) are dominated by American beech (*Fagus grandifolia* Ehrh.) and sugar maple (*Acer saccharum* Marsh.) (Braun, 1961). Species such as white oak (*Quercus alba* L.), red oak (*Quercus rubra* L.), slippery elm (*Ulmus rubra* Muhl.) and several ashes (*Fraxinus* spp.) are also important canopy species (Greller, 1988). Land use in the NCT is predominantly agricultural, since glacial scouring has created a flat topography (ridges are separated by shallow, sloping floodplains) and productive soils. 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 characterized by steep ridges and long, narrow drainages. In the WAP, xeric aspects are dominated by chestnut oak (*Quercus prinus* L.) and hickories (*Carya* spp.),
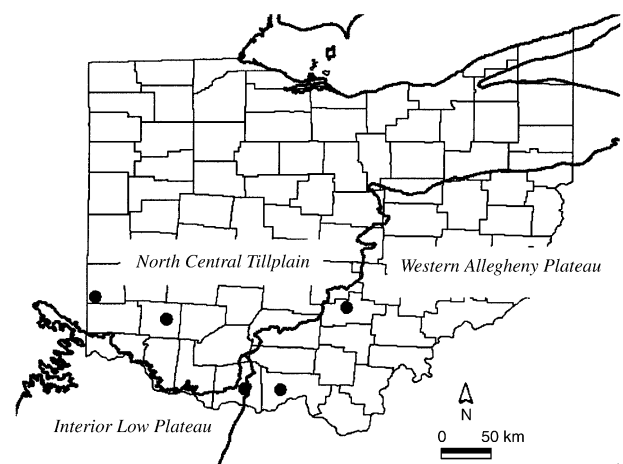

Figure 1 Map of Ohio showing ecoregions and study site locations. Dark lines represent ecoregional boundaries; ● represents study sites. Map adapted from The Nature Conservancy (1999). Study sites are listed clockwise beginning from the top of the Western Allegheny Plateau: Clear Creek MetroPark, Shawnee State Forest, Edge of Appalachia, Caesar Creek State Park and Hueston Woods State Park.

while mesic areas contain a more diverse assemblage of trees including American beech, tulip poplar (*Liriodendron tulipifera* L.), basswood (*Tilia americana* L.) and eastern hemlock (*Tsuga Canadensis* L. (Carr.)) (Greller, 1988). The ILP of southern Ohio is similar to the WAP in its glacial history and variable topography. Portions of the ILP, however, are underlain by dolomitic limestone and have more alkaline soils that tend to support a greater overall diversity of vegetation.

Our experimental design nested two sites within the NCT and the WAP (Fig. 1). Hueston Woods State Park (HWSP; Preble Co., OH) and Caesar Creek State Park (CACR; Warren Co., OH) occurred in the glaciated NCT, whereas Clear Creek MetroPark (CLCR; Hocking Co., OH) and Vastine Wilderness Area (VAST; Scioto Co., OH) occurred in the unglaciated WAP ecoregion. We included a fifth site in our study, Edge of Appalachia nature preserve (EDGE; Adams Co., OH) that falls within the ILP (Fig. 1). Within each site, we selected four forest stands (*c.* 1 ha) that represent typical mesic and xeric aspects and were separated by a minimum distance of 250 m from other stands as well as other ecotones. 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 geological formations more characteristic of the WAP. Mesic stands contained woody and herbaceous flora similar to bottomlands at Shawnee State Forest (Summerville *et al.*, unpublished data). A previous study demonstrated that the lepidopteran fauna of EDGE is closely affiliated with that of the WAP ecoregions (Summerville *et al.*, 2003).

Lepidoptera sampling

Within each forest stand, we sampled Lepidoptera using a single 12-W universal blacklight trap (BioQuip Products, Inc., Rancho Dominguez, CA) powered by a 12-V (26 amp h^{-1}) gel battery. Blacklight traps are widely recognized to be the standard technique for sampling moth communities, although the method is biased toward collecting phototactic species. To avoid disruption of the UV light by seedlings and shrubs in the understorey, we positioned UV traps on platforms *c.* 1.5 m above the ground. 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 EDT during both early and late seasons (four nights total per stand). Therefore, trapping accumulated 80 samples in the early and the late seasons combined, representing *c.* 60% of the moth fauna predicted to be present using the incidence-based coverage (ICE) diversity estimator (see Longino *et al.*, 2002).

