THE LEPIDOPTERA AS PREDICTABLE COMMUNITIES OF HERBIVORES: A TEST OF NICHE ASSEMBLY USING THE MOTH COMMUNITIES OF MORGAN-MONROE STATE FOREST

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Abstract.—The response of forest insect communities to disturbances such as timber harvest likely will depend on the underlying ecological assembly rules that affect community structure. Two competing hypotheses are niche assembly, which seeks to demonstrate significant species-environment correlations, and dispersal-assembly, which seeks to demonstrate spatial autocorrelation in the absence of species-environment correlations. Unfortunately, many studies of forest management never explicitly test what factors are responsible for maintaining community structure prior to harvest. The goal of this study is to examine variation in the community structure of forest Lepidoptera using the pre-timber harvest data on Lepidoptera from 18 forest sites within 3 management units of the Hardwood Ecosystem Experiment at Morgan-Monroe State Forest (MMSF) in Indiana.

We sampled 14,270 individuals representing 277 species of macrolepidoptera from MMSF in 2007. Canonical correspondence analysis suggested significant correlations between the moth assemblage found within a stand and levels of three environmental variables: importance of oaks, log-tree density, and percent basal area of shrubs and saplings. In contrast, Mantel tests suggested that forest moth communities at MMSF were, at most, weakly autocorrelated. The results here suggest some support of niche-assembly processes within forest macrolepidoptera. Still, a significant portion of the variation in species assemblages among forest stands remained unexplained, suggesting that stochastic factors and sampling bias may be important to consider when discussing patterns of lepidopteran diversity in space and time.

INTRODUCTION

The Lepidoptera is one of the most important insect orders in forest ecosystems, partly because of its constituent species' critical role in ecosystem functions such as trophic interactions and pollination and partly due to the irruptive potential of certain defoliators. Studies of bird communities in eastern deciduous forest systems regularly report the importance of lepidopteran larvae in the diet of birds (Holmes and Schultz 1988, McNulty et al. 2008, Robinson and Holmes 1982) and mammals (Burford et al. 1999). Species such as *Choristoneura rosaceana* (Har.), *Choristoneura fumifernana* (Clem.), *Malacosoma americanum* (F.), and *Lymantria dispar* (L.) can contribute to significant reductions in canopy cover, reduced tree growth increment, and in rare cases, direct mortality of tree species (Hennigar et al. 2007, Man et al. 2008, Tobin and Whitmire 2005). Therefore, understanding the key ecological processes that

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structure lepidopteran communities will be useful from the perspective of both forest conservation biology and forest pest management.

A small but growing body of literature suggests that both niche-based and dispersal-based assembly processes play a significant role in structuring forest lepidopteran assemblages. Niche-based assembly theory suggests that species diversity patterns are maintained by competitive resource partitioning, species sorting along environmental gradients, or some combination of both processes (Chesson 2000, Franklin et al. 2003, Lepš et al. 1998, Murakami et al. 2007). Species sorting is often a function of species traits, and can be a relatively predictable phenomenon (Summerville 2008).

In contrast, dispersal assembly is a neutral model that suggests that species membership within a community is more closely regulated by barriers to movement and founder effects associated with low frequency of colonization events (Leibold et al. 2004). Dispersal events are often modeled as stochastic processes related to interpatch distances rather than species traits per se. Under dispersal assembly, communities gain species from mass effects, where species that have established populations in favored habitat may colonize unsuitable habitat through dispersal dynamics (Leibold et al. 2004).

For Lepidoptera, tree species composition, herbaceous diversity, and stand volume all have been described as predictors of assemblage composition (reviewed in Summerville and Crist 2008). Dispersal limitation has proven difficult to disentangle from effects of habitat loss (which increases patch isolation but also diminishes habitat area) and biogeographic effects (Doak 2000, Kuussaari et al. 2007, Summerville et al. 2004). Donor pools for colonizing Lepidoptera are also poorly known (Holl 1996). Community studies have often focused on characterizing local assemblage structure and inferred landscape composition as an extension of local stand dynamics (Summerville and Crist 2008, but see Franklin et al. 2003).

Species sorting and dispersal assembly are processes that represent contrasting, but not mutually exclusive, answers to the basic question – why is this set of species found in this particular habitat? Testing for the relative importance of each process is critical for understanding how forest lepidopteran assemblages recover from disturbances. Studies of timber harvest have established that forest moth communities appear slow to recover from clearcutting, even when managed patches are small relative to the total stand area (Forkner et al. 2006, Holl 1996, Summerville and Crist 2004). Questions that remain to be answered include: (i) Did moth communities fail to recover an original lepidopteran species composition because of shifts in floristic composition? or (ii) Did moth communities fail to recover an original lepidopteran species composition because timber management created new barriers to recolonization? Before either of these questions can be answered, however, a test of the suitability of niche-based and dispersal-based assembly theory should be made pre-harvest. That is, prior to disturbance, what appears to be the proper hypothetical model explaining moth community structure? Does one process tend to explain the bulk of the variance in community structure or are both equally compelling?

