

ABSTRACT

Title of Dissertation: ECOLOGICAL DYNAMICS OF MACROLEPIDOPTERA
FEEDING ON BOX ELDER (*ACER NEGUNDO* L.)

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Understanding species abundances and distributions is a major goal of ecology. While manipulative experiments can reveal mechanistic properties of interactions among a small number of species, and macroecological studies can draw fundamental insights from patterns at a large scale, inference about local communities as a whole requires a combination of these approaches. I used a suite of techniques to better understand the ecological dynamics of a group of insect herbivores, the assemblage of moth caterpillars feeding on box elder, a common riparian tree. I examined the landscape ecology of the assemblage to determine the degree of turnover at multiple scales, and how diversity of the assemblage depended on host plant context. I found apparent homogeneity of caterpillar diversity masked important differences in co-occurrence even at small scales, though the expected influence of host plant diversity was not observed. Examining the species through time, I investigated how species abundance was related to body size,

intrinsic population growth rate, and diet breadth. Whereas body size did not scale significantly with abundance in this group of species, and diet breadth had a complex relationship with abundance, the population growth rate developed in association with the host plant explained the differential abundance of species on the plant quite well. Finally, I quantified elemental content of species in the group, to determine how stoichiometric constraints related to size and growth rates of caterpillars in the assemblage. I found some support for a theory connecting elemental composition to ecological interactions, though the results were species-dependent. Throughout these investigations I explicitly considered the evolutionary relatedness of co-occurring species using phylogenetic methods. By merging ecological and phylogenetic data, a more unified picture of the important mechanisms underlying species properties can be obtained. Through tests of theory at the landscape, community, and individual level, I have presented a clearer picture of the forces structuring this assemblage of caterpillars, and provided a template for investigations of community dynamics at a similar scale.

ECOLOGICAL DYNAMICS OF MACROLEPIDOPTERA FEEDING ON BOX
ELDER (*ACER NEGUNDO* L.)

by

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High beta diversity between trees drives landscape-level homogeneity of a temperate forest caterpillar assemblage

Abstract

Beta diversity in temperate forest herbivorous insect communities is thought to be low, in part due to polyphagy, but neither insects nor ecological interactions are distributed evenly in space. I investigated β -diversity of caterpillars feeding on a single host plant species at spatial scales from individual trees to the landscape. I used a spatially explicit, nested sampling design to document relative contributions of each scale to the landscape diversity using additive diversity partitioning, and to ask at multiple scales whether the vegetation context of the focal host plant explained any of the variance in herbivore species composition and abundance. Over two years, β -diversity of species richness was found to be partitioned proportionally among scales, and generally resembled the null model of random distribution of individuals across the landscape, though differences were significant at the lowest and highest scales. When species identity and abundance were considered, non-metric multidimensional scaling (NMDS) and analysis of similarity (ANOSIM) found β -diversity was low at multiple scales. Despite clear differences in vegetation type between sampled sites, vegetation context explained little to none of the β -diversity of the assemblage, while latitude was the only variable significantly associated with assemblage composition in both years. Finally, although β -diversity across the landscape was low, turnover was consistently high between individual trees without respect to distance, so that pairs of trees separated by 8 m or 80 km had similarly high turnover in their herbivore fauna. Heterogeneity of interactions at the tree level may thus lead to apparent homogeneity of the herbivore assemblage at higher scales.

Introduction

Beta (β) diversity in communities of herbivorous insects figures prominently in debates about global biodiversity patterns. Erwin's (1982) famous estimate of global insect species richness, and subsequent revisions (e.g., Novotny et al. 2002) are based on the turnover of herbivore communities between tree species, under the assumption that diet breadth of herbivores determines the β -diversity across host plants. High estimates of tropical insect species richness have therefore been premised on a higher degree of diet specialization in tropical than in temperate zones. Novotny et al. (2006) challenged this longstanding notion, instead positing that herbivore load per plant species remained fairly constant, while the latitudinal gradient in plant diversity explained much of the increase. Using rearing records from across a latitudinal gradient, Dyer et al. (2007) responded by showing generalized diets were more common at high latitudes in larval Lepidoptera, which supported the hypothesis that higher specialization in the tropics contributed to the latitudinal gradient in herbivorous insect β -diversity across host plant species. Both arguments presume temperate herbivore β -diversity to be relatively low among host species, as studies have demonstrated in neotemperate (Summerville et al. 2003b) and paleotemperate (Murakami et al. 2008) forests. However, no study to date has examined the spatial structure of temperate forest caterpillar β -diversity on scales from individual trees to the landscape.

Many eastern North American temperate forest caterpillars have a wide diet breadth (Dyer et al. 2007, Tietz 1972), but performance on all recorded hosts is not necessarily equivalent. Even some of the most polyphagous and abundant species vary widely in feeding performance on different host plants (Barbosa and Greenblatt 1979). From a tri-

trophic perspective, some host plant species provide increased protection from natural enemies at the expense of nutrition, and vice versa, potentially leading to trade-offs among hosts (Singer and Stireman 2005). Therefore a given plant host may provide a higher relative fitness in one stand of trees than in another, depending on the surrounding host plants, the oviposition preference of female moths and the success of their offspring. Thus, shifts in the composition of caterpillars present on a given host plant might be expected to depend on the vegetation context.

Variance in herbivore community composition among individuals of a given host plant species can also result from localized ecological interactions. Bottom-up factors such as genetically determined variation in host plant quality (Whitham et al. 2006) and other variation within and between individuals of the same host species (Gripengberg et al. 2007) can influence herbivore β -diversity. Behavioral patterns of oviposition and plant selection by adult females can lead to intraspecific aggregation (Veech et al. 2003), such that similarity of an herbivore assemblage might be expected to decline with distance between host plant individuals (Nekola and White 1999). The abundance of important members of an herbivore guild on a given plant individual can also influence community composition (Lill and Marquis 2003). Natural enemy pressure on herbivores is known to vary by host plant species (Barbosa et al. 2001, Lill et al. 2002), resulting in strong differences in the local food web across sympatric plant hosts of different species (Barbosa et al. 2007). These factors may vary across individuals of a single host plant species as well.

Despite the importance of interactions at the host plant scale for creating spatial dynamics in turnover, most recent investigations of β -diversity of Lepidoptera in the

temperate zone have focused on patterns of adult moths collected at lights (Miller et al. 2003, Summerville et al. 2003a, Summerville and Crist 2004, Grand and Mello 2004, Beck and Khen 2007, Hirao et al. 2007). To better quantify and explain the β -diversity of a group of temperate forest herbivores, I therefore focused on a group of caterpillars regularly found on the same host plant species. To understand the β -diversity of this assemblage on the focal host in the context of shifting host plant resources across a landscape, I used a spatially explicit, nested sampling design. I aimed to determine the relative contributions of hierarchical spatial scales to the overall landscape diversity of the assemblage, to quantify the relationship between β -diversity and geographic distance, and to test the hypothesis that the vegetation context of the host plant was correlated with the variance in composition of the caterpillar assemblage. Our results confirm temperate herbivore β -diversity can be low when considered across a landscape, but this apparent homogeneity masks high turnover in caterpillar composition at smaller scales, suggesting high variance in the strength of important ecological interactions.

Methods

Study System. In this study I focus on externally feeding caterpillars found in the mid-Atlantic region of the United States feeding on box elder maple (*Acer negundo* L.), an herbivore assemblage studied extensively over the past 15 years (Barbosa et al. 2000, Barbosa et al. 2001, Barbosa et al. 2004, Barbosa et al. 2007). In mid- to late-summer, the assemblage is heavily dominated by two species, each making up at least 20% of individuals collected: the maple Zale (*Zale galbanata* (Morr.), family Noctuidae) and the common angle (*Macaria aemulataria* (Wlk.), Geometridae). Four other species each are

typically encountered as more than 5% of individuals: the fall webworm (*Hyphantria cunea* (Dru.), Arctiidae); the one-spotted variant (*Hypagyrtis unipunctata* (Haw.), Geometridae); the white-marked tussock moth (*Orgyia leucostigma* (J.E. Smith), Lymantriidae); and the American dagger moth (*Acronicta americana* (Harr.), Noctuidae). I consider all other species observed (numbering nearly 60) numerically subdominant, in that each makes up less than 5% of individuals collected. Most species in this assemblage are known to feed as larvae on host plants in at least three families (based on host records in Tietz 1972), and can therefore be considered polyphagous.

Sampling. To investigate the effects of spatial structure and vegetation context on the constituent species of the assemblage, a nested sampling design was employed (Figure 1). Six mesic forests in central Maryland, USA were sampled: C&O Canal National Park (abbreviated CO; 38°58'17"N 77°09'58"W); Little Bennett Regional Park (LB; 39°16'07"N 77°17'13"W); Patapsco Valley State Park (PVSP; 39°19'25"N 76°52'12"W); Patuxent Research Refuge (PRR; 39°03'50"N 76°46'34"W); Patuxent River State Park (PRSP; 39°17'06"N 77°07'15"W); and Smithsonian Environmental Research Center (SERC; 38°53'04"N 76°33'17"W). The PRR and SERC sites are located in the Coastal Plain ecoregional province; all four other sites are in the Piedmont province (U.S.E.P.A. 2003). Within each forest, two large stands of box elder along a stream or drainage were identified and sampled, separated by 3-5 km within the forest (Figure 1). At each, 10 mature box elder trees of trunk diameter ≥ 15 cm were selected randomly.

In both 2006 and 2007, each tree within a stand was sampled for larvae on a single day over a two-week period in August. A timed (10 min) visual inspection of leaves and

branches of the tree (from base to up to 3m with the aid of a tree ladder) was performed, and all externally feeding Lepidoptera were collected. Following the timed search, branches which had been visually inspected were struck with a wooden rod, dislodging any remaining larvae onto a canvas sheet below. Larvae were returned to the lab and reared in plastic containers on field-collected box elder leaves until they could be identified as larvae or adults, parasitoids emerged, or individuals died. Due to our prior sampling efforts most caterpillars could be identified to species as larvae, though some died before pupating and could be identified only to family.

In July 2007, a vegetation sample was taken at each stand to quantify alternative host plant density. A geographic information system was used to generate three random lat-long pairs within the delineated boundary of each stand. In the field, a circular .04 ha plot (11.33 m radius) was marked out at each location. Within each plot, trees with diameter at breast height (dbh) greater than 1cm were identified, and dbh recorded. Plants were identified to species in most cases, with the exception of oaks (due to the high degree of hybridization occurring in Maryland, oaks were recorded as belonging to “red oak group” or “white oak group”). Using species-specific forestry regression equations (Wharton and Griffith 1993), dbh values were transformed to foliage biomass, a better approximation of the variable of interest to caterpillars than wood density.

Diversity Partitioning. I used an additive diversity partitioning approach to examine the contributions of different landscape scales to the diversity of the landscape assemblage (Crist et al. 2003). The hierarchical levels were defined as tree (n=120), stand (n=12), forest (n=6), and ecoregional province (n=2, piedmont with 4 forests and coastal plain with 2 forests). Diversity partitioning was carried out using the software package

PARTITION v.2 (Veech and Crist 2007). I used the individual randomization option with 999 randomizations, to evaluate both species richness and the Simpson diversity index against the null hypothesis that the contribution of diversity at each scale was no different from a random selection of individuals from the scale below.

Beta diversity and distance. In addition to testing for effects of scale, I also tested the hypothesis that turnover between samples increased with geographic distance (Nekola and White 1999). There are a wide variety of β -diversity measures which have been used in the literature (Koleff et al. 2003), but I chose a measure which includes relative abundance and uses rarefaction to estimate shared species in pairs of assemblages, a method which is particularly appropriate for samples containing large numbers of rarely observed species (Chao et al. 2005). For samples of tree, stand, and forest in both years, the pairwise β -diversity from a sample to all others was calculated (function *vegdist*, *method=chao* using the ‘vegan’ package in R software; Oksanen et al. 2007, R Development Core Team 2007). These β -diversity matrices were tested for correlation with the corresponding matrix of geographic distance between samples, using a mantel test (N=999 randomizations; Legendre and Legendre 1998).

Vegetation and spatial explanatory variables. Multivariate techniques (all performed using the ‘vegan’ package in R; Oksanen et al. 2007) were employed to characterize the caterpillar and vegetation communities, and to test explanatory relationships between variables measured at each stand and the β -diversity in the caterpillar fauna. Explanatory variables were: observed species richness of woody plants; foliar biomass by species of the local vegetation; total vegetation biomass per stand; relative density of the focal host *A. negundo*; total basal area (m^2 / ha) of trees in the stand; geographic area of the stand;

and the latitude and longitude of the center of the stand. Because there were many more plant species than caterpillar samples, the full stand-foliage matrix could not be correlated with the assemblage response. Instead, I attempted to find tree species which represented the different vegetation types found across the sampled area. The variance in the plant community types was characterized by principal components analysis (PCA) of the foliage biomass data, following Hellinger standardization by site total (Legendre and Gallagher 2001). I then tested for non-random correlation between plant species biomass and position of a stand in the PCA (R function *envfit*, 999 permutations), with foliage biomass of tree species found to be non-randomly associated with stand vegetation subsequently used in the analysis as explanatory variables.

Composition of caterpillar assemblages. The composition of larval assemblages at multiple scales was depicted using non-metric multidimensional scaling (NMDS), an ordination technique which graphically depicts relationships found in a dissimilarity matrix (Clarke 1993). I performed NMDS on the caterpillar assemblage samples at two scales: the tree level, and the stand level. At the tree level I sought evidence of clustering by stand, and asked which caterpillar species were important to defining assemblage types. At the stand level, I tested the ordination of stands by caterpillar community for association with the explanatory variables described above.

I first performed NMDS on the caterpillar-tree matrix which had been transformed by species maximum after removal of tree samples in which no caterpillars were found, reducing the effect of the assemblage shifts due to varying abundance of larvae from stand to stand. A Bray-Curtis similarity distance matrix was then used in the NMDS

ordination. Caterpillar species were plotted by their weighted averages (R function *wascors*) of abundance from each site.

To test the hypothesis that unique assemblages occurred within stands, I used analysis of similarity (ANOSIM, R function *anosim*; Clarke 1993). The technique uses a bootstrap randomization (we used 999 bootstrap replicates) to determine the relative fraction of within-stand versus between-stand variance in the community, and determine the probability of group membership of a given sample. Like NMDS, ANOSIM is based on rank distances between samples (we used the same Bray-Curtis distance matrices used for the NMDS). An overall ANOSIM within each year was conducted to test whether there was significant nesting of assemblages by tree into stands. Within a year I also conducted all pairwise comparisons between stands (66 comparisons in each year) to test whether the caterpillars found on trees within a stand were significantly different from those found in other stands. I used an experiment-wise Type I error of 0.05 with a Bonferroni correction for multiple comparisons in evaluating the ANOSIM results.

Influence of vegetation variables on caterpillar assemblage. I conducted an indirect gradient approach to determine whether any of the measured variables was non-randomly associated with the NMDS ordination of stand caterpillar composition. A randomization permutation procedure (R function *envfit*, 999 permutations) evaluated the strength and significance of the hypothesized correlations. I tested for correlations within in each year using NMDS ordinations of the 12 stand assemblages in the same manner as was constructed for the samples from individual trees.

Results

Caterpillar fauna. A total of 1168 caterpillars of 60 unique species were collected (437 individuals of 42 species in August 2006, 731 individuals of 34 species in August 2007). In both years the variance in number of caterpillars encountered per host plant was high, and larvae as a group followed an aggregated distribution. For instance in 2007, out of 120 trees there were 12 on which no larvae were encountered, whereas 44 caterpillars were collected from one tree and 27 larvae from two others.

The same six species were numerically dominant in both years, though the order of their rank abundance changed. The two specialist species made up the vast majority of caterpillars in each year, though not in the same proportions (*Z. galbanata* comprised 25% of individuals in 2006, 32% in 2007; *M. aemulataria* 39% in 2006, 12% in 2007). Together with the next four most abundant species [*H. cunea*, *H. unipunctata*, *Melanolophia canadaria* (Gn.) (Geometridae), and *Halysidota tessellaris* (J.E. Smith) (Arctiidae)], these six species comprised 72% of individuals in 2006 and 90% in 2007. The full stand-species abundance matrices are given in Appendix 1.

Diversity partitioning. Diversity partitioning found a consistent pattern across years, though patterns differed for the diversity measures (Table 1; Figure 2). Considering species richness, contributions to total diversity from mean alpha tree diversity and mean turnover between trees within a stand were lower than expected. Turnover among ecoregional provinces contributed the largest fraction of regional species richness in both years. While statistically significant, however, often the differences between expected and observed diversity components were not of great magnitude (e.g. in 2006 the expected mean number of species per tree sampled was 2.8

and observed mean was 2.6). Overall the contribution of each nested scale to regional diversity was approximately equal, with the exception of the within-forest stand pairs, which contributed fewer species.

The Simpson diversity index, which incorporates relative abundance of observed species, produced a different pattern when partitioned. In both years, the largest contributions to regional diversity were from the mean alpha values found on individual trees. Turnover between trees was expected to make a large contribution to regional diversity, but the observed mean β -diversity within stands was much lower than expected, and nearly nonexistent in 2007. As with the species richness measure, however, a larger than expected contribution to regional diversity came from turnover across the ecoregion boundary.

Beta diversity and distance. Mantel tests of the correlation between β -diversity and geographic distance matrices found a significantly positive relationship at the tree level in 2006, though it explained only a small fraction of the variance (mantel $r = 0.04313$, $p < .05$; Figure 3). This result appears to result from a lack of similar caterpillars on trees separated by > 60 km. No significant correlation was found at the tree level in 2007 or at the stand and forest levels in either year. Plots in all cases were similar to Figure 3, indicating a constant, high variation in caterpillar communities across the sampled area, such that at multiple scales, turnover between samples can be as high within short distances as across a larger landscape.

Vegetation type. Principal components analysis captured the vegetation data into orthogonal vectors of variance, of which the first five represented $>90\%$ of the variance in the site-vegetation matrix. The stands separated into groups along the first two axes,

associated with six significant tree species (Figure 4). The first PC axis, accounting for 35% of the variance in foliage biomass among stands, separates stands according to abundance of tulip poplar (*Liriodendron tulipifera* L.), sweetgum (*Liquidambar styraciflua* L.), and sycamore (*Platanus occidentalis* L.). The four stands in the coastal plain ecoregion grouped together, characterized by high density of tulip poplar and sweetgum, and low density of sycamore, while a group of three Piedmont stands (one each in PRSP, LB, and PRSP) grouped with high density of sycamore. The second PC axis, capturing 22% of the vegetation variance, separated stands on the basis of density of the focal host plant box elder (*A. negundo*) or red maple (*Acer rubrum* L.). Two stands (CO_E and PVSP_W) had extremely high densities of box elder, and separated from the remaining stands which had more red maple. The remaining three stands were variously intermediate in vegetation structure. The full stand-vegetation biomass matrix is given in Appendix 2, along with plant species loadings on the PCA.

Composition of caterpillar assemblages. Ordination of caterpillar assemblages by tree with NMDS (Figure 5a,b) revealed high within-site variance in both years, without clear clustering by forest. This overlap, or low β -diversity, of the composition of stands was due to the high variance in tree-level assemblages of caterpillars. Overall ANOSIM showed evidence of grouping of trees into stands (2006: $R=0.1795$, $p<0.001$; 2007: $R=0.1581$, $p<0.001$). However, of 132 pairwise comparisons only six significant differences between stands within a year were found using ANOSIM (Figure 5a,b). These significant differences in stand composition were all driven by large disparities in abundance of one or more of the dominant caterpillar species. In 2007, for instance, trees at the Little Bennett (LB) stands had an abundance of *Z. galbanata* with few to none of

M. aemulataria or the main subdominants, and were significantly different from trees in stands which had fewer *Z. galbanata* and a higher concentration of *Hyphantria cunea*. The same pattern occurred in 2006, between different pairs of stands but with the same contrast: *H. cunea* was present in large numbers on trees in two stands found to be different from two others that were rich in *M. aemulataria* or *Z. galbanata*. Plotting species onto the tree-level NMDS (Figure 5a,b) also emphasized the ubiquity of the abundant species *M. aemulataria*, which fell near in the center of the plots in both years.