Determining moth body size and diet breadth

We estimated body size as the mean of the maximum and minimum forewing length (in cm), as reported in Forbes (1923),

Table 1 Number of moth species and range in body sizes sampled from forest stands. Moth families are arranged in order of increasing species richness. Family names follow those in Hodges *et al.* (1983) with revisions according to Hodges (1999)

Family	Number of moth species	Observed range in body size (min.–max. in cm)
Argyresthidae	1	1.35
Bucculatracidae	1	0.45
Coleophoridae	1	1.20
Drepanidae	1	2.95
Epiplemidae	1	2.00
Heliozelidae	1	0.75
Incurvariidae	1	1.25
Plutellidae	1	1.30
Pterophoridae	1	1.35
Sessiidae	1	2.15
Tineidae	1	1.40
Zygaenidae	1	2.30
Acrolophidae	2	2.85–3.0
Apatelodidae	2	3.70
Megalopigidae	2	3.00–3.25
Mimaloniidae	2	2.60–4.25
Yponomeutidae	2	1.85–2.40
Amphisbatidae	3	1.35–2.05
Gracillariidae	3	1.10–1.30
Lasiocampidae	3	3.00–3.90
Lymantriidae	4	2.65–3.90
Oecophoridae	4	0.45–1.90
Cosmopterigidae	5	0.55–1.75
Sphingidae	6	5.75–9.40
Elachistidae	9	0.70–1.80
Saturniidae	10	4.30–12.70
Gelechiidae	12	1.15–2.50
Limacodidae	14	2.00–2.95
Arctiidae	26	1.65–7.4
Notodontidae	28	2.90–5.20
Crambidae	30	0.70–3.35
Pyralidae	32	1.10–3.80
Tortricidae	53	1.00–2.60
Geometridae	84	1.30–5.20
Noctuidae	144	1.25–7.75
Total	492	

Covell (1983) and other published monographs. Gaston and Reavey (1989) and Hawkins and Lawton (1995) considered this approach valid for large data sets, especially for insects. Using this approach, body size could only be estimated for those species we were able to identify. Summerville *et al.* (2003) collected a total of 636 species of moths, of which 492 were identified to species (Table 1). Some bias exists in the range of body sizes covered in our data as very small-bodied moths are difficult to identify even by experts ('microlepidoptera'; e.g. Gracillaridae, Gelechioidea), and published literature for species natural history is scant. Thus, our data set contained fewer tiny moths (wingspan < 0.4 cm) than likely occur in typical forest moth communities. Small
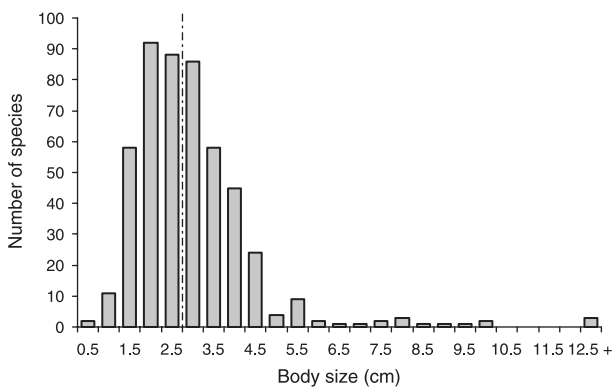
Figure 2 Distribution of body sizes for 492 moth species sampled in 2000. The dashed line breaks the distribution into two groups of moths that contained a similar number of species (small: average wingspan ≤ 2.75 cm; large: average wingspan > 2.75 cm).

moths represented body sizes < 2.75 cm in wingspan; wingspan of large moths was 2.75 cm (Fig. 2). Median body size for all moths was 2.70 cm, so this classification resulted in only slight differences in the total number of species within each group. Small moths were mostly Tortricidae, Pyralidae and Crambidae and Gelechiidae, while large moths were generally species of Noctuidae, Geometridae, Arctiidae and Notodontidae (Table 1).