The goal of this paper is to ascertain how moth community structure is maintained in a relatively undisturbed forest landscape. Specifically, we use data from macrolepidoptera sampled from 20 forest stands within Morgan-Monroe State Forest (MMSF) in Indiana to determine the degree to which niche-based or dispersal-based assembly mechanisms were significant in predicting moth species diversity and composition. Because many Lepidoptera are obligately connected to a narrow suite of host plants for larval development, we predicted that niche-based assembly processes would be of much greater importance than dispersal-based assembly processes. Further, we hypothesized that two critical floristic variables would determine moth species composition within forest stands: 1) the importance of oaks (*Quercus* spp.) because a large number of species are specialized on

this host plant (as opposed to maples [*Acer* spp.], for example), and 2) the density of the stand (because high tree density within a stand indicates prior disturbance and, perhaps, lower foliage quality among trees (see Fry et al. 2009, Summerville and Crist 2002). Moth diversity was expected to be higher in stands with a dominant oak component and a low stand density. If dispersal-assembly is more important in predicting moth species composition, then we expected to see stronger evidence of spatial autocorrelation in moth assemblages than observed in the stand tree assemblage (see Nekola and White 1999). Thus, moth species would be structured at a finer grain across the forest landscape than the food resources upon which their larvae are known to depend.

MATERIALS AND METHODS

Study Site

MMSF occurs within the north-central interior dry-mesic oak forest and woodland ecological system (39°31′28″N, 86°44′13″W). This system is widespread across the glaciated regions of the Midwest, from North Dakota to Ohio and Minnesota to Missouri. Soils are typically well-drained mollisols or alfisols from loam to sandy loam (Braun 2001). Located in the Central U.S. Mixed Hardwood Forest ecoregions, MMSF has dry slopes dominated by oak-hickory (*Carya*) forest. In unfragmented landscapes, canopy cover tends to be dense, although historic fire regimes likely maintained open canopy (Homoya et al. 1985). Chestnut oak (*Q. prinus*) is a dominant species with white oak (*Q. alba*), red oak (*Q. rubra*), and black oak (*Q. velutina*) present depending on soil moisture regimes. Bitternut hickory (*C. cordiformis*) and shagbark hickory (*C. ovata*) are also common. Additionally, this ecoregion is among North America's richest for herbaceous plants and shrubs, with >2,000 species described (Homoya et al. 1985). Most of the sites that were used for sampling have remained unlogged for at least 50 years. Salvage logging has occurred on a localized basis after major windstorm events, but these areas were avoided for the purpose of this study. Several forest stands, however, had not been cut after the mid-1920s.

Lepidoptera Sampling Methodology

In early 2007, we identified three management units within the Hardwood Ecosystem Experiment (HEE) at MMSF for lepidopteran sampling. Management units were ~500 ha in size, were 1-3 km apart, and were scheduled subsequent to our sampling to have forest harvest treatments applied to an inner core area that ranged from 78 to 110 ha in size (Kalb and Mycroft, this publication). Tracts were assigned to a specific timber management regime a priori, although the harvest schedule was crafted such that timber would be removed only after establishing a baseline biodiversity assessment. Management unit 1 was assigned an uneven-aged management regime using a combination of patch cuts and single-tree selection, unit 2 was dedicated as an unharvested reserve to serve as an experimental control, and unit 3 was assigned an even-aged management regime using three-stage shelterwoods and clearcut harvesting.

To develop a baseline assessment for forest moth biodiversity, we identified eight stands within each of the two managed units and four stands in the control unit (n = 20 total sites). Stands were separated by >150 m (range 150-750 m) and were grouped such that forest stands within each management unit were clustered into stand pairs. Stand pairs were generally 150 m apart and were chosen so that one occurred within the center of an area to be harvested and the other within the unharvested matrix adjacent to a harvest boundary (see Kalb and Mycroft, this publication).

Moths were collected from forest stands using Universal 12-watt blacklight traps (BioQuip Products, Inc., Rancho Dominguez, CA) powered by 12-volt, 26 ampere hr^{-1} batteries. On nights of operation, a single trap was placed at each site on a platform 2 m above the ground and remained lit from 2000 to 0700 CDT. We sampled Lepidoptera approximately every

14 days from 30 May to 30 August 2007, producing 100 total samples from the 20 sites (five per site). This level of sampling correlated with a sampling efficiency of 85 percent, which is equal to most other studies of Lepidoptera in temperate deciduous forests (Summerville and Crist 2008).