Influence of vegetation variables on caterpillar assemblage. Of the twelve vegetation and spatial variables tested in the indirect gradient analysis only latitude was significantly correlated with ordination location in both years (2006: $r^2=0.5659$, $p<0.05$; 2007 $r^2=0.5597$, $p<0.05$; Figure 5c, d). In 2006, the area of the box elder stand was also significantly correlated with the NMDS ordination ($r^2=0.5061$, $p<0.05$). In 2007, the foliar biomass of two trees was correlated with caterpillar composition: *Acer rubrum* ($r^2=0.6639$, $p<0.05$) and *Platanus occidentalis* ($r^2=0.7279$, $p<0.01$). The red maple gradient paralleled the latitudinal gradient, so that its significance may be more associated with the distribution of that host plant in northern sites, rather than a direct influence of the host plant on the caterpillar composition (Figure 5c, d).

Discussion

The β -diversity of this assemblage of caterpillars is highly dependent on scale and sampling unit. Though not as large as expected (Table 1), turnover is universally high between samples of the assemblage by tree (Figure 3). At this level, β -diversity,

measured by the complement of the probability of two samples sharing species (Chao et al. 2005), is nearly as high between trees separated by meters as it is between trees separated by 80 km. While this high variance in the assemblage may be due in part to the small sample size drawn from any given tree, it is striking that equivalent turnover could be captured through sampling within a stand as across a landscape. Summerville et al. (2003b) also found indications of higher than expected turnover in temperate caterpillar fauna between trees of the same species, though they sampled fewer trees, from a single site.

The high β -diversity observed at the lowest scales contrasts with the low turnover observed between aggregated groups of trees in stands and forests, as within-site variance overwhelms between-site variance. This was demonstrated by the lack of significant differences in assemblage composition by stand, except in a few cases (Figure 5a,b). The large contribution of the smallest scale to the overall diversity is also evident when relative abundance is taken into account in the partition analysis in the form of the Simpson index (Table 1). This index represents the probability of randomly drawing individuals from two different species (Magurran 2004), and that probability across the landscape is mostly determined by the diversity at the level of the tree. The low contributions from higher scales of β -diversity is probably due to the overwhelming dominance of the most common species. In other words, adding more samples at higher levels gives a greater chance of selecting two individuals of the same (dominant) species, which overwhelms any contribution of novel, scarce species to the regional diversity. Thus the overall picture at the landscape level is one of low turnover in the assemblage, but this masks a great deal of β -diversity at smaller scales.

On a similar landscape scale in the tropics, though with more intensive sampling, Novotny et al. (2007) recently reported a very similar pattern in caterpillars on selected tropical host plants, where the pattern of low β -diversity across long distances was more unexpected. Whether the latitudinal gradient in caterpillar specialization demonstrated in the Western Hemisphere by Dyer et al. (2007) is a general global pattern remains under investigation, but an assumption of both sides of the debate is that in the temperate zone, β -diversity is low due to more widespread polyphagy among herbivores. At the landscape level, this assumption holds for the polyphagous species I studied. However, the pattern of β -diversity in herbivores from tree to tree in the temperate zone may not be very different than that commonly observed in the tropics, where tree-to-tree variation has been the basis for macroecological speculation (Erwin 1982, Novotny et al. 2002).

Just as diversity can be partitioned into contributions of different scales, the mechanisms responsible for variation in assemblage composition may vary by scale as well (Loreau 2000). The large variance in tree-to-tree composition of caterpillar assemblage found here has also been observed as high β -diversity patterns at the smallest scale in other insect groups, including other caterpillar assemblages (Franklin et al. 2003, Hirao et al. 2007, Summerville and Crist 2004), moths at light traps (Summerville et al. 2003a), beetles (Gering et al. 2003), and entire arthropod communities (Gruner 2007). These results emphasize the generally clumped distribution of insects (Veech et al. 2003), but even in monospecific host plant stands clustering by herbivores has been well documented without being satisfactorily explained (Hunter et al. 1991). Local heterogeneity in plant nutrient content (Gripengberg et al. 2007), defensive chemistry (Haviola et al. 2007, Kapari et al. 2006, Singer et al. 2004), and natural enemy

interactions (Barbosa et al. 2007) could create the observed high tree-to-tree β -diversity if conditions favorable to the herbivores were scarce but effective in promoting survival when encountered. Further spatially explicit research into these factors on the landscape might help document the underlying causes of this basic pattern of herbivorous insect distribution.

At the stand level I hypothesized that the vegetation context of the host plant would be correlated with turnover in the assemblage found there. Clear differences in the vegetation types were observed between some stands, manifested as the dominance of different common tree species (Figure 4). If the identities of the generalist species collected from the focal host plant are influenced by the other potential host plants in a given site, then the composition of the assemblage should be correlated with the vegetation type to some degree. I found scant evidence for this, though the biomass of two host plants (red maple and sycamore) were correlated with the caterpillar community in 2007 (Figure 5d). The two stands with highest sycamore density were separated from the majority of stands in the NMDS plot, due to lower than average abundance of caterpillars, especially of the dominant *M. aemulataria* (Figure 5d).

Even though a clear gradient of plant species separated the stands by ecoregional province (Figure 4), longitude did not correlate with caterpillar composition. Surprisingly, a latitudinal gradient was observed instead in both years. The majority of caterpillars under study have wide distributions throughout the eastern half of the U.S. (Covell 2005), so edge-of-range effects are unlikely to be responsible for such a pattern. The north-south separation apparent in both years of caterpillar sampling was not reflected in the separation of stands by vegetation type (Figure 4) suggesting that other,

unmeasured environmental gradients may be structuring the moth assemblage. An obvious choice might be temperature, as even slight changes in microclimate can affect larval development patterns (Kingsolver 2000). The sampling procedure attempted to control for climate effects by cycling through each forest twice over two weeks, rather than sampling the same forest twice in a row. But climate may play a role in influencing the assemblage even across this short (30 km) gradient.

Understanding how biodiversity is structured through multiple scales on a landscape is one key to understanding the ecological dynamics of that biodiversity (Loreau 2000). While on a landscape scale β -diversity was low as represented by few differences in caterpillar species composition (Figure 5), β -diversity among host plant individuals was consistently high (Figure 3). Ecologically the latter pattern may be the more important one, since trophic interactions thought to be paramount to species abundance occur at this scale, and high variance observed in the caterpillars may also reflect heterogeneity in these selection pressures (Hunter and Price 1992). In addition, the diversity partitioning results, while significant, were often not qualitatively different from the null expectation of randomly distributed individuals. Taken together, these patterns suggest samples at multiple scales across the landscape were equivalent to random draws from a homogeneous regional species pool. In that case, variance in species composition may be modeled more effectively by considering dispersal limitation (Alonso and McKane 2004), about which little is known in forest moths.

Tables

Table 1. Results of diversity partitioning for species richness (S) and Simpson’s diversity index (D). Mean observed diversity at each level is compared against the mean of a null distribution generated by 999 randomizations of individuals within the site-species matrix. Observed diversity components significantly different from the random expectation are marked (* = p<.05, ** = p<.01, *** = p<.001.)

Level	2006				2007			
	S _{observed}	S _{expected}	1-D _{observed}	1-D _{expected}	S _{observed}	S _{expected}	1-D _{observed}	1-D _{expected}
α_{tree}	2.6***	2.8	0.7613***	0.7275	2.7***	3.1	0.7246***	0.6632
β_{tree}	8.3***	10.2	0.0456***	0.1108	7***	7.7	0*	0.0371
β_{stand}	5.9	5.5	0.0282***	0.0099	4*	4.7	0.0077	0.0091
β_{forest}	11.2	11.8	0.0144	0.0105	11.3	12	0.0235*	0.0502
$\beta_{ecoregion}$	14***	11.7	0.0085*	0	12**	9.4	0.0091***	0
<i>Total</i>	42	42	0.858	0.8587	37	37	0.7649	0.7596

Figures

Figure 1. Sampling areas in central Maryland, USA. Black dots represent locations of box elder stands, where 10 random trees were sampled for Lepidopteran larvae. Gray polygons are forest boundaries (CO: C&O Canal National Historical Park; LB: Little Bennett Regional Park; PRR: Patuxent Research Refuge; SERC: Smithsonian Environmental Research Center; PRSP: Patuxent River State Park; PVSP: Patapsco Valley State Park). The dashed line shows the approximate fall line between the Piedmont ecoregional province to the west and the coastal plain ecoregional province to the east.

Figure 2. Observed and expected diversity components of caterpillar communities across four scales in (a) August 2006 and (b) August 2007. Fractions of total gamma diversity are plotted for the mean contribution of each scale: mean diversity per tree sampled (“alpha tree”); mean turnover between trees within a stand (“beta tree”); mean turnover between stands within a forest (“beta stand”); turnover between forests within an ecoregion (“beta forest”); and turnover across ecoregions (“beta ecoregion”). Expected values are generated by 999 randomizations of individuals within a given site-species matrix using PARTITION v2 (Veech and Crist 2007).

Figure 3. Pairwise species turnover ($1 - \text{pr}[\text{shared species}]$) versus geographic distance between samples of herbivore assemblage by tree in August 2006. A mantel test shows a weak positive correlation between distance and turnover (solid line; mantel $r = 0.04313$, $p < .05$). A lowess smoothing curve (dotted line) shows the locally weighted relationship between turnover and distance is consistently high across the study area. No significant correlation between turnover and distance was found at the tree level in 2007 or at the stand or forest level in either year.

Figure 4. Principal components biplot of vegetation community, showing ordination of sampled stands and key tree species. Stem measures of trees sampled in three 0.04 ha plots in each stand were transformed to foliage biomass, then standardized by Hellinger transformation before PCA (Legendre and Gallagher

2001). The variance of vegetation explained by the first two components are labeled on the respective axes. Tree species (boxed abbreviations) are those non-randomly associated ($p < 0.05$ under 999 permutations) with stand position in the PCA, plotted by their loadings on the first two PC axes. Tree species codes: ACNE *Acer negundo* (the focal host plant); ACRU *Acer rubrum*; JUNI *Juglans nigra*; LIST *Liquidambar styraciflua*; LITU *Liriodendron tulipifera*; PLOC *Platanus occidentalis*. The foliage biomass of these six tree species was used in the indirect gradient analysis (Figure 5).

Figure 5. Non-metric multidimensional scaling (NMDS) of caterpillar assemblages and key species found on *Acer negundo* trees at 12 stands in 6 forests of central Maryland, for (a, c) August 2006 and (b, d) August 2007. (a, b) Ordination biplot of centroid NMDS axis values \pm standard error are plotted for trees sampled within a stand. Stands within a year sharing superscript (*, #) are significantly different according to ANOSIM. Only trees on which caterpillars were found ($n=112$ in 2006; $n=108$ in 2007) were included in the analysis. (c,d) Ordination tri-plot of caterpillar assemblage NMDS ordination by stand showing key species and vectors of significant explanatory variables. Significant (association with stand caterpillar assemblage composition $p < 0.05$ according to 999 permutations) vectors are plotted as arrows pointing in the direction of increasing variable value. Variable codes: “ACRU” biomass of *Acer rubrum* foliage; “Area” area of box elder stand; “Lat” latitude of centroid of stand polygon; “PLOC” biomass of *Platanus occidentalis* foliage. In all plots key caterpillar species (letters) are plotted by their weighted average of abundance by site. Species codes: “Aa” *Acronicta americana*; “Ec” *Eutrapela clemataria*; “Hc” *Hyphantria cunea*; “Ht” *Halysidota tessellaris*; “Hu” *Hypagyrtis unipunctata*; “Ma” *Macaria aemulataria*; “Mc” *Melanolophia canadaria*; “Os” *Oligocentria semirufescens*; “Tc” *Tetracis crocallata*; “Zg” *Zale galbanata*.

Figure 1.

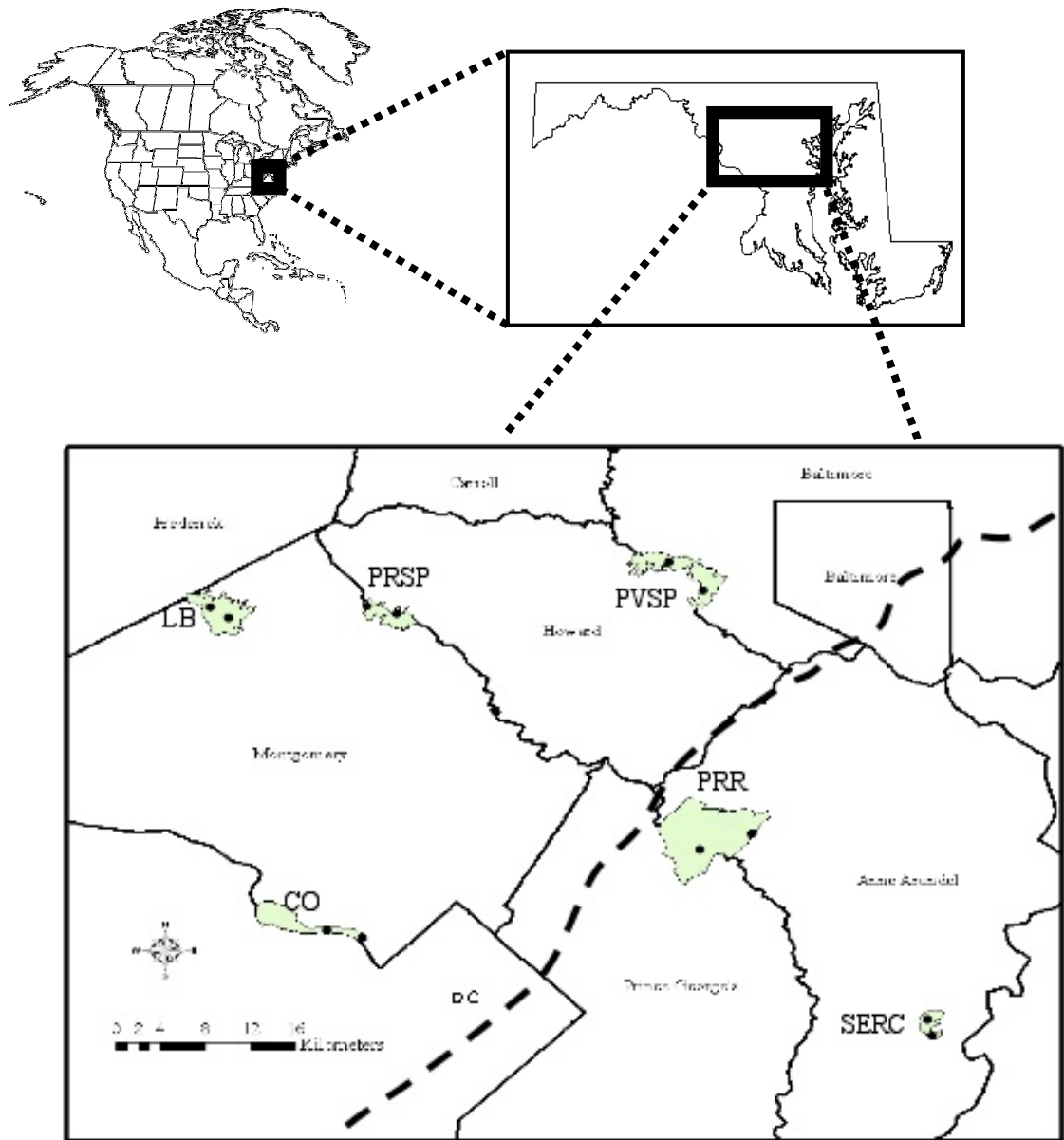
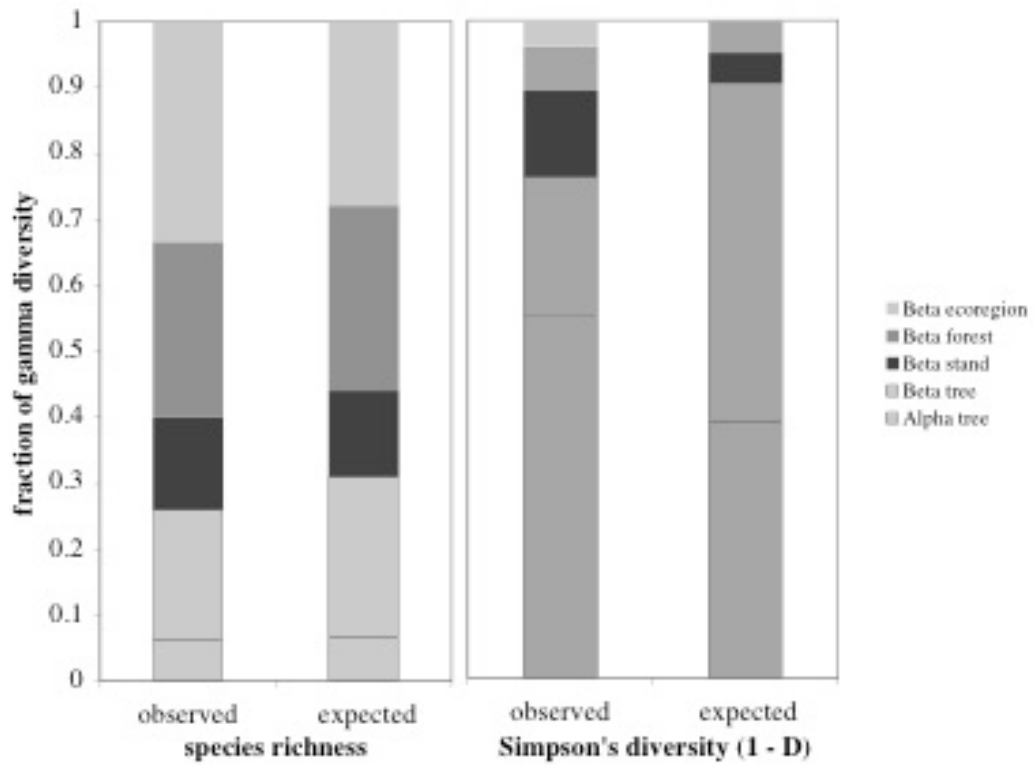


Figure 2.

(a)



(b)

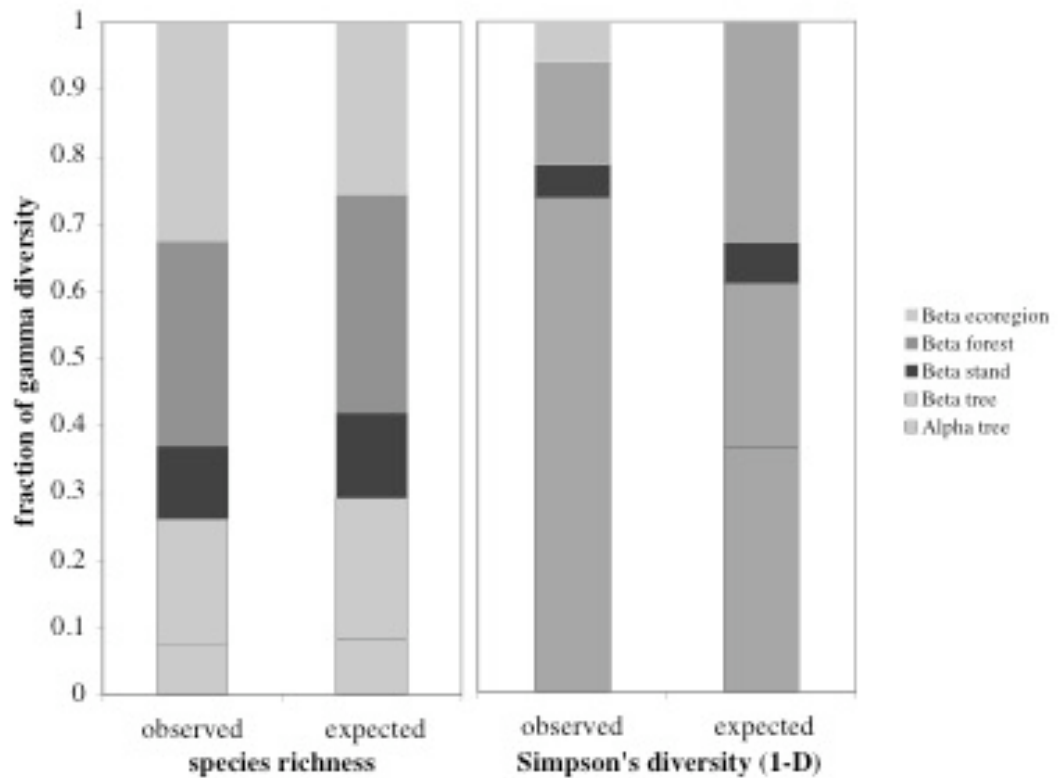


Figure 3.