We used the data on diet breadth in Robinson *et al.* (2002) to classify a total of 456 moth species as generalists, oligophagous or specialist. Following Lepš *et al.* (1998) and Summerville and Crist (2002), generalists were considered to be species known to feed on hosts in a number of plant families, oligophages were moths reported to feed on a number of host plant genera within a single family, and specialists were species known only to feed on plants within a single genus. This classification rendered relatively few oligophagous moths, so we combined the oligophagous and specialist species as a single diet-restricted group for our data analyses (Summerville & Crist, 2002).

Analysis using additive partitioning of species diversity across scales

Diversity partitioning is emerging as a powerful tool to detect changes in diversity and composition across sampling scales (Lande, 1996; Wagner *et al.*, 2000; Gering *et al.*, 2002; Ouin & Burel, 2002; Summerville *et al.*, 2003). The formal analytical basis of diversity partitioning has been well-developed elsewhere, but briefly, the method measures total species diversity (γ) and then partitions this measure into the additive components of alpha- (α) and beta-diversity (β) (see Lande, 1996). We compared observed α- and β-diversity at each hierarchical level of our sampling design to expected values obtained through a randomization technique (Crist *et al.*, 2003).

Within the context of our study, α- and β-diversity are defined relative to a given level of sampling within the nested design. 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 in a given sampling level is simply the sum of

the α- and β-diversity at the next lowest level (Wagner *et al.*, 2000), the overall moth species diversity within the five sites in our study can be expanded by the following formula:

$$\alpha_{2(\text{sites})} = \alpha_{1(\text{stands})} + \beta_{1(\text{stands})}. \tag{1}$$

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:

$$\gamma = \alpha_{1(\text{stands})} + \beta_{1(\text{stands})} + \beta_{2(\text{sites})} + \beta_{3(\text{regions})}. \tag{2}$$

The total diversity can therefore be expressed as the proportional contributions of diversity due to each level in the hierarchical sampling design (see Summerville *et al.*, 2003).

There is a multitude of ways to describe species diversity, but two of the most commonly employed measures are species richness and Simpson diversity (Magurran, 1988). Species richness is simply a count of the number of species present within a community, while the Simpson index is a measure of dominance within a community as determined from the relative abundance of species (Krebs, 1999). Simpson diversity was calculated as the Gini coefficient: $D = 1 - \sum P_i^2$, where p is the relative abundance of species i. Using these diversity indices, we conducted additive partitions for the entire data set in both sampling periods for a total of 16 partitions (two diversity metrics × two sampling seasons × four moth groups) using a self-contained computer program, PARTITION (Crist *et al.*, 2003).

For our analyses, we tested the diversity components from the hierarchical sampling design against the null hypothesis that the observed component of diversity at each level could have been obtained by a random distribution of species within samples. In effect, this hypothesis asks the question: for each class of body size or diet breadth, is an observed component of diversity at a given spatial level greater or less than one would expect by random distribution of species in space? To test this hypothesis, we used a reshuffling algorithm in PARTITION to randomize samples (i.e. trap catches within single forest stands or species sampled from stands within forest sites) while conserving the observed species-abundance and sample-size distributions. Samples at progressively higher levels in our design were obtained by pooling the appropriate samples at lower levels (just as done in our original partition, Crist *et al.*, 2003). For example, to test the significance of observed β-diversity within a site, we randomized samples from all the stands within a given ecoregion (Crist *et al.*, 2003).

We repeated these randomizations 10,000 times to form a null distribution of each α and β estimate (species richness and Simpson diversity). 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 or less than our observed estimate. For example, if 1 out of 10,000 null values is greater than the observed estimate, then the probability of obtaining (by chance) an estimate greater than the observed value is 0.0001. It is important to note that our diversity-partitioning algorithm will allow us to compare diversity components from different partitions in terms of whether one is

Table 2 Additive partition of α- and β-diversity components across a hierarchically scaled inventory of forest Lepidoptera. Separate partitions were performed on small- and large-bodied moths in early and late sampling seasons