Weather and moon intensity are known to affect sampling efficiency of blacklight traps, so trapping was restricted to nights that had a minimum temperature of 16 °C, no precipitation, and low levels of ambient moonlight (half to new moon phases) (cf. Yela and Holyoak 1997). Lepidopteran nomenclature and authorities follow Hodges et al. (1983) with revisions as noted in Ferguson (2008) and LaFontaine and Schmidt (2010). Voucher specimens were deposited at Drake University, Des Moines, IA.

Forest Vegetation Sampling Methodology

From September 2007 to August 2008, and before all harvesting, forest vegetation was sampled across each management unit using a systematic grid on a 75m × 150m spacing. All trees and standing snags ≥11.5 cm diameter at breast height (d.b.h.; = 1.37 m above ground) were inventoried within circular 0.10-ha plots on each grid point; saplings, shrubs, and standing snags 1.5-11.4 cm d.b.h. were measured within a nested 0.025-ha subplot.

Across the three units, 163 plots were established. For each tree, sapling, or shrub, species, d.b.h., condition, light field (sensu Bechtold 2003), stratum, and spatial location were recorded. Height and lowest live crown were recorded for a subsample of trees and saplings. For snags, species (if known), d.b.h., height, decay class (sensu Cline et al. 1980), and spatial location were recorded. More information regarding this inventory can be found in Saunders and Arseneault (this publication). This study included only those vegetation plots within 100 m of the moth sampling sites. Therefore, between two and five plots per moth sampling site were used for analysis. Data for 2 of the timber stands were not obtained (both from management unit 3), so 18 stands among the 3 management units were used in subsequent analyses.

Data Analyses

We tested whether communities of forest macrolepidoptera were structured by niche-based assembly rules using canonical correspondence analysis (CCA). This technique is a multivariate ordination approach that determines whether environmental variation is important in creating structure in a species-abundance matrix (ter Braak 1986). A detailed statistical treatment of CCA can be found in McCune and Grace (2006). To summarize, the algorithm for CCA defines linear combinations of orthogonal environmental variables that maximize the separation distance among species in ordination space. Site scores are derived as weighted averages of species scores and are plotted in 2- or 3-dimensional space. Thus, species with scores that are close to a given site point on a CCA ordination figure are likely to attain a high abundance at that particular site. The scatter of site scores in ordination space depicts how overall regional species composition varies across the measured environmental gradients. The influence of environmental variables on species abundances can be qualitatively modeled on the ordination figure through the use of joint bi-plots, which are graphic renderings of species sorting through niche dynamics (Jongman et al. 1995).

We performed CCA using PC-ORD for Windows (version 5.0, MjM Software Design 2006). We pooled species-abundance data from the 5 sampling nights for each stand, producing one, season-long characterization of lepidopteran community structure, as recommended by Summerville and Crist (2002). Microlepidopterans in families such as Gelechiidae, Tortricidae, and Gracillariidae were excluded due to the difficulty in validating species-level determinations.

Moth community data were then filtered in two ways to test for niche assembly. First, we ran a CCA using the entire species pool from each site minus species sampled as either singletons or doubletons (a total of 1 or 2 individuals sampled across all sites). Other authors have argued convincingly that exceptionally rare species can mask niche assembly dynamics because low abundance may be a consequence of sampling bias, species phenology, or weak photo-attraction (Hamback et al. 2007, Summerville and Crist 2008). Second, because the forest stands within MMSF were historically oak-dominated, we tested for niche assembly using only moth species known to feed on oaks as larvae (see Robinson et al. 2002). These two CCAs allowed us to differentiate between niche assembly at the level of the entire community and niche assembly within what should be the dominant guild of moths across MMSF.

We used the same secondary matrix of environmental variables for both CCAs. Initially, we included the following variables in the environmental matrix: total stand basal area (m^2 ha^{-1}, calculated using only those overstory sampling plots within 100 m of each moth sample point [n=2-5]), average tree density (# ha^{-1}), importance of oak, importance of maple, importance of sassafras (*Sassafras albidum*), importance of ash (*Fraxinus* spp.), elevation (m), aspect (°), and average percentage basal area of shrubs and saplings. Importance values were calculated as the arithmetic mean of basal area, density, and frequency values across all overstory plots adjacent to a moth sampling point. For analysis, shrubs and saplings were defined as individuals with stem d.b.h. ≤10.0 cm. Sassafras importance was included as an environmental variable because its occurrence is an indicator of past disturbance (Heitzman et al. 2007, Welch et al. 2000). Ash importance was included because its long-term viability within Indiana forests is compromised by range expansion of the emerald ash borer (*Agrilus planipennis*). Basal area and density measurements were log-transformed prior to CCA to normalize distributions (Jongman et al. 1995).