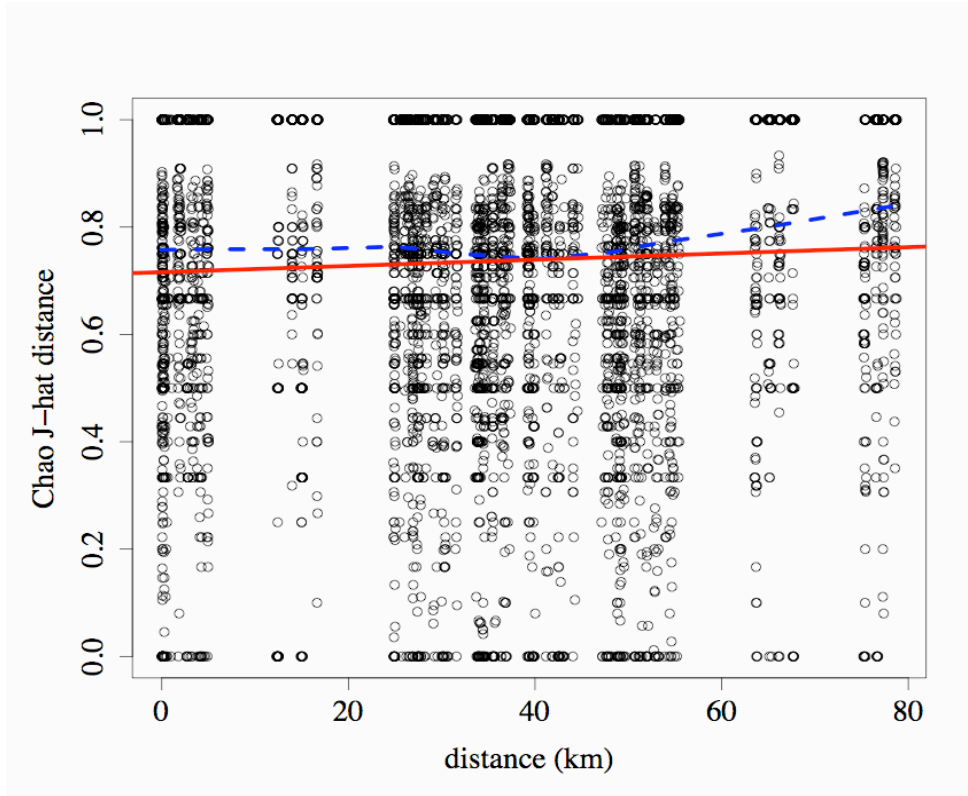


Figure 4.

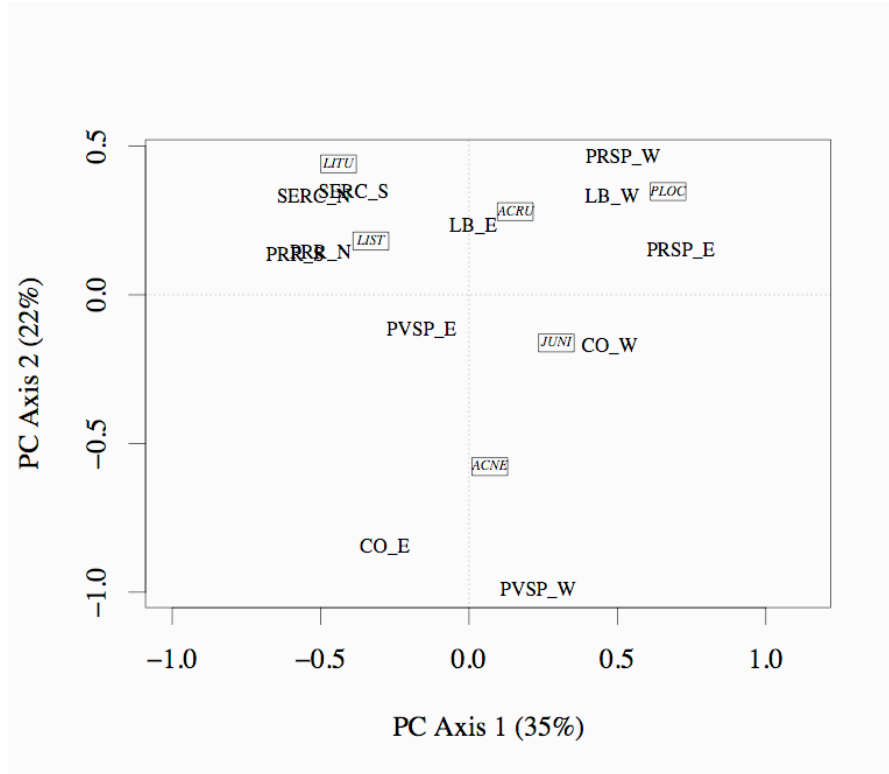


Figure 5.

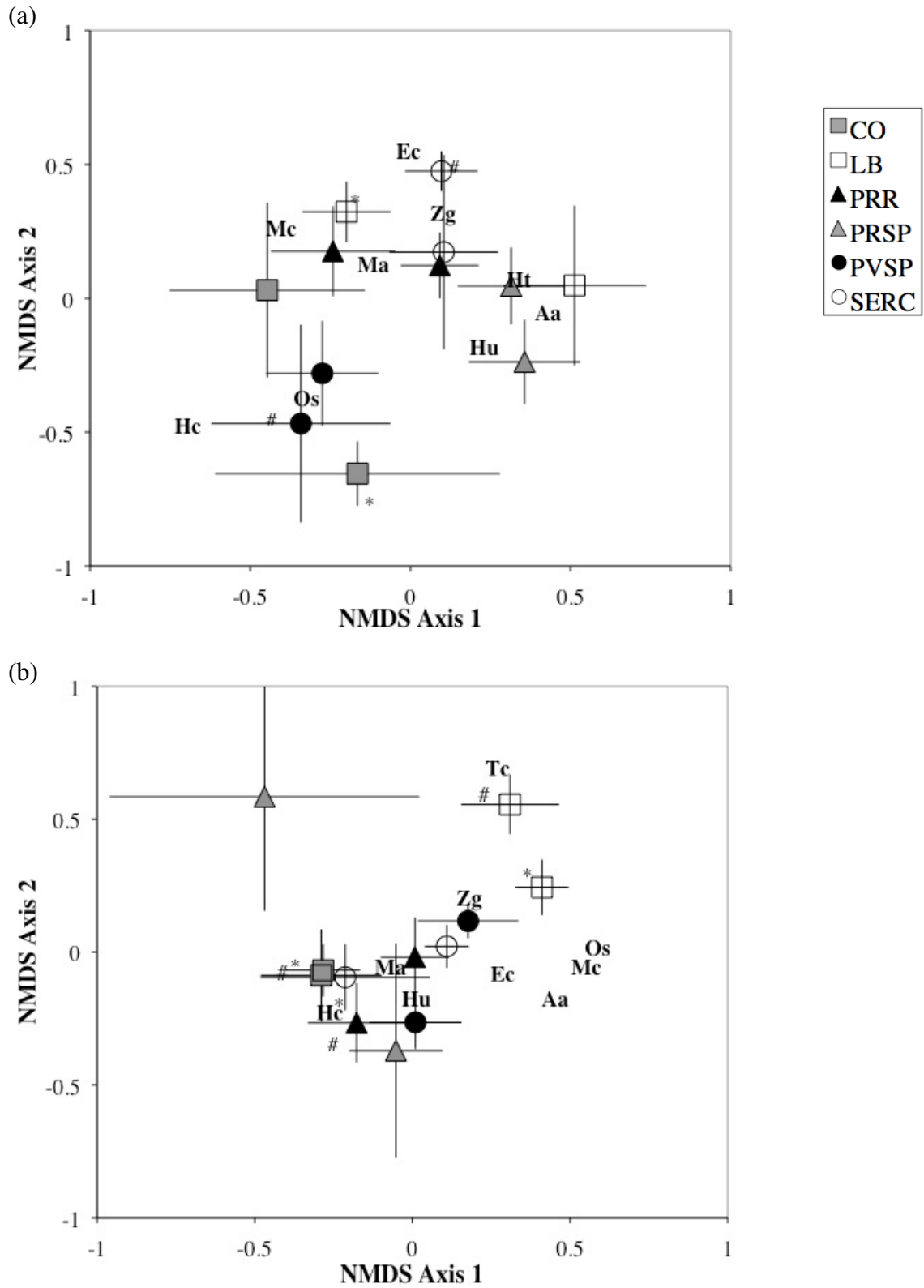
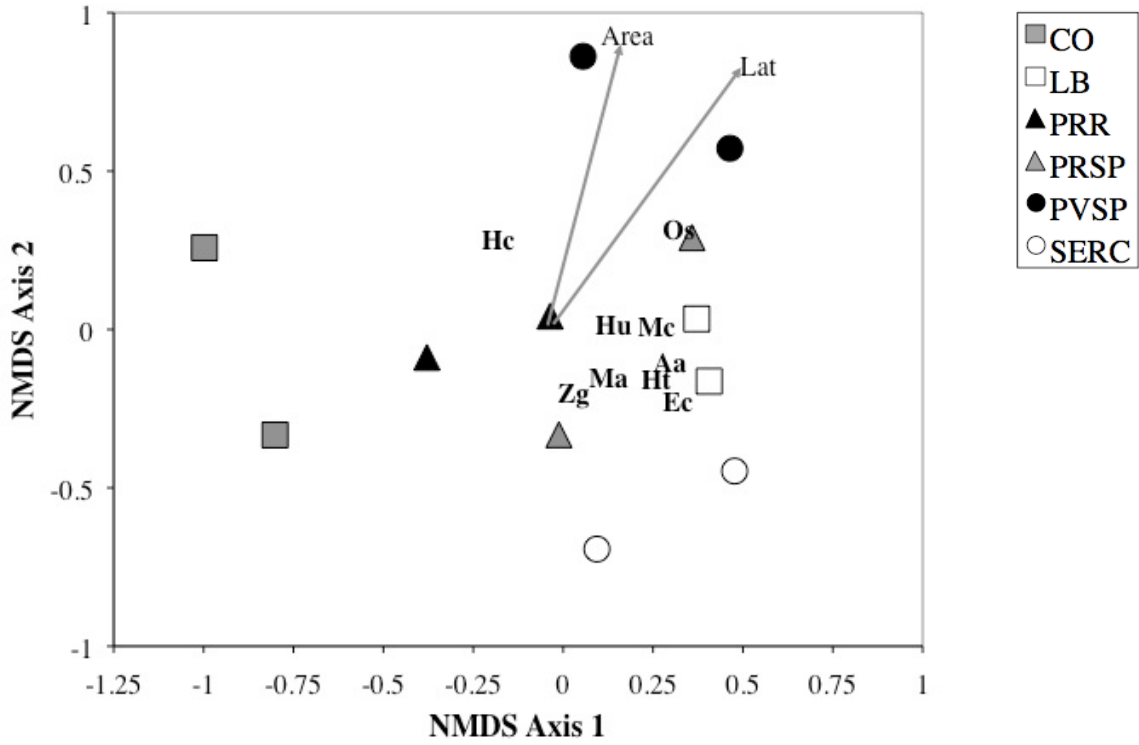
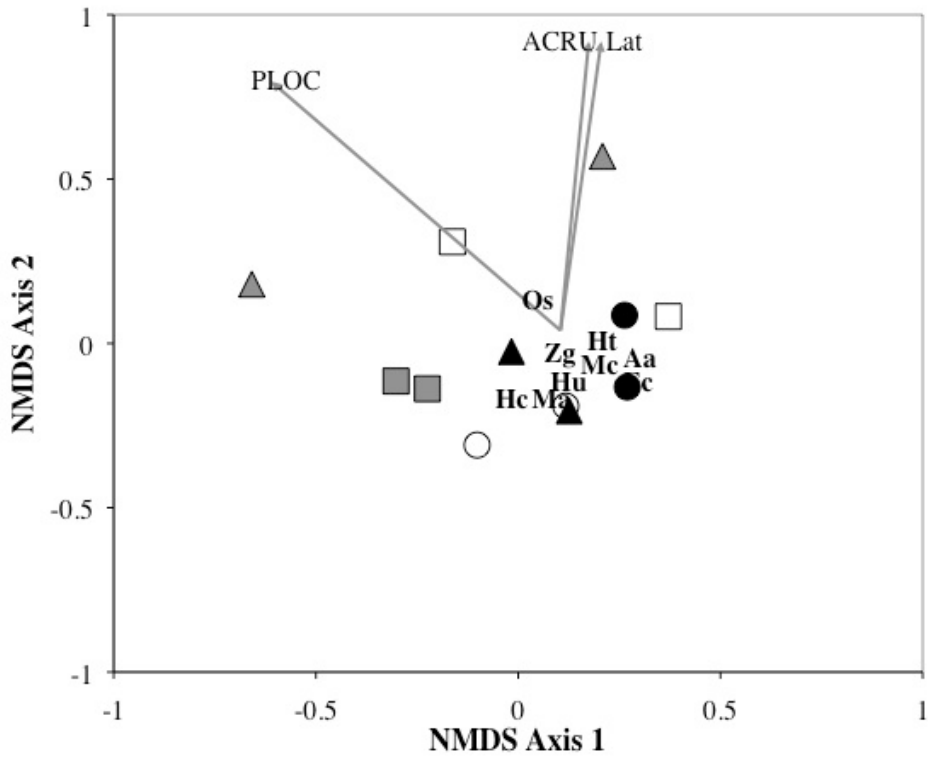


Figure 5
(c)



(d)



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Metabolic and life history models of abundance in an assemblage of forest caterpillars

Abstract

Metabolic ecology theory predicts abundance should be related to the mass of the constituents of a community of species sharing a resource base using a simple power equation. This relationship holds well at large spatial and temporal scales, but is not supported in many animal communities sampled at a relatively small scale. At these scales, ecological factors may be more important than the inherent limits to energy use set by allometric scaling of mass. I hypothesized that incorporating those factors (in the form of an estimate of intrinsic population growth rate for the species in the local community, and a quantification of resource availability) would improve the understanding of the mechanisms driving species abundance. Using an assemblage of forest caterpillars found co-occurring on a single host plant species, I tested whether species abundance could be explained by mass allometry, intrinsic population growth, diet breadth, or some combination of these traits. I included life history traits of the caterpillars in association with the host plant in both field and lab settings, so that the population growth estimate was specific to the plant on which abundance was measured.

Using a generalized least squares regression method incorporating phylogenetic relatedness, I found no scaling relationship between abundance and mass, but a strong positive relationship between abundance and intrinsic population growth rate, which was most affected by survivorship and larval development time on the host plant. Diet breadth showed a non-linear relationship with abundance. Metabolic constraints may determine limits to abundance levels for species, while abundance in a local community may be

better predicted by a quantification of the potential population increase of that species in a local environment.

Introduction

The theory of metabolic ecology (Brown et al. 2004) predicts density of species should be inversely related to body size due to fundamental limitations of metabolic processes. The prediction of an abundance-size relationship is derived from the scaling of metabolism and resource use according to a mass exponent (Brown et al. 2004). For species sharing a common resource base and experiencing the same temperature spectra, mass (M) is hypothesized to influence the density of species (N) in the form:

$$N \propto M^b \quad (1)$$

where the exponent b is close to -0.75 (Damuth 1987). This theoretical prediction often explains >80% in variation in density when applied to compilations of data from across large scales (White et al. 2007). However, when applied to groups of locally co-existing species, the hypothesized linear relationship often becomes more polygonal, and is reduced in terms of both slope and fit (Blackburn and Gaston 1997, White 2007).

One possible explanation for the decrease in explanatory power of the allometric relationship is that as species are not at their maximum density everywhere, in most communities most species are kept well below the limits to abundance that might be imposed by metabolic rates (Blackburn and Gaston 1997). Further obfuscation of the pattern occurs because species vary in body size and energy use within local communities (Ernest 2005). The increased variance in such a fundamental relationship suggests that ecological interactions modify the basic allometry of abundance and mass. Instead of being driven by metabolic limitation, local species density may be proportional to the fitness of individuals of that species in the local environment. For instance, the competitive ability of birds to acquire resources in a given forest type can result in a

positive slope of the mass-abundance relationship within ecological guilds (Russo et al. 2003). Thus, incorporating these types of dynamics into a model of abundance may improve our understanding of the mechanisms driving differences between species sharing a common resource.

In order to account for fitness in a local community, I summarize individual traits into an intrinsic population growth rate for the species on the shared resource, proportional to the vital rates of survivorship and fecundity through time. In population dynamics terms, given a starting density N_0 , species densities at time t [$N(t)$] may be predicted by the single-species population growth model:

$$N(t) = N_0 e^{rt} \quad (2)$$

where r is the intrinsic growth rate of the population. To examine the impact of local population dynamics on density with regard to body size, I substitute the expected density under the allometric metabolic relationship as the base density to be modified by the growth parameter:

$$N \propto M^b e^r \quad (3).$$

That is, the abundance of a species in a local system is proportional to the fundamental constraints of mass allometry, interacting with the potential for growth of the population in the local environment (Gaston and Lawton 1988). Because intrinsic growth (r) is a rate of change through time, the abundance expectation will change over the length of time this model is evaluated, and if there are significant differences in intrinsic growth rates the effect will be amplified with time. Nonetheless, if it is a property of a species in a given environment, r should also covary with abundance of the species in that environment independent of time.

Equation (3) forms the basis for examining the predictive power of local vital rates once the metabolic relationship has been taken into account. It predicts that density in a local community should depend both on limitations imposed by scaling metabolic functions due to size, as well as population dynamics driven by species-specific life history traits. The vital rates can vary within a species depending on local conditions and interactions with other species, as documented in studies of metapopulations (e.g. Hassell et al. 1991). At equilibrium densities in a given habitat, or at large scales where data are gathered from near-maximum densities of species, all species r would be expected to be at or near zero, and the equation would revert to the basic expectation of proportionality to mass-specific metabolic rate.

Herbivorous insects provide an ideal group for examining these dynamics for a number of reasons. Insect herbivores share a defined resource base in a local community, and quantification of vital rates is manageable. In addition, insect herbivore life histories are tied intimately to the host plant on which individuals develop, meaning resource acquisition and population growth may be different even among sympatric host plants of different species, which might also be reflected in their densities on those hosts.

Polyphagous insects are known to experience conflicting pressures regarding the chemical and nutritional properties of their plant hosts. For instance, individuals sometimes gain increased defense against parasitism (and thus increased survivorship) at the cost of growth (decreased fecundity or lengthened development time; Singer et al. 2004). Both predation (Murphy 2004) and parasitism (Barbosa et al. 2001; Lill 2002) rates are known to sometimes vary on the same herbivore, depending on the host plant on which it is feeding. Population success on a given host plant also may be diluted across

other possible hosts in polyphagous species. Abundance on a given host plant may be negatively associated with diet breadth, as oviposition choices or larval wandering spread local abundance of a species across multiple plants. Alternatively, species with wide diet breadth may be able to support a larger population size at a given site due to the greater availability of acceptable food resources, and therefore abundance may positively correlate with diet breadth. The interaction between body size, abundance and diet breadth can also change depending on the spatial scale considered (Summerville et al. 2006).