Season	Body size	Diversity component	Diversity measure	
			Species richness	Simpson diversity
Early	Small	Within stands (α_1)	67.5	0.616
		Among stands (β_1)	55.3	0.035
		Sites (β_2)	47.2	0.015
		Regions (β_3)	38.0	0.036
		Total	208.0	0.701
	Large	Within stands (α_1)	54.1	0.826
		Among stands (β_1)	43.6	0.013
		Sites (β_2)	38.9	0.003
		Regions (β_3)	32.4	0.038
		Total	169.0	0.881
Late	Small	Within stands (α_1)	52.0	0.939
		Among stands (β_1)	50.2	0.015
		Sites (β_2)	49.2	0.009
		Regions (β_3)	44.6	0.006
		Total	196.0	0.970
	Large	Within stands (α_1)	51.9	0.948
		Among stands (β_1)	48.7	0.012
		Sites (β_2)	39.0	0.007
		Regions (β_3)	35.4	0.011
		Total	175.0	0.978

Table 3 Additive partition of α- and β-diversity components across a hierarchically scaled inventory of forest Lepidoptera. Separate partitions were performed on generalist and diet-restricted moths in early and late sampling seasons

Season	Diet breadth	Diversity component	Diversity measure	
			Species richness	Simpson diversity
Early	Restricted	Within stands (α_1)	32.3	0.332
		Among stands (β_1)	30.7	0.019
		Sites (β_2)	32.7	0.014
		Regions (β_3)	18.3	0.030
		Total	114.0	0.395
	Generalist	Within stands (α_1)	77.1	0.891
		Among stands (β_1)	60.3	0.011
		Sites (β_2)	46.3	0.003
		Regions (β_3)	44.3	0.023
		Total	228.0	0.928
Late	Restricted	Within stands (α_1)	27.1	0.891
		Among stands (β_1)	32.8	0.029
		Sites (β_2)	32.4	0.021
		Regions (β_3)	32.7	0.009
		Total	125.0	0.950
	Generalist	Within stands (α_1)	68.6	0.956
		Among stands (β_1)	61.0	0.010
		Sites (β_2)	51.0	0.007
		Regions (β_3)	41.4	0.009
		Total	222.0	0.981

greater than or less than null expectation while another is not. Our goal here was not to test for difference between two values of α- or β-diversity that were both greater than (or less than) expected by chance.

RESULTS

Of the 492 species for which we were able to obtain estimates of body size, roughly equal numbers of species were considered small and large, a pattern that did not vary much with season (Table 2, Fig. 2). A far greater number of forest moth species were considered dietary generalists compared to the number of restricted feeders, however (Table 3). Body size did not appear to differentially affect the spatial partitioning of α- and β-diversity across sampling scales. In the early season, the partitions of species richness for large and small-bodied species were virtually identical (Fig. 3a). In contrast, using the Simpson index, small-bodied species contributed 1.25–1.5 times as much observed β-diversity among stands, sites and regions compared to larger-bodied species (Table 2). Because the Simpson index is a measure of dominance within communities, this result suggests that the species-abundance distribution for smaller moths is less biased by a few, highly abundant species. Indeed, the species-abundance distribution of small moths more closely mirrors the log-series distribution rather than the log-normal distribution characteristic

of larger-bodied species. In the late season, the observed partition of species richness modestly reflected a non-significant bias towards smaller species contributing a greater proportion of β-diversity (Fig. 3b). There was no difference between partitions for Simpson diversity (Table 2). For larger-bodied moths, α-diversity was greater than that expected by chance, while observed β-diversity was lower than expected among stands and greater than expected among sites, and in the early season, between ecoregions ($P < 0.01$ for each test of significance; Fig. 3a,b). For smaller moths, β-diversity was significantly different from random expectation (< than expected among stands, > than expected among sites) only in the late season ($P < 0.025$, Fig. 3b). Thus, the general trend to emerge from these diversity partitions was that species richness of larger-bodied moths was more similar than expected by chance among forest stands within a single site, while sites and ecoregions contained significantly greater levels of β-diversity than expected.