Using an exponential relationship to account for the different possibilities of potential host plants on herbivore abundance, the interaction of diet breadth (D) with mass and population growth can be modeled as:

$$N_{host} \propto M^{b_1} e^{b_2 r_{host}} D^{b_3} \quad (4)$$

where the b_1 and b_3 exponents are the forms of the relationships and b_2 represents the influence of time on the growth model. This equation quantifies the interaction of allometric mass limitation, local population dynamics, and resource availability on abundance of herbivores on a host plant sampled as a local community.

I used an abundance dataset together with vital rates developed from lab rearings and field collections, and published information on diet breadth, to test the combined metabolic and life history model on an assemblage of forest caterpillars. Because in comparative work, the relatedness of species cannot be ignored (Felsenstein 1985, Nee et al. 1991, Blackburn and Gaston 1998, Harvey and Pagel 1991), I used a newly developed phylogenetic hypothesis of the Lepidoptera (Mitter et al. *in prep*) to test for effects of evolutionary lineage on the traits used in the analysis, and to correct for this effect in the

model where appropriate. I sought to determine the relative ability of the parameters, alone or in combination, to predict abundance in this group of insects. Specifically, I asked (1) how phylogenetic relatedness influenced the distribution of trait values among species; (2) whether mass predicts species abundance in the local community, and if so with what exponential slope; (3) whether intrinsic population growth as calculated from vital rates predicts abundance; and (4) whether diet breadth predicts abundance in a community of mostly polyphagous herbivores.

Methods

Abundance dataset. Barbosa et al. (2000, 2001) quantified abundance of externally feeding macrolepidopteran caterpillars on host plants including box elder (*Acer negundo* L.) as part of a study on differential parasitism across host plants. When summed across five years of collections, the relative abundance of species in the assemblage follows a typical pattern of relative abundance, with most members occurring as scarce species (Fig 1; McGill et al. 2007). With the exception of a handful of species including the two most abundant ones, most caterpillars in the assemblage are known to feed from host plants in at least three families (Tietz 1972). I collected enough data to parameterize the full statistical model (equation 4) for 27 of the species in the assemblage, including ten of the twelve species comprising the top 85% of the abundance spectrum (filled circles in Fig 1).

Rearing. The vital rates of survivorship, fecundity, and generation time can be combined to determine the per capita population growth rate, r :

$$r = \frac{\ln \sum l_x m_x}{T} \quad (5)$$

where l_x and m_x respectively represent survivorship to, and fecundity at, age x ; and T represents generation time (Clark 2007). Life history parameters (Table 2) were estimated from both laboratory rearings and field collections. Adult moths of target species were collected from UV and mercury vapor lamp traps placed in box elder stands in the Patuxent Research Refuge (Laurel, MD; 39° 03.639' N, 76° 44.244' W) during summer 2005-2007. Eggs laid from females were counted and monitored daily. Upon hatching, larvae were kept in plastic deli containers with field-collected box elder leaves which had been sterilized for 20 minutes in a 10% sodium hypochlorite (bleach) solution, rinsed twice with fresh water for 20 minutes, and air dried. After five days, 25 larvae per egg mass were placed individually into 8-inch plastic Petri dishes with moistened filter paper and a sterilized box elder leaf. These dishes were kept in a growth chamber set to mimic seasonal temperature and light patterns (Table 1). Every other day leaves were changed and the dishes cleaned of frass. Upon pupation the individual was set aside for two days, and then pupal mass was recorded. For those species not entering diapause to overwinter as pupae, adults were mated as they emerged, paired with adults from egg batches different than their own whenever possible. Any eggs resulting from these matings were likewise counted and used in rearing trials where appropriate.

Survival. The survival estimate for each species was modeled as a joint probability of two mortality processes intimately associated with the host plant: development or “bottom-up” survivorship, and parasitism, which is specific to the host plant (Barbosa et al. 2001). Bottom-up survivorship was modeled as an exponential process with a constant mortality rate ρ throughout development while feeding on the host plant. The time from hatch to either death or pupation for each reared larvae was

used to fit ρ for each species (function *survreg* in the *survival* package of R; R Development Core Team 2008). Parasitism rate was modeled as a binomial process with constant probability of survival θ throughout the development of a caterpillar on the host plant. The maximum likelihood estimator of θ is given by the fraction that survived without being parasitized from the collection dataset (Clark 2007). I estimated parasitism rate from the five year survey dataset (Barbosa et al. 2001). This estimate is biased by sample size, and for some scarce species no parasitoids were collected. The estimate of $S(pupa)$, the mean species probability of survivorship from hatching to pupation in association with the host plant, is

$$S(pupa) = e^{-\rho T} \theta \quad (6)$$

where T = species mean development time from hatching to pupation.

Fecundity. Fecundity was calculated as lifetime number of eggs per female, based on females reared on box elder in the lab, and supplemented with data from wild-caught females where lab data was absent or of low replication. Both mean and maximum values were calculated, the latter as a measure of the influence of unusually productive individuals to the growth of the population. While fecundity and mass are often correlated within and across insect species, I did not correct for mass in the fecundity variable within the intrinsic growth calculations because it was explicitly contained in the larger model.

Generation Time. In population dynamics using life tables, generation time can be represented as $\frac{\sum x l_x m_x}{R_0}$, where x is a given age class, l is probability of survival to the beginning of age class, m is the reproductive output of the age class, and R_0 is $\sum l_x m_x$

(Clark 2007). Here I reduce survivorship to a single value to the reproductive step. This reduces the sum to $\frac{x l_x m_x}{R_0} = \frac{x l_x m_x}{l_x m_x} = x$. Thus generation time can be represented by T, mean species time from egg to pupation. This measurement does not address development time of eggs and pupae, or adult longevity. However, evaluation of the length of these parts of the life cycle is complicated by species overwintering in one or more of the life stages. Additionally, stages outside the larval period may not be as directly influenced by the host plant.

Diet breadth. For polyphagous species, relative abundance on any one host may be a function of the available host species. I used the number of plant genera occurring in Maryland known to be utilized as food by each species (Tietz 1972, Wagner 2005, Covell 2005) as a measure of diet breadth.

Phylogenetic relationships. While the abundance of a given species is an emergent phenomenon unlikely to be directly inherited by common ancestry, other species properties such as mass or fecundity are not necessarily independent of evolutionary history and cannot be treated as independent observations in traditional statistics (Felsenstein 1985). To account for this possible influence I used a permutation test to evaluate the significance of association between the phylogenetic relatedness of species and the trait values (Blomberg et al. 2003). A phylogenetic hypothesis was constructed using a recently inferred tree of the “backbone” relationships of all Lepidoptera (Mitter et al. *in prep*). I substituted the taxa in this study for members of the same genus or tribe in the tree, keeping the branch lengths as developed in the full analysis (Fig 2). Where I had more taxa at a given tip than were resolved in the original tree, I added equal branch lengths of arbitrarily short size (0.01 change units) below the

given node. I modeled the variance of each variable using generalized least squares (GLS), a modification of linear models which incorporates phylogenetic distance into the error structure (Martins and Hansen 1997; Blomberg et al. 2003). For this analysis I assumed a Brownian motion model of evolution of the trait variables, which treats variables as randomly evolving along branches (Martins and Hansen 1997). The significance of the phylogenetic component of the trait variance was evaluated following Blomberg et al. (2003) using log Likelihood scores from the GLS model of each trait against a constant (function *gls* of the package *ape* in R software; Paradis et al. 2004). The likelihood value of the observed data was compared against a distribution of 1000 values calculated after permuting the trait data on the tips of the phylogeny. In this one-tailed test, if the observed likelihood value was larger (smaller $-\text{Log likelihood}$) than 95% of the permutation values, the phylogenetic relatedness of the species was said to significantly impact the trait variance. The phylogenetic variance of traits showing significant signal in this way was incorporated into the statistical analysis.

Data analysis. I evaluated the impact of mass, intrinsic population growth, and diet breadth using the log-transformed version of equation (4):

$$\ln(N) = b_0 + b_1 \ln M + b_2 \frac{\ln(S_{pupa} m)}{T} + b_3 \ln D + \varepsilon \quad (7)$$

where N = mean abundance, M = pupal mass (g), D = diet breadth, S_{pupa} = joint probability of survival to pupation, m = maximum number of eggs laid, T = time to pupation (d), b_1 , b_2 , and b_3 are exponential slopes indicating the form of the relationships of the variables with abundance, b_0 = an intercept, and ε = a residual variance term. The middle term is shown in its component parts but was evaluated as the single variable, r , the intrinsic rate of population growth for the species on the host plant. To include the

impact of relatedness of the species (where necessary as tested above), I used a GLS version of the linear model where error terms are structured according to the phylogeny (function *gls* of the *ape* package in R).

I used a model selection approach (Stephens et al. 2006) to determine the significance of each of the variables mass, intrinsic growth rate, and diet breadth. I used likelihood ratio tests to evaluate the contribution of each term by evaluating the fit of data to the models with and without that term. Individual terms were dropped from the full model, and the significance of a difference in likelihood was evaluated by comparing the ratio of log likelihoods and change in degrees of freedom against a chi-square distribution. Variables which did not significantly decrease the likelihood of the model when absent were dropped, and the process repeated to find the best model. Finally, to explore potential interaction of life history variables, I calculated covariance and Pearson correlation statistics between the measured traits.

Results

Nearly all measured traits of species were above or near the threshold for non-random phylogenetic signal, including the calculated intrinsic population growth rate (Fig 3). The exception was number of eggs produced by females, which did not show evidence of influence of phylogeny (Fig 3c). As expected, species abundance showed no evidence of being correlated with phylogeny (Fig 3a). However, because each of the predictor variables in the model did show such evidence, the GLS analysis including phylogenetic structuring of the error was used to fit the linear model.

The results of the model selection show that abundance on the host plant is best explained by the calculated intrinsic growth rate alone (Table 4, Fig 5a). Neither mass (LR=0.511168, $\Delta df=1$, $p=0.4746$) nor diet breadth (LR=0.292784, $\Delta df=1$, $p=0.5884$) significantly affected the likelihood of the model when dropped. In contrast, the likelihood of the model was significantly worse when intrinsic growth rate was not included (LR=18.55188, $\Delta df=1$, $p<0.0001$, $\Delta AIC=16.5519$). Sequentially removing terms resulted in the single best model including only r , regardless of the order in which terms were dropped.

The value of the mass exponent in relation to abundance differed based on the model used. The full linear model coefficients (given in Table 4) suggested an allometric mass exponent around 0.14, while the GLS model of abundance including only mass as an explanatory variable estimated the coefficient at -0.10. In neither case was this relationship significantly different from zero (mass only model tested against null model of abundance set to a constant, LR=0.0279542, $\Delta df=1$, $p=0.8672$).

Measured traits showed surprisingly few significant correlations among species (Table 3). Mean pupal mass was positively correlated with egg production across species (Pearson $r=0.385$, $p=0.048$). However, mass did not correlate with development time or the calculated intrinsic growth rate. One surprising significant correlation was between egg number and diet breadth, which covaried positively across species (Pearson $r=0.441$, $p=0.021$).

Species differed strongly in survivorship on the host plant in lab rearings (Fig 3a). The joint model incorporating parasitism rates differentially lowered survival estimates for the most abundant species (Fig 3b), since they carry a disproportionate load of recorded

parasitism (Barbosa et al. 2004). In species for which no parasitism was recorded the joint estimate was treated as equal to the bottom-up estimate. Joint survivorship was not correlated with any of the other measured variables, but was significantly correlated with intrinsic population growth (Pearson $r=0.552$, $p=0.003$).

Discussion

I did not find a significant relationship between the metabolic rate, as expressed in an allometric mass exponent, and abundance in this assemblage of caterpillars. In addition, the calculated exponents for the abundance-mass relationship ranged from -0.1 to 0.14, depending on the model, but not close to the -0.75 expected under metabolic ecology theory. This weakening or changing of the abundance-body size relationship is still somewhat of a puzzle (White et al. 2007), and has been demonstrated in numerous other locally surveyed groups including fish (Ackerman et al. 2004), mammals (Ernest 2005) and birds (Nee et al. 1991, Russo et al. 2003), though the predictive power of mass for abundance appears relatively scale-invariant for trees (Enquist and Niklas 2001). The reasons for the mismatch between theory and empirical data in local systems result from mechanisms other than metabolic rate limiting species density. Two mechanisms tested here are the amount of available resources, and the match of the species to the local conditions as measured by intrinsic population growth rate.

Carbone et al. (2007) attempted to address the lack of fit of the metabolic theory in local animal communities by modeling the spatial distribution and amount of the resource base of the community, arguing dimensionality of resources could skew or flatten the abundance-mass relationship. In this study the insects shared a common resource (the

focal host plant) but most of the species had alternative resources (alternative known host plant genera), possibly diluting their abundance on the focal host. There was not a significant linear effect of diet breadth on the abundance of species in the model (Table 4). However, diet breadth (and thus resource availability) may have a more intriguing relationship with abundance. Of the top four most abundant species, two (*Zale galbanata* (Morr.) and *Macaria aemulataria* (Wlk.)) feed on two or fewer genera of host plants, while the other two (*Hyphantria cunea* (Dru.) and *Orgyia leucostigma* (J.E. Smith)) are each known from over 80 genera occurring in Maryland (Table 2). This “u-shaped” relationship between diet breadth and abundance is not captured in the linear modeling approach tested here, and suggests divergent life history strategies (specialist and generalist) associated with high abundance on the host plant. This idea is reinforced by the strong positive correlation between diet breadth and fecundity in the group (Table 3). A combination of high reproductive output and large diet breadth is known to be indicative of outbreaking Lepidoptera (Hunter 1991), and may play a similar role in non-outbreak high density populations as well. Insect herbivore species with high resource availability by way of wide diet breadth may be more limited by their metabolic ability to process those resources, if not limited in abundance by other factors.

In keeping with the idea of local interactions rather than metabolic limitation determining species densities, I found that abundance was best predicted by an estimate of intrinsic population growth, reflecting interactions with the resources of the herbivores as well as mortality sources from natural enemies. Survivorship and development time on the host plant had strong, independent impacts on the overall intrinsic growth rate (Table 3). These variables describe the probability of successful growth of individuals of

different species in their larval association with the host plant, in terms of extracting nutrition, processing or avoiding plant defensive chemicals, avoiding parasitism, and successfully pupating.

Individual development time on the host was especially important in predicting r , and thus abundance, in our model. On average the most abundant species grew fastest, independent of mass, suggesting abundant species may be those better able physiologically, or even behaviorally, to extract needed nutrition from the host upon which they feed. This match between herbivore and host plant could lead to higher abundance through the preference-performance hypothesis (Thompson 1988), wherein females oviposit on host plants on which their offspring will do best. Evidence for this hypothesis has been mixed, though there have been well-documented cases in support (Poykko 2006). At least two other explanations for the association of fast development with abundance exist. Development time may reflect the influence of voltinism, since abundance of the species I studied reflects counts through time, and more abundant species may simply be the ones with multiple generations per season. This explanation is not well supported because species such as *Pyrharctia isabella* and *Xanthotype urticaria* undergo multiple generations in our area (Covell 2005), but, nevertheless, are scarce and develop slowly on the focal host plant. Although multiple generations may be a necessary element it is not sufficient to explain higher abundance. Second, the faster development time may correlate with a lower risk of natural enemy attack, under the slow-growth-high-mortality hypothesis (Clancy and Price 1987). However, this hypothesis has not been well supported with experimental evidence (Medina et al. 2005), and the strongest

evidence in favor to date (Benrey and Denno 1997) involved mortality from parasitoids, which was included in our model.

I did not account for mortality sources from predation, which may affect the results by skewing survivorship estimates. Predation by birds and invertebrate predators such as wasps may depend on morphological or behavioral differences of the caterpillars (Castellanos and Barbosa 2006), as well as preferences of the predators (Altegrim 1992). Incorporating predation into the population growth model may improve the explanatory power of r with regard to abundance.

I found one glaring exception to the success of the intrinsic population growth rate to predict abundance in the assemblage: the most abundant species (*Z. galbanata*) is a clear outlier (Fig. 5b). This species has high survivorship on the host plant in the lab, relatively high parasitism in the field, and slightly lower than average fecundity and development time (Table 2), which led the model to place it among most species scarce on the host plant. Yet *Z. galbanata* abundance is orders of magnitude greater than that of most of the other species in the assemblage, suggesting a missing component to understanding numerical dominance in this species. That missing component may be the impact of diet breadth: *Z. galbanata* feeds only on plants the genus *Acer*, and may well be a functional specialist on box elder locally (Barbosa et al. *unpublished data*). Whatever population growth occurs will be reflected solely on this host plant, in contrast to species with wider resource bases.

Overall, the success of our estimate of intrinsic population growth rate in predicting abundance raises an interesting possibility in the light of the documented relationships between abundance and mass in other local animal communities. The expected

relationship of abundance to a -0.75 mass exponent is reduced on average to -0.25 in these studies (Blackburn and Gaston 1997, White et al. 2007). Notably, metabolic ecology theory predicts expected population growth rates should also vary with respect to mass to the -0.25 (Brown et al. 2004). This correspondence suggests ecological interactions impacting the abundance of animals through their population growth rates may be stronger than metabolic limitations in some local communities. While I did not see a significant abundance-mass relationship in this study, I did demonstrate the power of intrinsic population growth to explain differential species abundance. Local animal communities with an log-transformed abundance-mass slope of -0.25 may be reflective of similar underlying dynamics.

Tables

Table 1: Temperature and light settings for caterpillar growth chamber used in rearing.

Month	Light Cycle (hours light : hours dark)	Temperature Cycle min : max °C
May	14 : 10	11.5 : 23
June	15.5 : 8.5	16.8 : 28.5
July	16 : 8	19 : 31
August	14.5 : 9.5	18.7 : 29.6
September	12.5 : 11.5	14.9 : 26.3

Table 2. Species, data sources and parameters used in regression model.

Species	Code	Mean N	Pupal mass (g)	rho	theta	Mean lifetime eggs / female	Max lifetime eggs / female	Mean development time (d)	Diet (No. Genera)
<i>Acronicta americana</i> (Harr.)	Aa	34.4	0.5665 ± 0.4321	0.0270	0.6744	549.8 ± 407.0	1128	44.5 ± 7.5	23
<i>Acronicta impleta</i> Wlk.	Ai	0.6	0.3048 ± 0.0432	0.0278	0.6667	143.7 ± 83.7	208	64.3 ± 6.7	15
<i>Achatia distincta</i> (Hbn.)	Ad	0.6	0.3199 ± 0.0957	0.0011	1.0000	148.0 ±	148	53.7 ± 1.5	5
<i>Acronicta obliquata</i> (J.E. Smith)	Ao	0.2	0.4426 ± 0.1530	0.0127	1.0000	469.0 ±	469	103.7 ± 22.9	25
<i>Acharia stimulea</i> (Clemens)	As	4	0.0663 ± 0.0086	0.0073	0.6000	75.4 ± 87.0	229	63.3 ± 12.3	14
<i>Automeris io</i> (F.)	Aui	0.6	0.3217 ± 0.1334	0.0065	1.0000	179.0 ± 119.6	360	76.2 ± 13.0	39
<i>Euchlaena amoenaria</i> (Gn.)	Ea	2.6	0.1044 ± 0.0910	0.0054	1.0000	199.7 ± 138.7	433	50.8 ± 4.4	2
<i>Euclea delphinii</i> (Bdv.)	Ed	0.2	0.1300 ± 0.0344	0.1024	1.0000	191.5 ± 72.4	279	66.3 ± 6.9	9
<i>Euchlaena obtusaria</i> (Hbn.)	Eo	0.8	0.1474 ± 0.0834	0.0082	1.0000	158.7 ± 133.7	269	56.8 ± 9.8	6
<i>Eutrapela clemataria</i> (J.E. Smith)	Eucl	18	0.2912 ± 0.1967	0.0047	0.8444	485.1 ± 313.0	889	37.9 ± 4.7	19
<i>Glena cribrataria</i> (Gn.)	Gc	1.8	0.2056 ± 0.0864	0.0270	0.8889	55.0 ± 62.7	162	30.8 ± 3.5	6
<i>Heterocampa biundata</i> Wlk.	Hb	7.2	0.1634 ± 0.0196	0.1000	0.7500	115.0 ± 124.4	271	30.8 ± 3.2	8
<i>Hyphantria cunea</i> (Dru.)	Hc	50.2	0.2989 ± 0.1450	0.0020	0.6972	627.3 ± 462.4	1066	34.6 ± 5.9	81
<i>Halysidota tessellaris</i> (J.E. Smith)	Ht	15.4	0.1308 ± 0.0733	0.0116	0.9091	105.5 ± 91.0	287	60.9 ± 10.2	29
<i>Hypagyrtis unipunctata</i> (Haw.)	Hu	45	0.0464 ± 0.0090	0.0163	0.8844	213.7 ± 289.1	793	36.5 ± 4.8	11
<i>Macaria</i> (= <i>Semiothisa</i>) <i>aemulataria</i> (Wlk.)	Ma	140.2	0.1451 ± 0.1106	0.0077	0.7347	48.7 ± 58.4	253	22.4 ± 3.6	2
<i>Melanolophia canadaria</i> (Gn.)	Mec	21.2	0.2263 ± 0.0611	0.0349	0.8396	168.3 ± 198.8	397	39.1 ± 4.5	14
<i>Morrisonia confusa</i> (Hbn.)	Moc	10.6	0.2622 ± 0.0361	0.0043	0.8868	156.0 ±	156	104.9 ± 17.3	22
<i>Nemoria lixaria</i> (Gn.)	Nl	0.4	0.2386 ± 0.0384	0.0166	1.0000	25.7 ± 6.1	31	51.0 ± 11.2	3
<i>Orgyia definita</i> (Pack.)	Od	13.4	0.4788 ± 0.2429	0.0000	0.8060	190.2 ± 70.6	281	29.9 ± 3.1	11
<i>Orgyia leucostigma</i> (J.E. Smith)	Ol	77.4	0.6065 ± 0.3575	0.0033	0.7028	205.1 ± 180.0	574	29.3 ± 8.3	89

<i>Pyrrharctia isabella</i> (J.E. Smith)	Pi	2.8	0.5123 ± 0.0818	0.0225	1.0000	494.8 ± 383.4	1076	97.3 ± 14.8	10
<i>Prochoerodes lineola</i> (Goeze)	Pl	7.6	0.2497 ± 0.1986	0.0118	0.8947	61.2 ± 40.1	140	39.0 ± 4.1	27
<i>Spilosoma virginica</i> (Dru.)	Sv	0.6	0.1554 ± 0.1148	0.0099	1.0000	383.6 ± 228.5	639	50.3 ± 9.8	56
<i>Tetracis crocallata</i> Gn.	Tc	4.4	0.2352 ± 0.1261	0.0127	0.9545	206.0 ±	206	42.8 ± 4.8	6
<i>Xanthotype urticaria</i> Swett	Xu	1.4	0.2781 ± 0.1608	0.0022	0.8571	148.3 ± 119.0	221	47.3 ± 6.8	13
<i>Zale galbanata</i> (Morr.)	Zg	167.8	0.2759 ± 0.0347	0.0078	0.6961	67.0 ± 39.2	102	32.1 ± 3.6	1

Table 3. Trait correlation matrix for life history measurements of 27 caterpillar species feeding on box elder (*Acer negundo*). Values below the diagonal indicate covariance between variables. Values above the diagonal are Pearson correlation r statistics. Correlation values in bold are significantly different from random at $p < 0.05$. *Pupal mass*: mean mass (g) recorded two days after pupation of caterpillars reared on box elder in the lab; *survival*: joint probability of caterpillar survival on box elder due to successful development and avoiding parasitism (see text for details); *Max egg*: maximum lifetime number of eggs laid by a female moth; *T*: mean development time (d) from hatching to pupation for caterpillars reared on box elder in the lab; *diet*: number of host plant genera occurring in Maryland recorded in literature as hosts for each species; r : estimated intrinsic population growth rate, calculated as $\ln(\text{Survival} * \text{Max egg}) / T$.

	Pupal mass	survival	Max egg	1/T	diet	r
Pupal mass		-0.0017868	0.38468736	0.00640599	0.37259026	0.16673484
survival	-6.516E-05		-0.1218667	0.23957329	0.16167255	0.55182165
Max egg	17.9664088	-9.5939823		-0.0034462	0.44099329	0.30244114
1/T	8.2918E-06	0.00052271	-0.0096292		0.0962347	0.81887936
diet	1.2297198	0.89943845	3141.94872	0.01900235		0.34853176
r	0.00143987	0.00803257	5.63804823	0.00042307	0.45914681	

Table 4. Model selection to determine significance of parameters shows intrinsic population growth r , but not body mass or diet breadth, explains significant variance in abundance of an assemblage of caterpillars feeding on box elder (*A. negundo*). Data from Table 1 were used to parameterize the full log-transformed linear model, using generalized least squares to structure the error term according to phylogenetic relatedness. Likelihood ratio tests were used to evaluate the significance of each term by comparing the full model to one without the specified variable. Where the reduced model was not significantly (probability <0.05 in Chi-square test) worse than the full model, the term was dropped, and the tests repeated with the remaining terms. The best model was identified through this sequential dropping procedure. Δdf : difference in degrees of freedom between models being evaluated (full model $df=23$); LR : ratio of likelihood values; p -value: probability of observed ratio under Chi-square distribution; ΔAIC : difference in Akaike Information Criterion between reduced and full model. The AIC values for the full and best models are also reported.

Model term dropped from full model	Δdf	LR	p value	ΔAIC
r	1	18.55188	<0.0001	16.5519
log(mass)	1	0.511168	0.4746	1.4888
log(diet)	1	0.292784	0.5884	0.5884
Full model				AIC
log(N) = -1.302 + 0.143*log(mass) + 26.19*r + 0.0554*log(diet)				124.919
Best model				
log(N)=-1.382 + 26.31*r				121.1031

Figures

Figure 1. Dominance-diversity curve showing abundance of species collected 1993-1997 from box elder (*Acer negundo* L.) in central Maryland. Species are ordered by rank abundance and plotted as a fraction of total caterpillars collected (overall N=4220). Filled circles indicate species used in the current analysis.

Figure 2. Phylogenetic hypothesis used to structure variance in GLS model for species in the assemblage. Tree is based on a Lepidoptera-wide phylogenetic analysis by Mitter et al. of 26 protein-encoding nuclear loci, constructed using heuristic branch swapping evaluated by Maximum Likelihood (details of the loci and protocol available at <http://www.leptree.net>). Species in the assemblage were substituted at the lowest possible taxonomic level (usually tribe) with arbitrarily chosen equal branch lengths of 0.01 change units below the most resolved node. Species codes are as in Table 1.

Figure 3. Histograms depicting permutation tests of influence of phylogeny on measured species traits (a) abundance, (b) pupal mass, (c) fecundity, (d) survival, (e) development time, (f) diet breadth, (g) calculated intrinsic population growth rate. Likelihood of each trait as observed (dotted line) was compared against the distribution of 1000 permutations of the trait data across the tips of the phylogeny (Fig. 2). Observed values outside the 95% range of the permutation results (solid lines) were considered significantly influenced by phylogenetic relatedness.

Figure 4. Survival probability curves for 27 caterpillar species from (a) host plant and (b) joint host plant and parasitism sources. Host plant-derived mortality was estimated by rearing caterpillars on box elder, recording time to death or pupation, and fitting an exponential decay parameter representing constant mortality through time (ρ , Table 1). This was multiplied by the mean length of development time. Parasitism was estimated from field collections on the host plant (Barbosa et al. 2001), modeled as a binomial probability, and multiplied by bottom-up rearing through time. Caterpillars with few collected individuals often had zero recorded parasitism, and so for these species the curves do not differ between (a) and (b).

Figure 5: Intrinsic population growth rate predicts observed caterpillar abundance on box elder, with an important exception of the most abundant species (*Zale galbanata*). (a) Best-fit linear model (Table 3) of log mean abundance versus intrinsic growth rate: $\ln(N) = -1.382 + 26.31 * r$. Circled point depicts *Z. galbanata*. (b) Observed, and predicted count data transformed from the best model, by species, showing misplacement of *Z. galbanata* by orders of magnitude.

Figure 1.

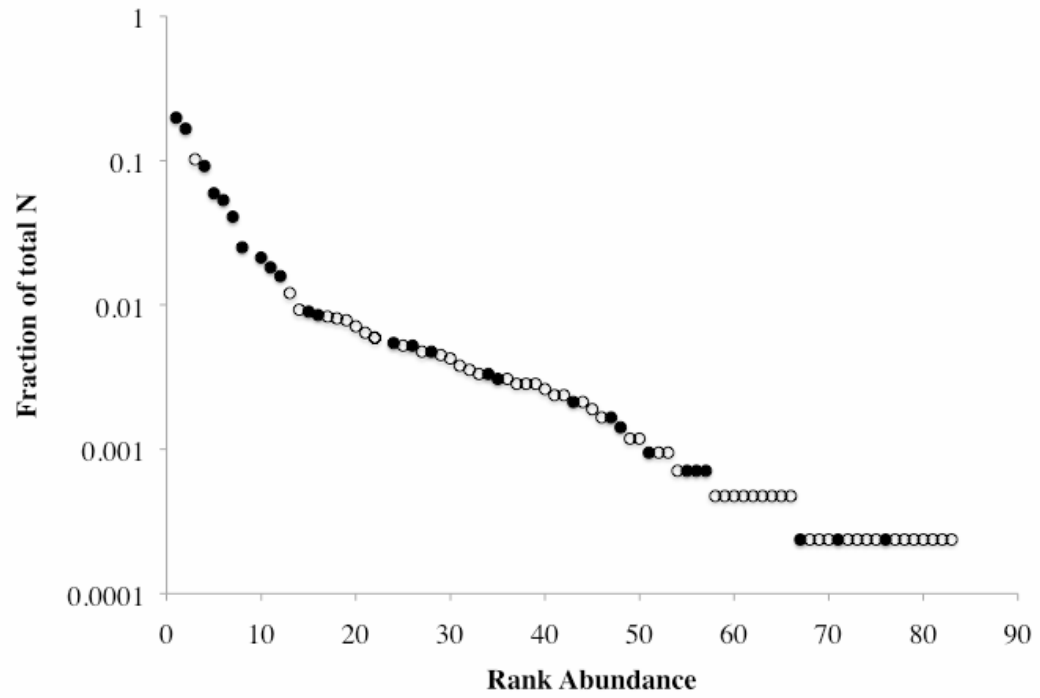


Figure 2.

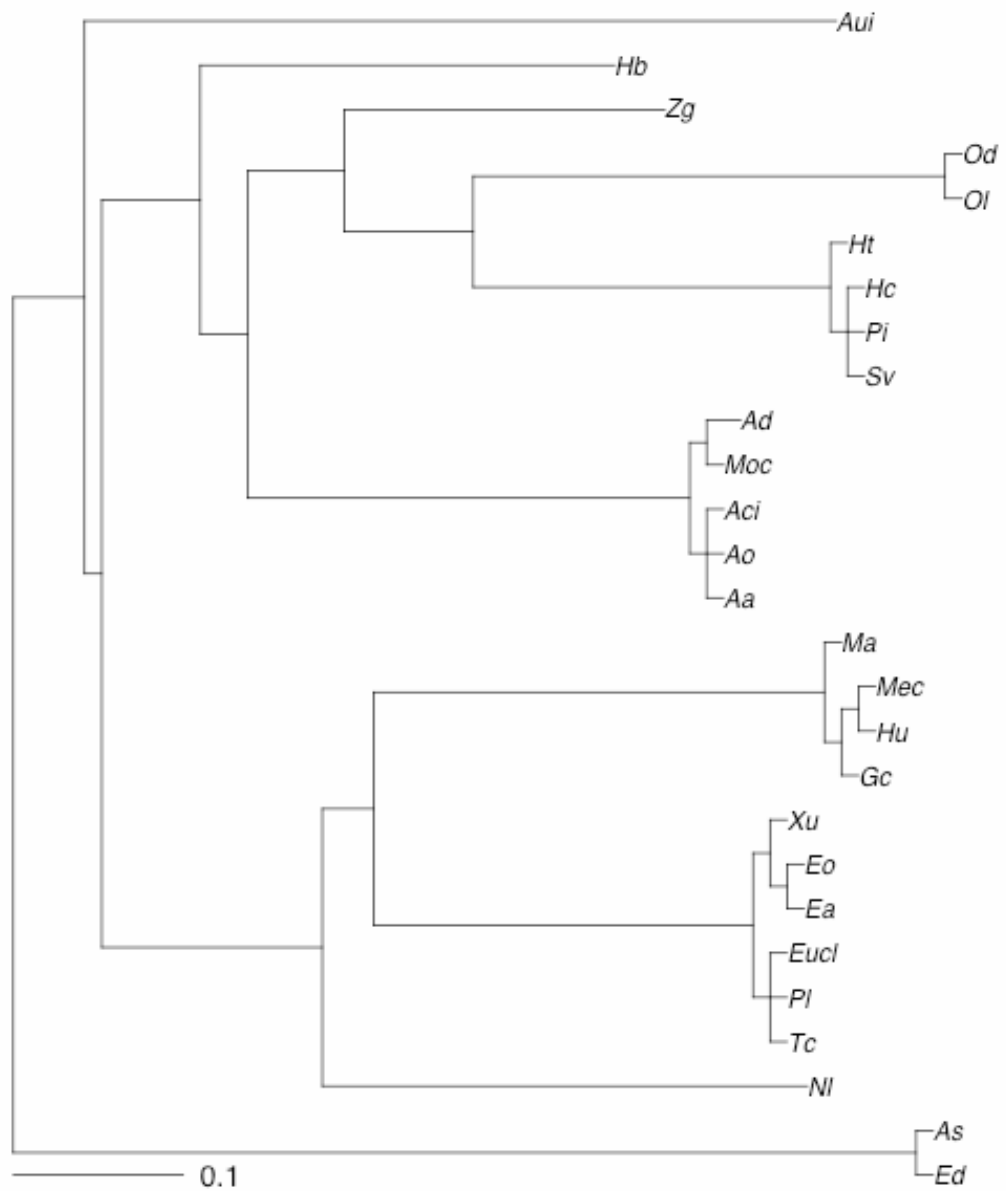


Figure 3.

Density for 1000 permutations

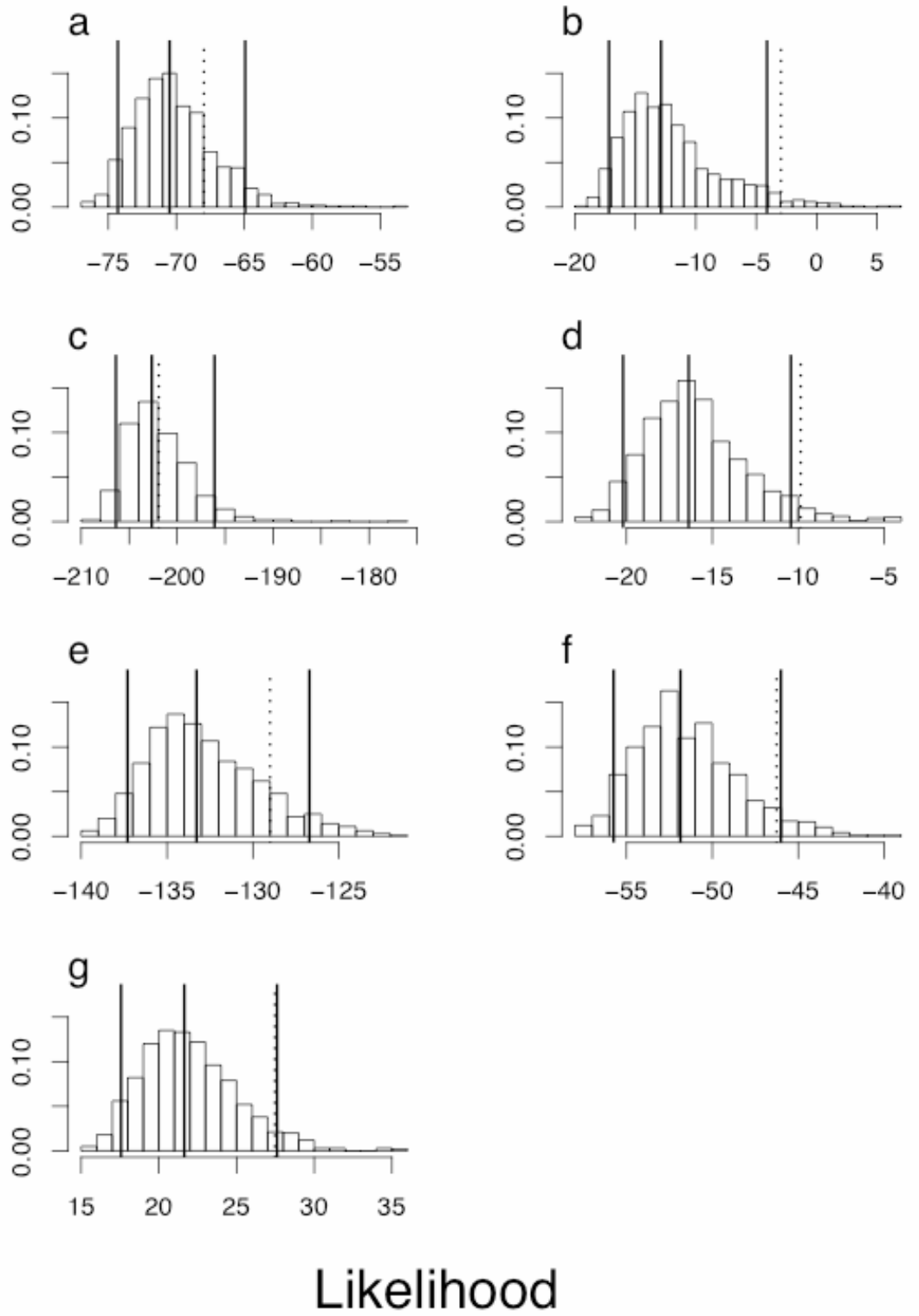
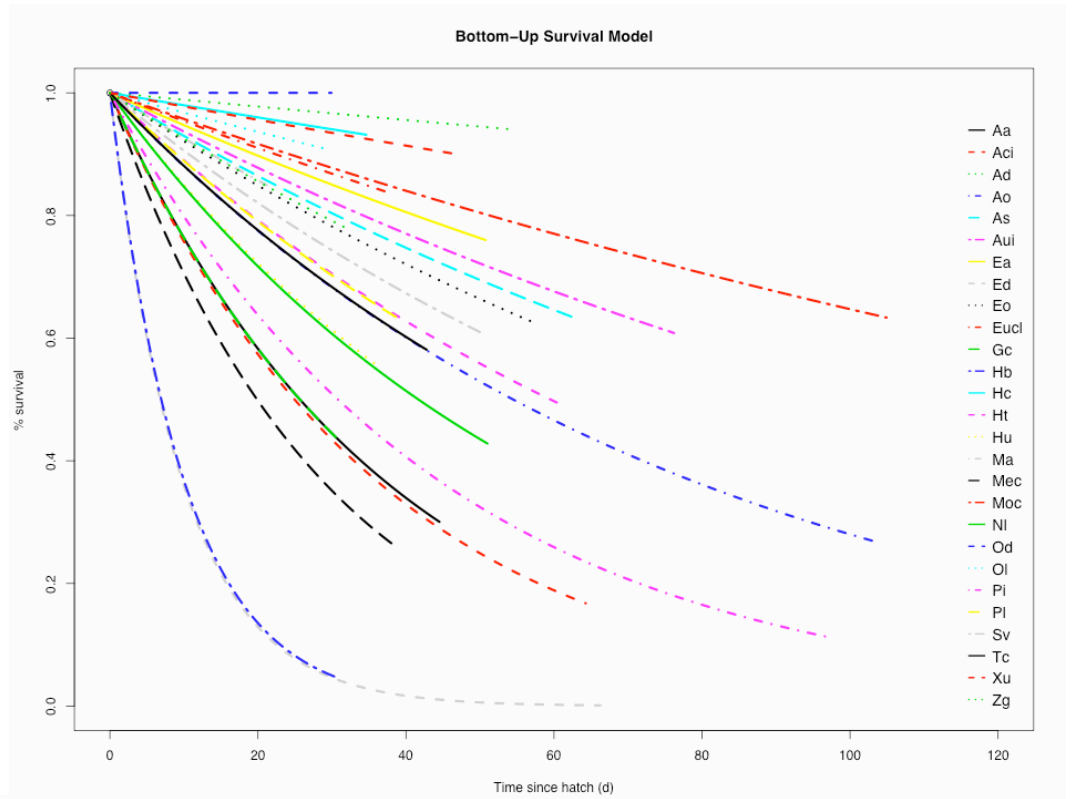