The effect of diet breadth on the contribution of species to either α- or β-diversity was significantly different and less susceptible to seasonal variation (Fig. 4a,b). In general, moth species that were more restricted feeders had higher levels of β-diversity among stand, sites and ecoregions but lower levels of species diversity within stands (Table 3, Fig. 4). Furthermore, this trend was observed for both species richness and Simpson diversity. In contrast, generalists had higher levels of α-diversity, both in
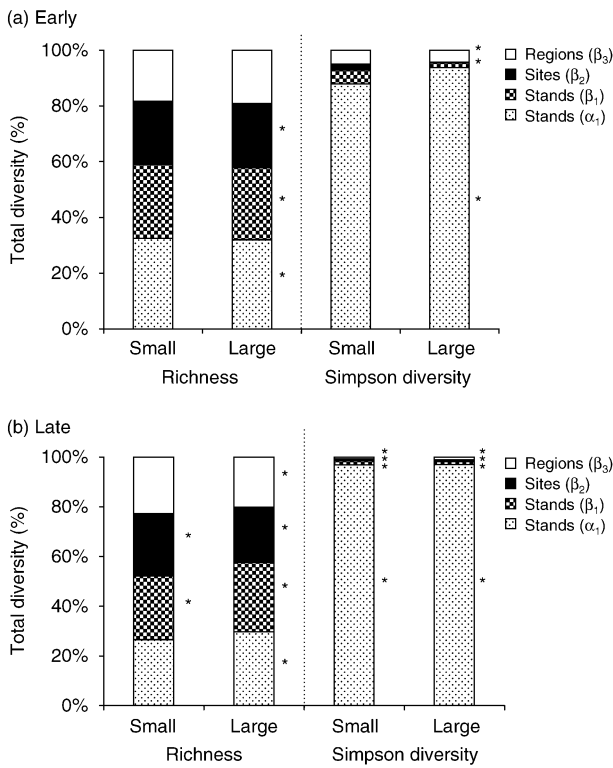
Figure 3 Percentage of total moth species richness and Simpson diversity explained by α and β components of regional diversity. Observed species diversity was partitioned for both large and small-bodied moth species within forest stands (α_1), among forest stands (β_1), among sites (β_2) and between regions (β_3). Separate diversity partitions were performed in (a) early and (b) late seasons. Asterisk indicates that the observed diversity at a level is significantly different than random expectation ($P < 0.025$).

Figure 4 Percentage of total moth species richness and Simpson diversity explained by α and β components of regional diversity. Observed species diversity was partitioned for moths considered to be either dietary generalists or restricted feeders within forest stands (α_1), among forest stands (β_1), among sites (β_2) and between regions (β_3). Separate diversity partitions were performed in (a) early and (b) late seasons. Asterisk indicates that the observed diversity at a level is significantly different than random expectation ($P < 0.025$).

terms of absolute species numbers (Table 3) and as a proportion of the total species diversity (Fig. 4). Generalists also had higher levels absolute measures of β-diversity at progressively large spatial scales (Table 3). Simpson β-diversity for restricted feeders at each spatial level was > 2 times that for generalists (Table 3), suggesting that specialists were less variable species-abundance distribution compared to generalists. Finally, observed α-diversity components for the diet breadth comparisons were always significantly greater than expected for dietary generalists and significantly lower than expected by chance for dietary specialists (Fig. 4a,b; $P < 0.01$). This result is consistent with expectation when specialized species are aggregated in space, fewer species will be present in a single forest stand, but community divergence among stands is substantial (e.g. higher β-diversity). Generalists, however, may appear more equitably distributed across spatial scales, leading to higher α-diversity and lower β-diversity among stands (Fig. 4a,b). Finally, β-diversity among sites and ecoregions were greater than expected by chance for both specialists and generalists, indicating that considerable species turnover occurs regardless of diet breadth beyond the sampling scale of sites (e.g. > 15 km) (Fig. 4a,b).
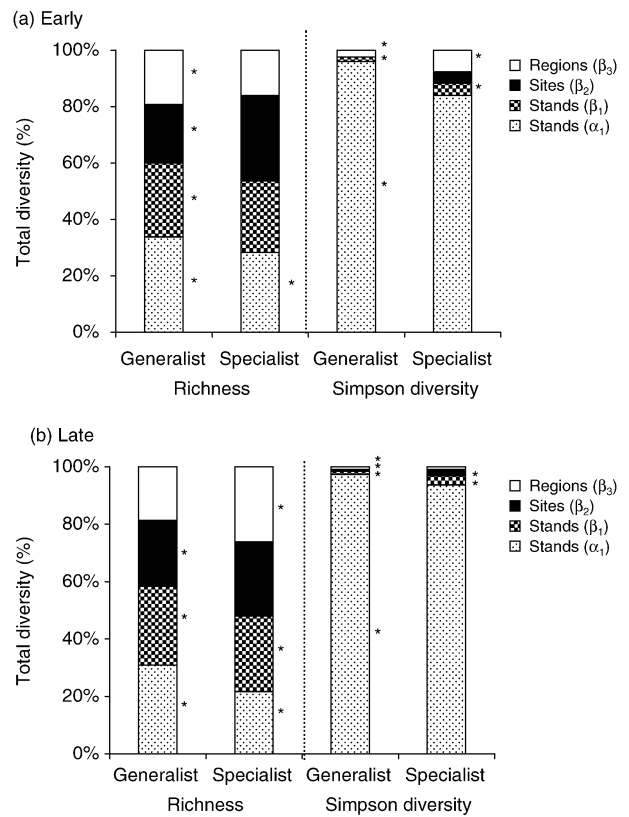
DISCUSSION