Figure 4.
(a)



(b)

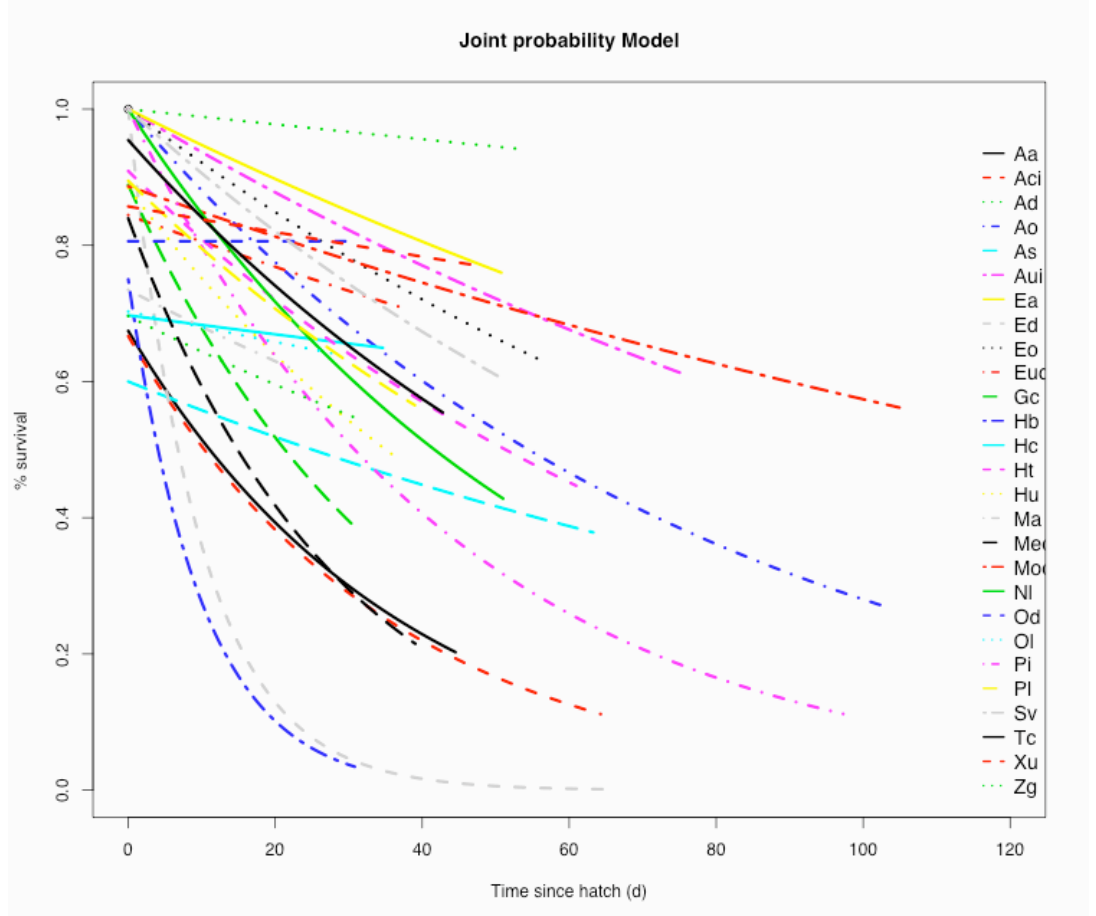
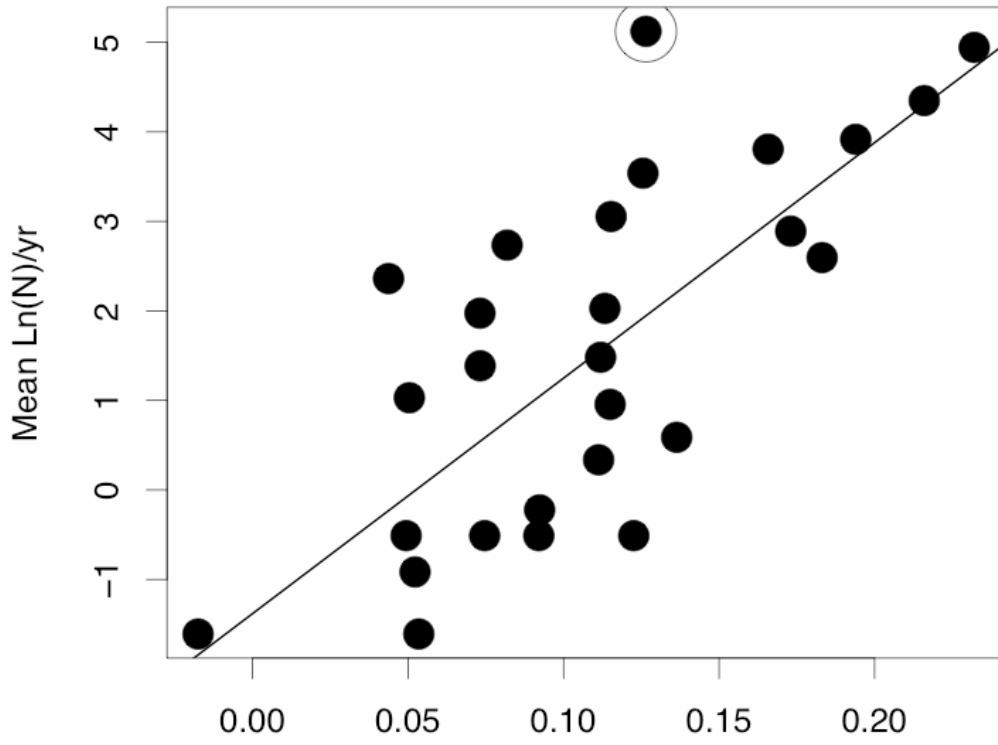
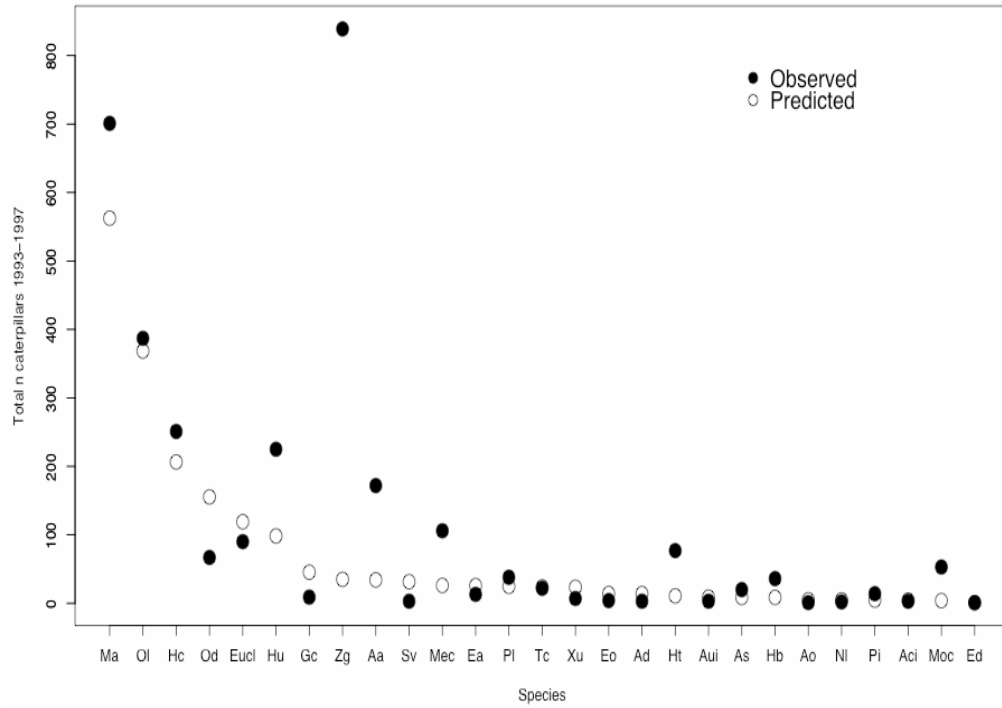


Figure 5.
(a)



(b)



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Variation in phosphorus content in an ecological assemblage of Lepidoptera: testing predictions of mass allometry and relationship to growth rate

Abstract

Ecological stoichiometry connects biochemical processes to organismal interactions through a common currency of elemental composition. A central hypothesis of ecological stoichiometry, termed the growth rate hypothesis (GRH), proposes that organismal development rates should covary positively with phosphorus (P) content, since growth depends ultimately on cellular reproduction using P-rich RNA. Despite the knowledge that terrestrial phytophagous insects face strong P limitation in their food, as well as selection pressure to develop rapidly, little is known about how the P levels of these herbivores vary among species, and whether they correspond with growth rates in an ecological setting. I used a group of moth caterpillar species known to feed on a shared host plant to ask how whole-body P varied with mass and phylogenetic relatedness, and to examine the relationship between P content and growth rates at the individual and species level.

Species differences in whole-body percent P were significant despite small within-species replication ($n \leq 5$), and the low percent P of two species including the gypsy moth was primarily responsible for the observed differences. The percent P of individuals sampled did not scale negatively with mass. Across individuals I found a non-significant relationship between mass-specific growth rate on the host plant and percent P.

Comparing species mean values and accounting for phylogenetic relatedness showed a

significant positive relationship between growth rate and percent P at the species level. These data suggest P limitation could have ecological impacts on success of insect herbivores, and call for additional investigation into the heretofore underappreciated role of P in plant-insect ecology, including the role of P limitations in insect outbreaks and the success of invasive species.

Introduction

Ecological stoichiometry (Sterner and Elser 2002) attempts to connect biochemical processes to properties of individuals, species, and communities through the common currency of elemental ratios (Elser 2006). One fundamental pattern revealed by quantifying stoichiometric ratios is the strong difference in micronutrients such as nitrogen (N) and phosphorus (P) across trophic levels, for instance between terrestrial insect herbivores and their plant hosts (Fagan et al. 2002), or between insect predators and their prey (Fagan and Denno 2004). While plant-herbivore theory has long considered the role of host plant quality in herbivore performance, ecological stoichiometry provides a new framework for understanding the connection between nutrient limitation and life history in herbivorous insects.

Elemental nutrients are characteristically associated with different essential cellular processes (Elser et al. 1996; Sterner and Elser 2002; Elser et al. 2003). Phosphorus is particularly important because individual growth is ultimately driven by cellular division, which is in turn limited by the amount of P-rich ribosomal RNA. The growth rate hypothesis (GRH) formally proposes that organismal P content should vary with growth

rates, reflecting differential allocation to the molecular machinery of growth (Elser et al. 2000). Research supporting the GRH in herbivores has come mainly from freshwater and marine aquatic systems (Elser et al. 2003; Hessen et al. 2007). Relatively few studies have considered the role of P limitation in the performance of terrestrial herbivorous insects (but see Fagan et al. 2004; Huberty and Denno 2006). Although the linkage between growth rates and P can be complicated by other limiting nutrients (Elser et al. 2003), the GRH is a fundamental hypothesis in need of exploration in a terrestrial ecological setting.

The larval stage is often a key factor influencing the population dynamics of Lepidoptera (Dempster 1983), and growth rate is a commonly used metric of performance and fitness in caterpillars (e.g. Coley et al. 2006). Historically, most field and laboratory studies of insect herbivore performance have focused mainly on the roles of nitrogen and plant defensive chemistry (Awmack and Leather 2002). However, experimental evidence demonstrates P content of food can also be a limiting factor in growth of the tobacco hornworm *Manduca sexta* L. (Perkins et al. 2004). There is also suggestive ecological evidence for the importance of P to herbivores. In deserts, herbivore density increases with increasing plant percent P (Schade et al. 2003). Leaf phosphorus content has been found to predict winter moth caterpillar outbreaks in a monospecific host plant stand, where most other variables did not (Hunter et al. 1991). Similarly the spatial distribution of high densities of herbivores can correspond with the distribution of plants with low C:P ratios (i.e., high percent P) (Fagan et al. 2004). However, in an explicit test of P limitation in a lace bug feeding on oaks under different

burning regimes, other environmental factors overwhelmed any stoichiometric effect (Kay et al. 2007).

In this study I focused on a group of caterpillars feeding on a shared host plant. First, I determined whether differences in percent P were detectable across species sharing a resource base, and asked whether some species face a stronger nutrient limitation than others. I also evaluated the relationship between percent P and mass, as P has been hypothesized to decline with body size in an allometric relationship (Gillooly et al. 2005). Finally, to explore the relevance of the GRH to this group of herbivores, I examined the relationship between mass-specific growth rate and percent P by comparing the percent P of individuals reared on the same host plant, and determining whether there is a relationship between mean species growth rates and mean species percent P.

Methods

Herbivore species and host plant. I focused on a group of caterpillars known to feed on leaves of box elder (*Acer negundo* L.), a maple occurring alongside streams and in moist soils throughout the much of the USA. Field surveys have shown P content of box elder leaves is highly variable from tree to tree, and declines from May (0.31 ± 0.006 , mean \pm standard error %P by mass) to August (0.19 ± 0.003 %P; n=120 trees in each month; E. M. Lind unpublished data). To standardize measurements of percent P by species I conducted stoichiometric analysis on the adult moths. Moths for analysis were either reared (see below) or in some cases collected as adults.

Rearing and growth rate measurements. I reared caterpillars from eggs laid by adults collected by light trap from the Patuxent Research Refuge (Laurel, MD; 39° 03.639' N, 76° 44.244' W). Larvae were reared on field-collected, sterilized box elder leaves under controlled light and temperature regimes (further details in Chapter 2). Five days after hatching 25 larvae were weighed and then placed individually into 8" Petri dishes with moistened filter paper and a box elder leaf. Leaves were changed every other day from hatching until pupation. I measured pupal mass two days after pupation. The mass-specific growth rate μ (d^{-1}) was calculated as $\ln(M_2/M_1)/T$ where T is time in days between measurements of mass M_1 and M_2 (Elser et al. 2003).

Chemical analyses. Upon collection or emergence adults were placed in a -22°C freezer until processing. Moths were placed in a drying oven at 60°C for at least three days. Each whole body mass was recorded and the moth was ground to powder using a mortar and pestle. Two to five moths (females wherever possible) of each species were used to quantify elemental composition. Two subsamples (1-2 mg) of each individual were used to quantify whole body percent P using the method of persulfate digestion followed by colorimetric analysis (Clesceri et al. 1998). Subsample values were averaged to get a percent P estimate for individuals, and individual estimates were then averaged to get species-specific values. Twenty-two species from the assemblage of macrolepidoptera co-occurring on box elder were analyzed.

Phylogenetic relatedness. I included the influence of evolutionary relatedness on the P composition of the moth species using a recently developed phylogenetic hypothesis (Mitter et al. *in prep*). I substituted moth species used in this study into a

phylogeny generated from 26 nuclear genes sampled from across the Lepidoptera. I placed the species included in this study at the lowest corresponding sampled taxonomic unit (usually tribe, though some of our sampled species were included in the original phylogeny). Where there were more than one species to insert into the given point on the tree, uniform branch lengths of arbitrarily short size (0.01 change units) were used to join our focal taxa to the tip.

Statistical analyses. Statistical analyses were conducted in R software (R Development Core Team 2008). I tested for species differences in mean percent P using a fixed effects analysis of variance with species identity as the explanatory variable. I tested all pairwise mean differences using Tukey's honestly significant difference (function *TukeyHSD* in R).

To analyze relationships of P to mass and growth rate I used a generalized least squares (GLS) approach. This approach allows incorporation of relatedness into the error structure of a linear model, by utilizing a covariance matrix of species phylogenetic distance (Martins and Hansen 1997). I used a Brownian model of evolution where traits evolve randomly along branch lengths (Martins and Hansen 1997), using the assembled phylogeny. Because this analysis includes phylogenetic distance (and thus differences between species), the GLS models did not include a separate species term.

Using the *gls* function of the R package *ape* (Paradis et al. 2004), I tested for linear effects of log-transformed dry mass (GLS model $\%P = \ln(\text{dry mass})$). To test for effects of percent P on individual growth rate, I regressed percent P on mass-specific growth rate for individuals (GLS model $\%P_{\text{IND}} = \mu_{\text{IND}}$). To account for species for which individual

growth rate data was not available, I used the same model using the species means (GLS model $\%P_{SP} = \mu_{SP}$). For each GLS model, I tested the significance of the explanatory variable using log likelihood ratio tests, evaluated against the expectation of a Chi-square distribution with degrees of freedom equivalent to the difference in degrees of freedom between the models.

Results

As expected, the overall mean percent P by mass was much higher in the herbivores (grand mean \pm SE, 0.875 ± 0.106 %P) than in their shared host plant foliage. Though within-species replication was low (n=2-5), species differed, in some cases strongly, in their mean percent P (Fig 1; overall $F_{21,58}=7.911$, $p<0.001$). Two species had extraordinarily low P content, *Lymantria dispar* L. (0.473 ± 0.027 percent P) and *Automeris io* (F.) (0.501 ± 0.032 percent P). These two species were significantly lower in P than all other species, except each other. Few other pairwise mean comparisons were significantly different from random using Tukey's HSD, though *Zale galbanata* (Morr.) (1.079 ± 0.056) was significantly higher in percent P than *Hyphantria cunea* (Dru.) (0.783 ± 0.047), which is notable because both species are found in high numbers on the host plant. Interestingly, the four numerically dominant caterpillar species (*Z. galbanata*, *H. cunea*, *Alsophila pometaria* (Harris), and *Orgyia leucostigma* (J. E. Smith)) were significantly higher in percent P than the subdominant species included in this analysis (*post-hoc* contrast $p<0.001$), though without the two low percent P species this pattern was less well-supported (*post-hoc* contrast $p=0.08$ without *L. dispar* and *A. io*).

When phylogenetic distance is incorporated using the GLS model, percent P did not decline significantly with body mass (Fig 2; LR=0.048, $\Delta df=1$, $p=0.8266$). At the individual level, percent P_{IND} did not relate significantly to μ_{IND} , the mass-specific growth rate, though the trend was positive (Fig 3; LR=0.833, $\Delta df=1$, $p=0.3613$). In contrast, mean species P (percent P_{SP}) was significantly associated with faster mean species growth rate (Fig 4; LR=5.1998, $\Delta df=1$, $p=0.023$). The difference in the results was the inclusion of the mean values for *L. dispar* and *A. io*, both of which have low μ_{SP} on the host plant, but for which there were no samples in the individual analysis (individuals analyzed for percent P did not have individual growth rate information). Removing these two low P species, and redoing the GLS model of mean percent $P_{SP} = \mu_{SP}$ gives a non-significant relationship similar to the individual analysis (LR=1.038, $\Delta df=1$, $p=0.3083$).

Discussion

This ecological assemblage of species sharing a host plant is marked by strong differences in P between the herbivores and their food source, as has been found in other taxa (Woods et al. 2004) and within different trophic levels (Martinson et al. 2008). The overall mean percent P by mass of 0.875 ± 0.106 reported here falls within the range of estimates given by the one published study on P content in Lepidoptera, in which 12 species of Lepidoptera surveyed from the Sonoran Desert averaged around 0.9 percent P by body mass (Woods et al. 2004). The greater mean percent P by mass content of the caterpillars compared to that of the foliage they consume occurs even in the early

growing season, when foliar nutrient levels are highest. Most species were not significantly different from each other in percent P. This was both because within-species variation was not negligible, and because sample sizes (n=2-5) were low. Recent evidence indicates this type of intraspecific variation in stoichiometric ratios can be extensive and should not be discounted (Bertram et al. 2008), which may make resolution of patterns more difficult with the small sample sizes used to date in most studies of ecological stoichiometry.

Contrary to the general pattern, the extremely low whole body percent P values for the gypsy moth (*L. dispar*) and io moth (*A. io*) nearly overlapped the mean percent P found in early season leaves, a surprising finding given the severe limitation in herbivore diet usually revealed when analyzed in a stoichiometric context (Fagan et al. 2002). This may be important for understanding the ecology of the gypsy moth, an invasive exotic caterpillar of economic importance. Gypsy moths complete one generation per year on early season foliage, and the low percent P by mass demonstrated here implies they are much potentially less limited by that micronutrient than most other Lepidoptera. Release from this particular limitation could mirror the release from natural enemies known to accompany the exotic herbivore (Elkinton and Liebhold 1990), reinforcing the potential for large population growth rates.

Mechanistic explanations for the low percent P observed in gypsy moth and io moth are not clear. One possible explanation is morphological, as a connection between ecological context, morphology, and stoichiometry has been proposed for groups such as ants (Davidson et al. 2005) and detritivores (Martinson et al. 2008). Both *L. dispar* and *A.*

io have thick, hair-like wing scales which in the case of gypsy moth are used by the flightless female to encase an egg mass, but may also have defensive purposes as the scales readily dislodge from the animal upon disturbance in both species. As these scales are composed of chitin, an N-rich structural molecule, these species may be expected to exhibit much higher percent N and N:P ratio than similar species lacking such scales.

Although the two low P species were also among the largest by dry body mass, I did not find the hypothesized negative allometric relationship between percent P and body size (Fig 2; Gillooly et al. 2005). The species sampled here may represent too narrow a range of sizes to detect such a pattern, which as demonstrated in Gillooly et al. (2005) has a slight negative exponential slope across 10 orders of magnitude in animal body size. Woods et al. (2004) found an overall negative relationship between body size and percent P across eight Orders of arthropods, but across their 12 species of Lepidoptera this pattern was not significantly different from random. Martinson et al. (2008) did not find an overall mass-percent P relationship for detritivores, but suggested that within-taxa negative scaling relationships did exist. However, in the group of herbivores in this study, body mass did not predict percent P.

One question related to mass scaling of P elided by the whole-body analyses conducted here and in other stoichiometric studies is the elemental composition of cells with different functional roles, for instance the eggs of a female adult moth. In some moth females, like the flightless *Orgyia* species studied here, eggs make up a large proportion of overall body mass. Given the connection between percent P and RNA in ecological stoichiometry (Sterner and Elser 2002), and the fact that egg cells are built

specifically for rapid growth and division, egg number per female should vary strongly with whole body adult female percent P. If such a relationship can be demonstrated, it will be important to untangle the causation loop as to whether, for instance, higher P food in larvae results in more eggs in an adult female. Especially in non-dispersing females which do not feed as adults, larval access to P may be crucial to determining fecundity, and thus may impact population dynamics of the herbivore.

To examine the importance of the GRH in this group of Lepidoptera I explored the relationship between percent P and growth rate in these herbivores. Such an approach has revealed strong correspondence of percent P to growth rates for a range of aquatic animals under conditions where P is limiting (Elser et al. 2003). Growth rate of individuals has previously been demonstrated to influence abundance of macrolepidoptera on box elder (Chapter 2). In addition, fast development on a host has long been associated with higher fitness in caterpillars, whether because of associations with increased fecundity (Awmack and Leather 2002) or because of a decreased time of exposure to natural enemies (Benrey and Denno 1997). Yet P has been neglected in the plant-insect literature on both sides of the trophic interaction. Finding a link between growth rate and P content of these herbivores would thus have important new ecological implications.

I did find such a relationship when I tested the relationship between percent P_{SP} and the mass-specific growth rate μ_{SP} while accounting for their phylogenetic relatedness (Fig 4). I found no such pattern when analyzed across individuals (Fig 3). The main difference between the two was the inclusion of the two very low percent P species in the species

mean model. It happened that I did not have μ , and percent P, for the same individuals in these two species, which meant they could only be included at the species mean level. In any case the relationship between percent P_{SP} and μ_{SP} was driven by *A. io* and *L. dispar*, as shown by the non-significance of the relationship without the inclusion of those two points in the model (dashed line in Fig 4).

Is the significant statistical relationship between percent P_{SP} and μ_{SP} ecologically meaningful? One complication in comparative work across species is standardizing measurements, and to do here I evaluated percent P in the adult of each species. In doing so I avoided the complications of comparing life stages, instars, and feeding behavior. However I also assumed an as-yet untested relationship exists between larval percent P and adult percent P within individuals. Formalizing this relationship will be difficult given the destructive nature of the P analysis as conducted here. But stronger evidence for the GRH in caterpillars may be provided by utilizing late-stage caterpillars, or perhaps pupae, in the growth rate-percent P comparison. To the degree to which percent P does correlate with life history strategies or morphological differences, the observed correspondence between low percent P and low growth rate in the two outlying species may indicate a fundamental difference in the ecology of these species. These species may face much less of a limitation from acquiring P through their foliar food, which may then emphasize other limiting factors such as N content in their development.

Although much of the debate over the control of population cycles such as observed in the gypsy moth has contrasted natural enemy effects with those of plant quality as measured in terms of nitrogen and defensive chemistry, future models may wish to take

into account the apparently low relative need of gypsy moths for P. This may be among the factors contributing to the success of this invasive outbreak species in eastern North America.

Figures

Figure 1. Whole-body percent phosphorus and phylogenetic relationships of moth species used in the study. Phylogenetic relationships shown as cladogram without branch lengths, though data analysis was conducted with branch lengths included (tree from Mitter et al. *in prep*). Percent whole body percent P calculated from two averaged subsamples of n=2-5 adult moths. Bar shows mean percent P +/- pooled SE for the ANOVA model percent P = species. All pairwise contrasts with Tukey's HSD adjustment found species Ld and Aui were significantly different than every species except each other. Species in order as drawn (taxonomic family in capital letters): ARCTIIDAE: **Sv** *Spilosoma virginica* (Dru.); **Hc** *Hyphantria cunea* (Dru.); **Ht** *Halysidota tessellaris* (J.E. Smith); LYMANTRIIDAE: **OI** *Orgyia leucostigma* (J.E. Smith); **Od** *Orgyia definita* (Pack.); **Ld** *Lymantria dispar* L.; NOCTUIDAE: **Zg** *Zale galbanata* (Morr.); **Aa** *Acrionicta Americana* (Harr.); NOTODONTIDAE: **Hb** *Heterocampa biundata* Wlk.; GEOMETRIDAE: **NI** *Nemoria lixaria* (Gn.); **PI** *Prochoerodes lineola* (Goeze); **Eucl** *Eutrapela clemataria* (J.E. Smith); **Alp** *Alsophila pomataria* (Harris); **Ea** *Euchlaena amoenaria* (Gn.); **Eo** *Euchlaena obtusaria* (Hbn.); **Xu** *Xanthotype urticaria* Swett; **Gc** *Glena cribrataria* (Gn.); **Pp** *Protoarmia porcelaria* (Guenee); **Hu** *Hypagyrtis unipunctata* (Haw.); **Mec** *Melanolophia canadaria* (Gn.); **Ma** *Macaria* (= *Semiothisa*) *aemulataria* (Wlk.); SATURNIIDAE: **Aui** *Automeris io* (F.).

Figure 2. Relationship between percent P and whole body dry mass (g) for individuals sampled (note log scale of x-axis). Line indicates best fit for GLS model: percent P =

$0.898 + 0.006 \cdot \log(\text{body mass})$. Model including mass was not significantly different from random.

Figure 3. Relationship between individual percent P and mass-corrected growth rate μ (d^{-1}) on the host plant. Individual caterpillars were reared from eggs on field-collected box elder under controlled conditions (see text). Growth rate calculated as $\mu = \ln(M_2 / M_1) / T$ where M_i = mass at time i , and T = time in days between measurements. Adult moths were used for the percent P calculations. Line is best fit for GLS model: percent P = $0.86 + 0.474 \cdot \mu$. Model was not significantly different from random.

Figure 4. Relationship between mean species percent P and mean species μ on the host plant. Using species means expands dataset to include the two species lowest in percent P, *L. dispar* and *A. io*, which also have very low mean μ values. Solid line is best fit for GLS model: percent $P_{SP} = 0.655 + 1.43 \cdot \mu_{SP}$. Model was significantly different from zero (LR=5.1998, $\Delta df=1$, $p=0.023$). Dotted line shows best fit GLS model without *L. dispar* and *A. io*: percent $P_{SP} = 0.863 + 0.394 \cdot \mu_{SP}$. This reduced model was not significantly different from random.

Figure 1.

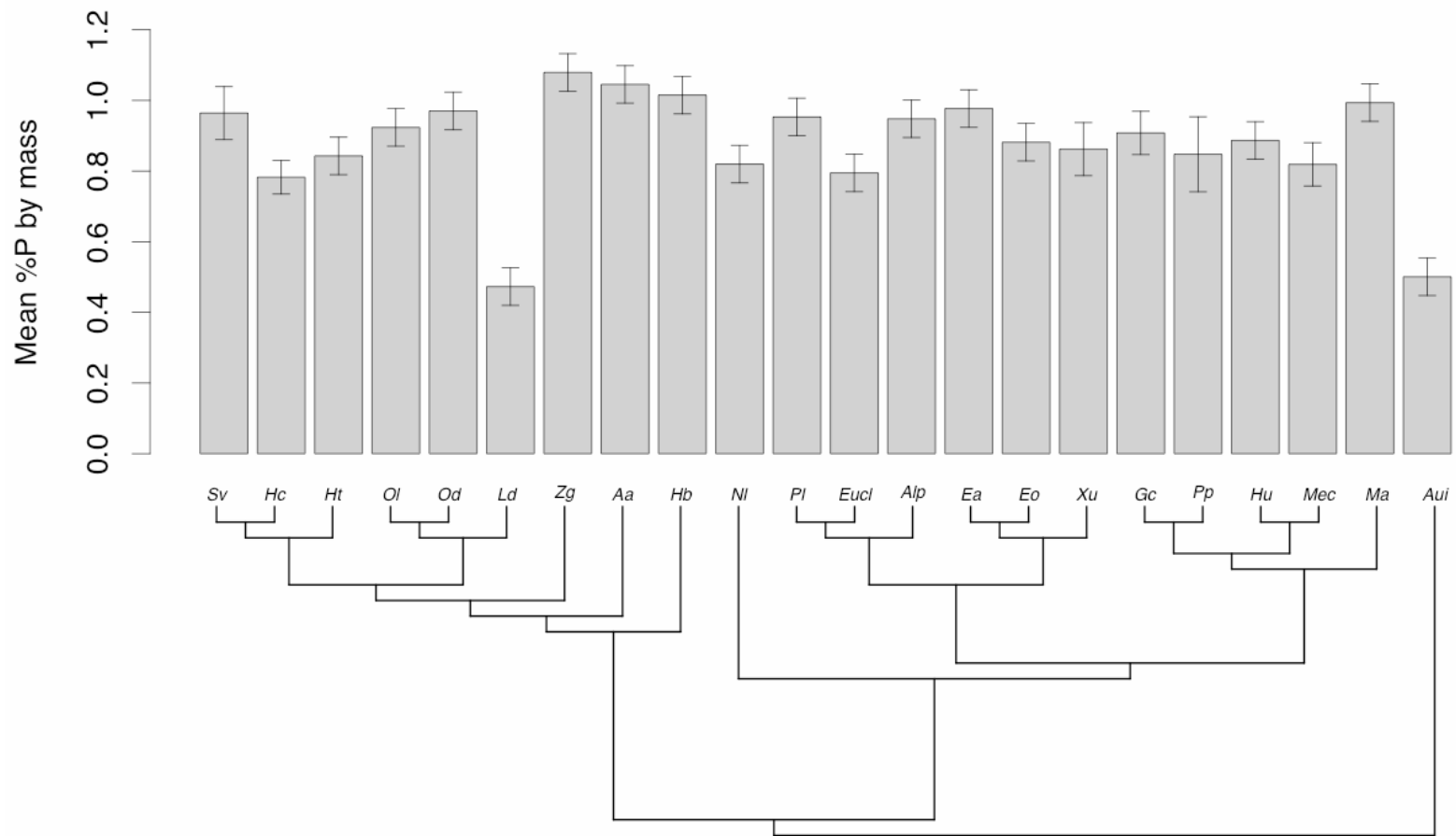


Figure 2.

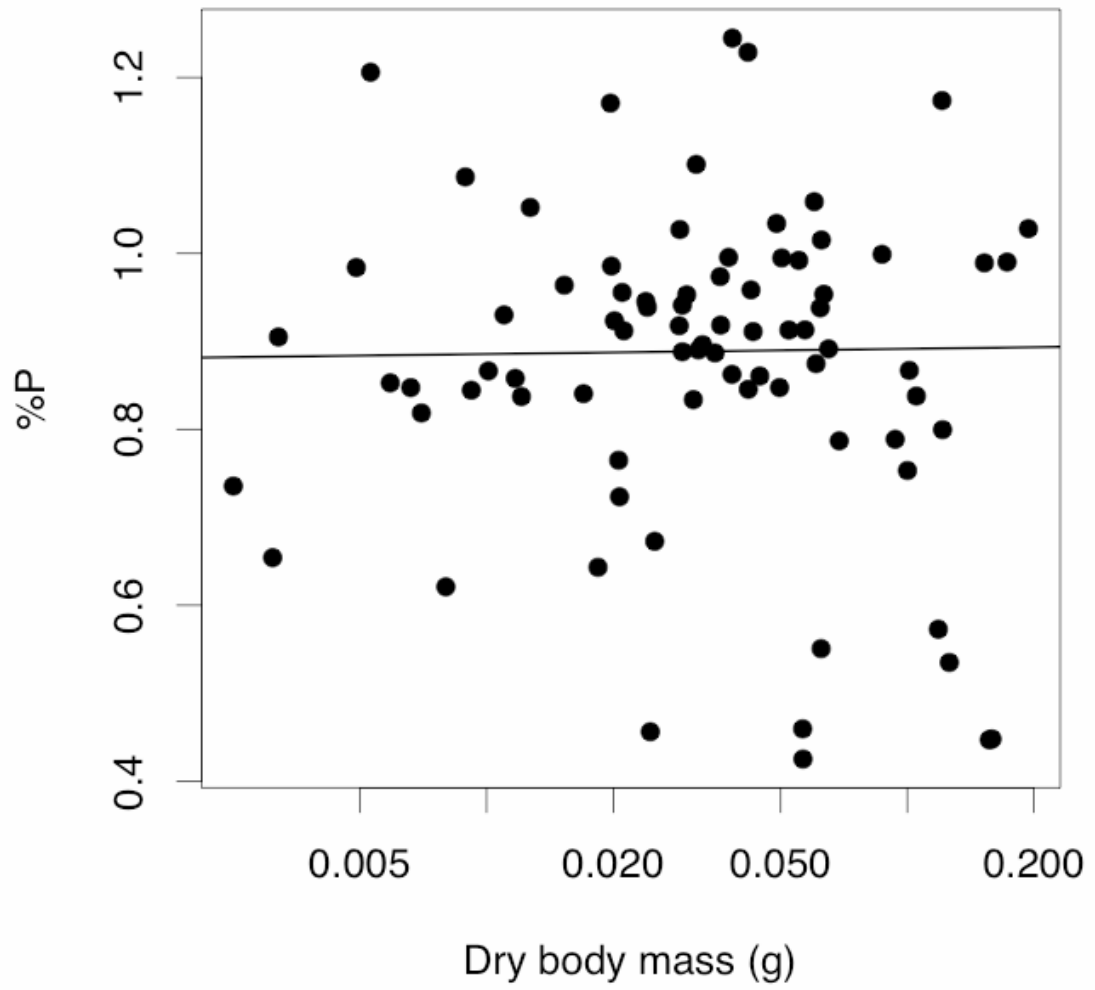


Figure 3.

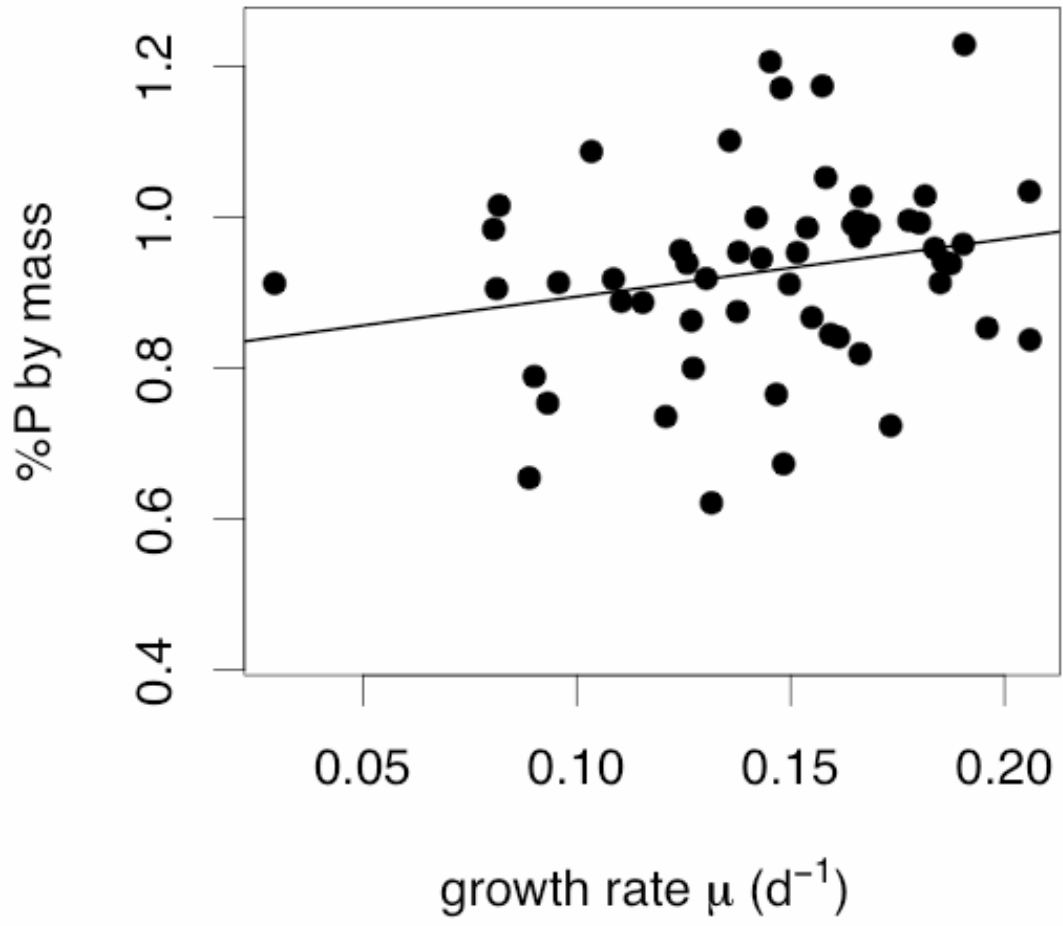
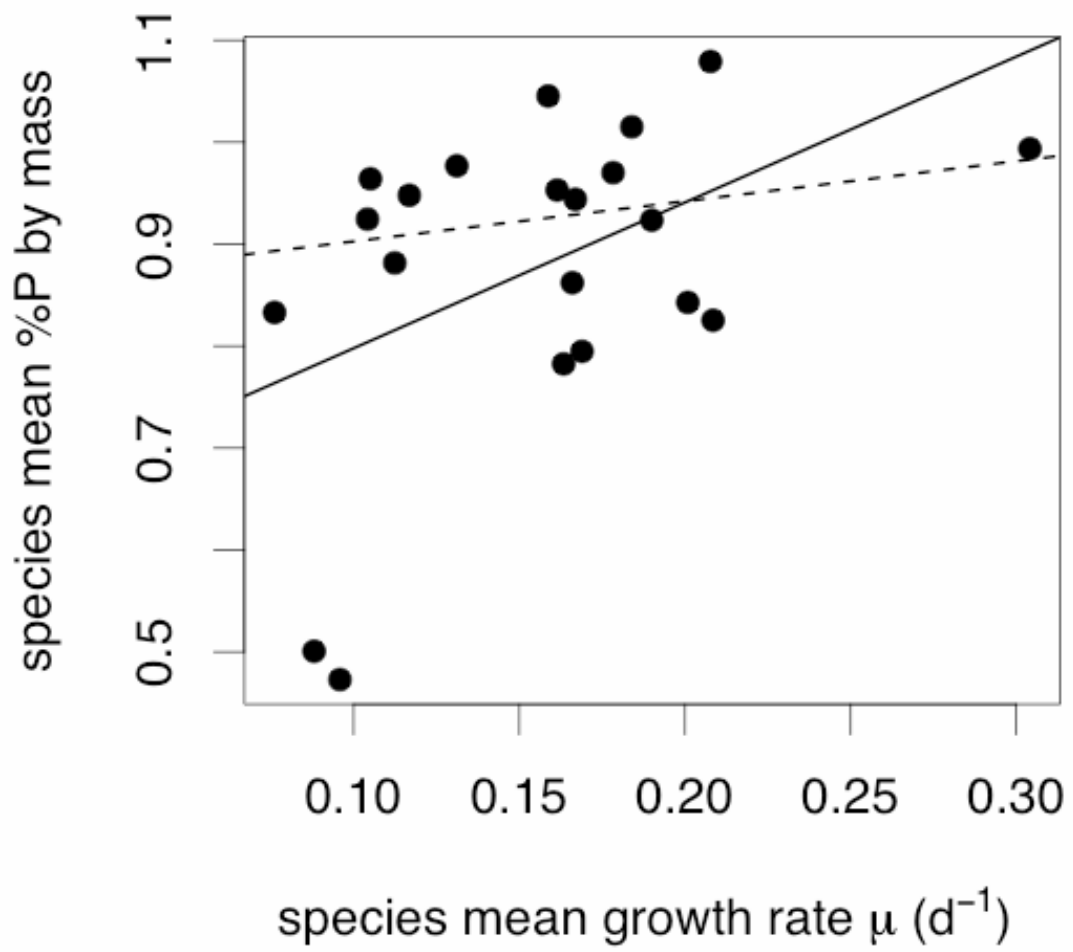