The principal goal of this study was to assess whether body size or niche breadth influenced the partitioning of species diversity across a hierarchy of spatial scales. We determined that differences in body size did not greatly affect the partitioning of species diversity, while differences in partitions based on diet breadth were pronounced. This is consistent with the hypothesis that host-plant distribution affects insect community composition at local and regional scales (i.e. within and among forest stands), and may exert a greater influence on species turnover and changes in dominance within communities compared to dispersal limitation (at least as measured using body size). Similar results are emerging from several recent studies of the effects of habitat loss on insect communities (see Tscharntke *et al.*, 2002; Collinge *et al.*, 2003; Summerville & Crist, 2004). Therefore, occupancy of a given forest habitat may be due to the presence of suitable vegetation and consequent aggregation of specialized

herbivores rather than colonization dynamics *per se* (Brändle *et al.*, 2002).

Our test for body size, however, may have failed because, by itself, body size is not a good predictor of geographical range in forest moths (Blackburn & Gaston, 2003). Different life-history traits may interact to determine species distribution (e.g. Gaston *et al.*, 2000; Ribeiro *et al.*, 2003; but see Blackburn *et al.*, 1997 for a contrary case), so some very small species may actually have wide distributions if they are highly vagile, have large fecundities, or are general feeders (e.g. Chapman *et al.*, 2002). *Plutella xylostella* L. (Plutellidae), *Argyroytaenia velutiana* Clem. (Tortricidae) and *Dichomeris ligullela* Hbn. (Gelechiidae) are small species that fit such a description. Alternatively, large species may be patchily distributed if necessary resources are themselves patchy, if adults are relatively sedentary, or of the female is often flightless as in some Lymantriidae and Geometridae (Nieminen, 1986; Doak, 2000). Nevertheless, studies at larger spatial scales than ours have demonstrated positive correlations between body size, geographical distribution, fecundity and dispersal ability in the Papilionoidea (butterflies) (e.g. Gaston *et al.*, 1998; Cowley *et al.*, 2001). Thus, chance effects and dispersal limitation may still have an important role in determining lepidopteran community structure, especially in highly disturbed or fragmented systems and at larger spatial scales than considered in our study (Thomas & Harrison, 1992; Doak, 2000; Thomas *et al.*, 2000).