Figure 4.



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Appendix 1

August 2006 Caterpillars collected from <i>Acer negundo</i>												
	CO_E	CO_W	LB_E	LB_W	PRR_N	PRR_S	PRSP_E	PRSP_W	PVSP_E	PVSP_W	SERC_N	SERC_S
Acronicta americana	0	0	1	1	0	0	5	4	0	0	0	3
Acronicta obliqua	0	2	0	0	0	0	0	0	0	0	0	0
Acronicta retardata	0	0	0	0	0	0	0	0	0	1	0	0
Adoneta spinuloides	0	0	0	0	0	0	0	0	0	2	0	0
Anacamptodes defectaria	0	0	0	0	1	0	0	0	0	1	0	0
Cepphis armataria	0	0	0	0	0	0	0	0	0	2	0	0
Cepphis decoloraria	0	0	0	0	0	0	0	0	1	0	0	0
Ectropis crepuscularia	1	0	0	0	0	0	0	1	0	0	0	0
Elaphria versicolor	0	0	0	0	0	0	1	1	1	2	0	0
Euchlaena amoenaria	0	0	0	0	0	0	0	0	1	0	0	0
Euchlaena delphinii	0	0	0	0	0	0	0	0	0	0	1	0
Eutrapela clemmataria	0	0	1	1	1	0	1	1	0	1	0	5
GEOM10	0	0	0	0	1	0	0	0	0	0	0	0
GEOM11	0	0	0	0	0	0	0	0	0	0	0	1
GEOM12	0	0	0	0	0	0	0	0	0	0	0	1
GEOM13	0	0	0	0	0	0	0	0	0	0	0	1
GEOM14	0	0	0	0	0	0	0	0	0	2	0	0
GEOM15	0	0	0	0	0	0	0	0	0	1	0	0
GEOM16	0	0	0	0	0	0	0	0	0	1	0	0
GEOM7	0	0	0	0	0	0	0	0	0	0	1	0
GEOM8	0	0	0	0	0	0	0	0	0	0	1	0
GEOM9	0	0	1	0	0	0	0	0	0	0	0	0
Halysidota tessellaris	0	0	2	4	2	0	4	6	1	2	3	4
Heterocampa umbrata	0	0	0	0	0	0	0	0	0	1	0	0
Hypagyrtis unipunctata	0	2	3	1	4	3	6	1	0	5	1	5
Hyphantria cunea	2	5	0	0	3	4	0	0	3	8	0	0
Lithacodes fasciola	0	0	0	0	0	0	0	0	1	0	0	0
Macaria aemulataria	2	0	10	1	3	12	1	3	1	3	4	10
Melanolophia canadaria	1	0	6	1	2	2	3	4	5	6	2	8
Nemoria sp	0	0	0	0	0	0	0	1	0	0	0	0
NOCT5	0	0	0	0	0	0	0	0	6	0	0	0
NOCT6	0	0	0	0	0	0	1	0	0	0	0	0
Oligocentria semirufescens	0	0	2	1	1	0	2	0	2	3	0	0
Orgyia definita	1	0	0	0	2	1	6	0	0	5	0	0
Orgyia leucostigma	0	1	0	0	2	0	1	0	0	1	0	9
Palthis angulalis	0	0	0	1	1	0	0	0	0	0	0	0
SATR1	0	0	0	0	0	0	0	0	0	1	0	0
Sibine stimulea	0	0	3	2	1	0	1	0	0	1	0	0
Tetracis crocallata	0	0	1	0	0	0	0	0	1	0	0	0
Thyridopteryx ephemeraeformis	0	0	0	0	0	0	0	2	0	0	1	0
Zale galbanata	7	6	13	8	20	14	6	16	3	7	13	27
Zanclognatha cruralis	0	0	0	0	0	0	1	0	0	1	0	0

August 2007 Caterpillars collected from *Acer negundo*

	CO_E	CO_W	LB_E	LB_W	PRR_N	PRR_S	PRSP_E	PRSP_W	PVSP_E	PVSP_W	SERC_N	SERC_S
Acronicta.americana	0	0	5	0	0	1	0	0	2	2	1	1
Anacamptodes.defectaria	0	0	0	0	1	0	0	0	0	0	0	1
Bomolocha.baltimoralis	0	0	0	0	0	0	0	1	0	0	0	0
Dasychira.obliquata	0	0	0	0	0	0	0	0	0	1	0	0
Euchlaena.amoenaria	0	0	0	0	0	0	0	0	1	1	0	1
Euchlaena.sp	0	0	0	0	0	0	0	0	0	0	1	1
Eutrapela.clemmataria	0	0	0	0	0	0	0	0	3	1	0	0
GEOM1	0	0	0	0	0	0	0	0	1	1	0	0
GEOM2	0	0	0	0	0	0	0	1	0	0	0	0
GEOM3	0	0	0	0	1	0	0	0	0	0	0	0
GEOM4	1	0	0	0	0	0	0	0	0	0	0	0
GEOM5	0	0	1	0	0	0	0	0	0	0	0	0
Halysidota.harisii	0	0	0	0	0	0	1	0	0	0	0	0
Halysidota.tessellaris	0	1	1	0	1	0	0	1	2	5	0	3
Heterocampa.biundata	0	0	0	0	0	0	0	0	0	1	0	0
Heterocampa.sp	0	0	1	0	0	0	0	0	0	0	0	0
Hypargyrtis.unipunctata	3	4	9	0	10	9	1	2	3	10	4	11
Hyphantria.cunea	6	10	0	0	7	22	0	0	0	3	5	28
Iridopsis.larvaria	0	0	0	0	0	0	0	1	0	1	0	0
Isa.textula	0	0	0	0	0	1	0	0	0	0	1	0
Lophocampa.caryae	0	0	0	1	0	0	0	0	0	0	0	0
Lytrosis.unitaria	0	0	1	0	0	0	0	0	0	0	0	0
Macaria.aemulataria	12	36	2	3	50	16	2	3	21	45	23	70
Melanolophia.canadaria	1	1	5	2	2	1	0	0	6	4	1	4
NOCT1	0	0	2	0	0	0	0	0	0	1	0	0
Oligocentria.semirufescens	0	0	0	4	0	0	0	0	2	2	0	0
Orgyia.definita	0	0	3	0	0	1	0	1	0	2	0	0
Orgyia.leucostigma	0	0	3	0	1	2	0	0	0	0	0	1
Prochorodes.lineola	0	0	0	0	1	0	0	0	1	0	0	0
Protoboarmia.porcelaria	0	0	0	1	0	1	0	0	0	0	0	0
Pyrrhactia.isabella	0	0	0	0	0	0	0	0	0	1	0	0
Tetracis.crocallata	0	0	1	3	0	0	0	0	0	0	0	0
Thyriodpteryx.ephemerata	0	0	1	0	0	0	0	0	0	1	0	0
Zale.galbanata	5	8	33	21	24	9	3	2	26	10	8	35

Appendix 2

Biomass of foliage by species (values are kg foliar biomass estimated by regressions from diameter of trunk)														
Abbreviation	Species	CO_E	CO_W	LB_E	LB_W	PRR_N	PRR_S	PRSP_E	PRSP_W	PVSP_E	PVSP_W	SERC_N	SERC_S	
ACNE	Acer nugundo	1216.70674 5	243.497641 7	0	301.036661 8	12.8677717 7	103.738263 9	238.002100 4	4.68346333 5	256.731452 8	715.191612	68.3513904 9	113.513697 6	
ACRU	Acer rubrum	0	122.838659 7	186.290150 8	299.264860 6	93.6945117 4	0	80.2006747 4	742.303242 8	20.6289482 9	0	50.9764257 6	99.2644045 4	
ACSA	Acer saccharinum	237.687673 2	0	0	0	0	0	0	0	0	0	0	0	
ASTR	Asmina triloba	94.5594853 6	10.7643615 3	0	0	1.77394554 2	25.4374469 7	0	0	0	0	0	6.52185954 9	
BELE	Betula lenta	0	0	0	0	0	0	0	52.1191391 4	0	0	0	0	
BENI	Betula nigra	0	0	0	0	1.51646303 2	0	0	0	0	0	0	0	
CACA	Carpinus caroliniana	0	3.59216566 8	16.4934600 9	0	98.2201188 6	94.5085848 2	38.4736774 6	0	15.1229253 9	0	24.1892364 2	0	
CAGL	Carya glabra	0.02506576 5	136.194078 9	0	0	15.8312305 5	0	0	0	79.5919637 5	13.5957979 9	0	0	
COFL	Cornus florida	0	0	5.46246544	0	31.0106389 1	0	0	0	0.89655911 3	0	20.4593062 4	0	
CRAT	Crataegus sp.	0	0	0	0.75082119 1	0.89655911 3	0	0	0	0	0	0	0	
DIVI	Diospyros virginiana	0	0	0	0	0	0	89.9315502 6	0	0	0	0	0	
FAGR	Fagus grandifolia	0	0	0	0	135.646878 8	798.403530 4	0	0	20.1310818 4	0	0.75082119 1	0	
FRAM	Fraxinus americana	0.50334717 6	10.4147847 8	236.954962 8	0	33.2364829 8	144.987041 7	0	137.881416 6	16.4800701 2	128.583805 9	10.0258025 7	7.44627525 2	
GYDI	Gymnocladus dioica	0	0	0	0	0	0	0	0	0	32.3373250 4	0	0	
HAVI	Hamamelis virginiana	0	0	0	0	0	0	0	0	0.28476807 1	0	0	0	
ILOP	Ilex opaca	0	0	0	0	0	0	0	0	0	0	1.05755678 3	0	
JUNI	Juglans nigra	0	560.689920 9	125.908114 1	127.429049 3	0	0	35.6179990 1	212.542798 8	0	272.142434 2	0	0	
JUVI	Juniperus virginiana	0	0	21.5516432	0	0	0	0	0	0	0	0	0	
LIBE	Lindera benzoin	0.99551017 6	0.48211282 8	4.50671834 8	4.05874065 2	0.21028680 7	0.19122319 6	2.77593978 5	4.08407867 5	0.21028680 7	3.29954514 1	3.80799660 4	2.31512935 7	
LIST	Liquidambar styraciflua	0	0	0	0	317.656399 9	478.692193 9	0	0	0	0	720.788833 8	42.4409613 6	
LITU	Liriodendron tulipifera	324.941918 8	126.088805 3	224.014770 4	1326.22175 6	780.927884 9	2040.95642 2	59.5375190 7	352.730004 4	1078.49859 2	0	1192.36889 1	2513.59625 1	

MOAL	Morus alba	0	0	0	0	0	0	0	0	0	0	0	0	9.53753834	7
NYSY	Nyssa sylvatica	0	35.4297784	12.5455736	0	9.78692510	0	0	0	0	0	0	0	0	0
OSVI	Ostrya virginiana	0	0.17060249	0	0	0	8.41421864	0	0	0	0	0	0	0	0
PLOC	Platanus occidentalis	0	434.017748	20.7030934	3498.34208	26.5857088	0	2747.86494	1246.29139	350.973284	0	0	0	0	0
PRSE	Prunus serotina	0	0	413.973577	0	0	0	9.59537658	145.963110	0	10.9959225	26.387297	527.545315	4	
QUAL	Quercus alba	0	0	0	0	0.50334717	0	0	0	9.08377797	0	0	0	0	
QUPR	Quercus prinus	0	0	0	0	0.13172691	154.479357	0	0	1.63623091	0	0	0	0	
QURU	Quercus rubra	1775.77671	0	8.61692674	0	447.385015	73.5144598	0	0	781.737254	0	0	0	0	
RHCA	GROUP Rhamnus cathartica	0	0	0.22771699	0	0	6.65017332	0	0	0	0	0	0	0	
ROPS	Robinia pseudoacaci a	0	0	0	0	0	0	0	0	0	137.353998	0	0	0	
SAAL	Sassafras albidum	0	0	57.1290904	0	2.36645985	0	0	0	6.01153598	42.0545197	7.62729888	12.3958288	2	
STTR	Staphylea trifolia	1.4691161	2.12637229	0	0	0	0	0	0	0	0	0	0	0	
TILI	Tilia sp.	0	0.31135155	0	0	0	0	0	0	0	0	0	0	0	
ULRU	Ulmus rubra	0.92359368	216.922245	106.863679	0	121.195209	326.502765	0	0	79.1022692	12.2297997	39.3596236	0	8	

First five PC Axis loadings by plant species (captures 90% of overall variance in stand-vegetation matrix)

Abbreviation	Species	PC1	PC2	PC3	PC4	PC5
ACNE	<i>Acer nugundo</i>	0.030279338	-0.196774199	-0.018694423	-0.034453062	-0.060155728
ACRU	<i>Acer rubrum</i>	0.067181694	0.097795567	0.042171783	0.051368497	0.037438668
ACSA	<i>Acer saccharinum</i>	-0.014032815	-0.041891272	-0.027174241	0.03144782	-0.009161561
ASTR	<i>Asimina triloba</i>	-0.016836128	-0.023177244	-0.013904797	0.006770383	0.003028768
BELE	<i>Betula lenta</i>	0.013515418	0.012051802	0.003275423	0.009057633	0.002387333
BENI	<i>Betula nigra</i>	-0.002586196	0.000738597	-0.001427158	-0.000464702	0.003539988
CACA	<i>Carpinus caroliniana</i>	-0.031498843	0.021447696	-0.007599775	-0.020648499	0.041257982
CAGL	<i>Carya glabra</i>	0.015343358	-0.030136489	-0.001943566	-0.019332461	0.04370177
COFL	<i>Cornus florida</i>	-0.021935803	0.011915034	0.004776208	-0.001881165	0.014366661
CRAT	<i>Crataegus sp.</i>	-0.000899011	0.001315067	-0.00200218	-0.000686351	0.001935064
DIVI	<i>Diospyros virginiana</i>	0.022855667	0.004854432	-0.01452703	-0.006764285	-0.007336662
FAGR	<i>Fagus grandifolia</i>	-0.078183221	0.017576736	-0.024633652	-0.054682358	0.05986603
FRAM	<i>Fraxinus americana</i>	-0.002720078	-0.011637166	0.101749076	0.021365957	0.049337711
GYDI	<i>Gymnocladus dioica</i>	0.006964521	-0.029647165	0.020075004	-0.01192273	-0.008345326
HAVI	<i>Hamamelis virginiana</i>	-0.00031688	-0.000230297	-0.001157671	0.000663257	0.000502971
ILOP	<i>Ilex opaca</i>	-0.002241224	0.001412358	0.000725132	-0.00224057	-0.001877193
JUNI	<i>Juglans nigra</i>	0.126900395	-0.053873178	0.111223488	-0.025766375	0.052790292
JUVI	<i>Juniperus virginiana</i>	0.000356048	0.005505169	0.020051086	0.017674726	0.011366979
LIBE	<i>Lindera benzoin</i>	0.00504079	0.000458419	0.011960971	0.002780066	-0.004684414
LIST	<i>Liquidambar styraciflua</i>	-0.142520641	0.063887008	0.003165092	-0.099055601	0.001443217
LITU	<i>Liriodendron tulipifera</i>	-0.189536699	0.153008894	-0.032395207	0.007271691	-0.039927419
MOAL	<i>Morus alba</i>	-0.004032097	0.003577362	0.003057005	0.003772688	-0.009085273
NYSY	<i>Nyssa sylvatica</i>	0.006261535	0.001476531	0.016407909	0.001332888	0.032640757
OSVI	<i>Ostrya virginiana</i>	-0.004176256	0.000844688	0.0001219	-0.00630246	0.003476098
PLOC	<i>Platanus occidentalis</i>	0.289155757	0.121070646	-0.136438822	-0.015297554	0.013442716
PRSE	<i>Prunus serotina</i>	-0.005477591	0.06225448	0.12667908	0.10032614	-0.030395274
QUAL	<i>Quercus alba</i>	-0.003279686	-0.000875172	-0.007360641	0.003478289	0.004880214
QUPR	<i>Quercus prinus</i>	-0.023150558	0.004652688	-0.004081212	-0.02228952	0.012690775
QURU	<i>Quercus rubra</i> GROUP	-0.114075069	-0.106961111	-0.147376669	0.107523694	0.07650534
RHCA	<i>Rhamnus cathartica</i>	-0.004450987	0.001600607	0.001877337	-0.003109321	0.003334919
ROPS	<i>Robinia pseudoacacia</i>	0.014353568	-0.061101486	0.04137369	-0.024572215	-0.017199345
SAAL	<i>Sassafras albidum</i>	-0.006780316	-0.017110453	0.053869754	0.015930855	0.000324201
STTR	<i>Staphylea trifolia</i>	0.001973727	-0.004420368	-0.000976353	-0.000215516	0.00294836
TILI	<i>Tilia sp.</i>	0.001177412	-0.000431228	0.000443895	-0.001028533	0.001403814
ULRU	<i>Ulmus rubra</i>	-0.038239102	-0.001336172	0.038100828	-0.034448704	0.100420376

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