Flight ability and body size are also both known to be constrained by phylogeny in the Lepidoptera (Lindström *et al.*, 1994), and a posteriori test on our data revealed a significant effect of family level phylogeny on body size (SAS PROC GLM, $F = 24.44$, d.f. = 33, $P < 0.01$) despite some degree of overlap in range of sizes represented by species in small-bodied families (e.g. Tortricidae, *Choristoneura* spp.) and large-bodied families (e.g. Noctuidae, *Tarachidia* spp.) (see also Koh *et al.*, 2004). There was also broad overlap in the range of body sizes for geometrid and noctuid moths, but Geometridae are generally regarded as less vagile than Noctuidae because of differences in body shape, wing morphology and internal structure (Scoble, 1995). Because diversity partitions for large- and small-bodied moth species were so similar, however, we suggest that the lack of strict phylogenetic independence in our data does not detract from the central conclusion of our analyses: diversity of large and small species appears to scale the same way among forest stands, sites and ecoregions. Species of Saturniidae, Sphingidae and Noctuidae (at the upper end of our size range) were not necessarily more likely to have lower β-diversity than species of Gelechiidae, Pyralidae or Tortricidae.

He and Legendre (2002) predicted and Veech *et al.* (2003) demonstrated that α-diversity tends to be lower than expected by chance and β-diversity tends to higher than expected by chance when there is significant intraspecific aggregation among patches. The significantly low levels of α-diversity within forest stands for diet-restricted species are consistent with these patterns and suggest that specialists tend to be aggregated in space. Furthermore, restricted feeders had higher levels of β-diversity among stands than generalists, a pattern that would be expected if host resources are patchy in distribution (Taylor, 1984; Ribeiro *et al.*, 2003; Summerville *et al.*, 2003). Generalists, however, also had significantly high levels of β-diversity at broad sampling scales. We posit two mechanisms may contribute to high levels of β-diversity in generalist moths. First, polyphagous moth species are frequently characterized by substantial inter-annual variation in population sizes compared to specialists (Rajmánek & Spitzer, 1982; Spitzer *et al.*, 1984), so during poor years, populations may not be readily detected in all sites. Second, Roy *et al.* (1998) noted that the relationship between diet breadth and the geographical distribution of British butterflies was complex and nonlinear. Importantly, generalist species tended to have smaller ranges than predicted by the presence of suitable host species, and this would contribute to regional β-diversity if the same pattern applied to forest moths.

As with body size, differences in diet breadth are widely known to be constrained by phylogeny (e.g. Janz & Nylin, 1998), but our data did not possess significant family level phylogenetic effects on diet specialization (SAS PROC GLM, $F = 1.43$, d.f. = 28, $P c.$ 0.10). This may not be a robust approach to resolving whether phylogeny contributes to our diversity partitions because many of the moth families listed in Table 1 contain both specialist and generalist moths. Effects of phylogeny on diet breadth may be most apparent at the level of tribe or genus. For example, within the noctuid subfamily Catocalinae, species are reported to feed on a wide variety of plants (Covell, 1983), but the genus *Catocala* contains many species restricted to feeding on foliage from a single family, or species, of host tree (Robinson *et al.*, 2002). The phylogeny of host plants within a site may also be important in determining regional patterns of α- and β-diversity for Lepidoptera. Studies of broadscale geographical similarities among insect communities emphasize the role of higher-level host plant relatedness as a determinant of species turnover in phytophagous insects (Ødegarrd *et al.*, 2005). Thus, these studies posit an alternative, evolutionary mechanism that is consistent with our diversity partitions — communities of specialist species may appear aggregated in space when phylogenetic similarity (and thus plant chemistry and palatability — see Bernays & Chapman, 1994; Ødegarrd, 2005) among host plants is high locally and divergent regionally.

In conclusion, in order to properly design a conservation plan for this moth fauna, land managers will need to understand that actions such as logging within a single stand will have a disproportionately adverse affect on specialized species, which often have even small home ranges than their host plants and can be entirely lost from a region if highly aggregated at small spatial scales (Quinn *et al.*, 1997; Spitzer *et al.*, 1997; Roy *et al.*, 1998; Summerville & Crist, 2002). Because β-diversity of specialists among stands within a given forested site is relatively low but is quite high at large sampling scales, preservation of single areas such as watersheds in managed ecosystems will also fail to protect more than a small subset of specialized species within an ecoregion (see also Hamer *et al.*, 1997). A preferred scheme for conservation of forest Lepidoptera should therefore emphasize a stratified approach to the design of preservation schemes. Such a design might emphasize creating numerous forest preserves within ecoregions even if each site is perceived to be relatively small (e.g. *c.* 10 km^2 in size).

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