Because CCA requires that all environmental variables in the final model be orthogonal, we removed correlated variables through a process of pre-screening with Spearman Rank-Correlation Analysis (McCune and Grace 2006). Five environmental variables were selected for subsequent analyses: oak importance, sassafras importance, average percentage shrub/sapling basal area, total stand basal area, and average tree density. To assess the significance of CCA ordination axes, we used the Monte Carlo simulation option within PC-ORD. This step allowed us to test the specific null hypothesis that there was no correlation between the moth species-abundance matrix and the environmental variable-site matrix (McCune and Grace 2006). We selected a conservative r^2 value (0.20) for the minimum level of species-environment correlation for bi-plot display on the CCA ordination.

Finally, we performed Mantel tests to assess the degree of spatial autocorrelation among moth communities within and among management units. As with CCA, two separate Mantel tests were generated, using all species minus singletons and doubletons and using only oak-feeding species. The overall species-abundance matrix was used to calculate community similarity among forest sites. The distance matrix consisted of Euclidean distances among each pair of sites as measured in kilometers. Finally, a third Mantel test was performed to assess whether the overstory tree community displayed significant spatial structure. As with CCA, Mantel tests were generated using PC-ORD.

RESULTS

A total of 14,270 macrolepidopteran individuals representing 277 species were sampled from MMSF in 2007 (Table 1, Appendix 1). Of these, 213 species contained total abundances >2 (i.e., were not singletons or doubletons) and 94 species were determined to be capable of feeding on oak. Most of these oak-feeding species would fit the description of host plant “generalist,” however, as host plant breadth

Table 1.—Number of macrolepidopteran species and individuals of forest Lepidoptera sampled from Morgan-Monroe State Forest, 2007.

Family	Number of species	Number of individuals
Apatelodidae	2	56
Cossidae	1	6
Drepanidae	1	37
Erebidae	67	5,138
Geometridae	72	2,008
Lasiocampidae	3	172
Limacodidae	9	72
Megalopygidae	2	114
Mimalonidae	1	1
Noctuidae	75	3,117
Nolidae	4	29
Notodontidae	28	2,724
Saturniidae	12	685
Sphingidae	6	103
Yponmeutidae	1	8
Total	277	14,270

for all but 39 oak-feeding moths exceeded two plant families. Regardless, nearly 34 percent of all of the species we sampled could be described as oak feeding, making this the largest guild of species sampled in 2007. In addition, a few species that tend not to be sampled in high abundance in oak-hickory forests of Indiana and Ohio were found, including *Zanclognatha jaccusalis* (Erebidae), *Lacosoma chiridota* (Mimalonidae), and *Anistoa virginiensis* (Saturniidae). Overall, however, most of the species sampled from MMSF are reasonably well represented in collections or have been previously reported in the literature from across Indiana, Ohio, and Kentucky.

Both of our CCAs revealed significant evidence of niche assembly in the Lepidoptera of MMSF. First, the analysis of species-environment correlations for all moth species (excluding singletons and doubletons) suggested two significant ordination axes and explained approximately 25 percent of the variance in community structure (Table 2). Sites appeared to weakly separate from one another according to management unit (Fig. 1), but variation in moth species composition within a given management unit was roughly equal to variation among management units. Three environmental variables had an r^2 >0.20: importance of oak, percentage basal area of shrubs and saplings, and log-tree density (Fig. 1).

The importance of oak loaded most significantly onto ordination axis 1 and separated a few stands in management unit 1 (which has oak importance >50 percent) from the remainder of the forest areas in MMSF (Table 3). Species associated with high values of oak importance included *Catocala micronympha* (Erebidae), *Dasylophia thyatiroides* (Notodontidae), *Crambidia pallida* (Erebidae), *Cisthene plumbea* (Erebidae), *Cosmia calami* (Noctuidae), *Besma quercivoraria* (Geometridae), and *Catocala retecta* (Erebidae). Several sites in management unit 3 had very high overstory density and thus contained moth communities different from those in units 1 or 2

Table 2.—Summary of canonical correspondence analyses (CCAs) relating moth communities to stand-level environmental variation. Two analyses were performed: (i) using all moth species sampled except singletons and doubletons and (ii) using only oak-feeding species.

Moth community	Ordination axis	Eigenvalue	Explained variance (percent)	Cumulative variance (percent)	P-value
All species (total abundance >2)	Axis 1	0.085	10.4	10.4	0.025
	Axis 2	0.074	8.8	19.2	0.044
	Axis 3	0.048	5.7	24.9	0.270
Oak-feeding species	Axis 1	0.097	10.8	10.8	0.030
	Axis 2	0.052	6.0	16.8	0.050
	Axis 3	0.027	5.0	21.8	0.340

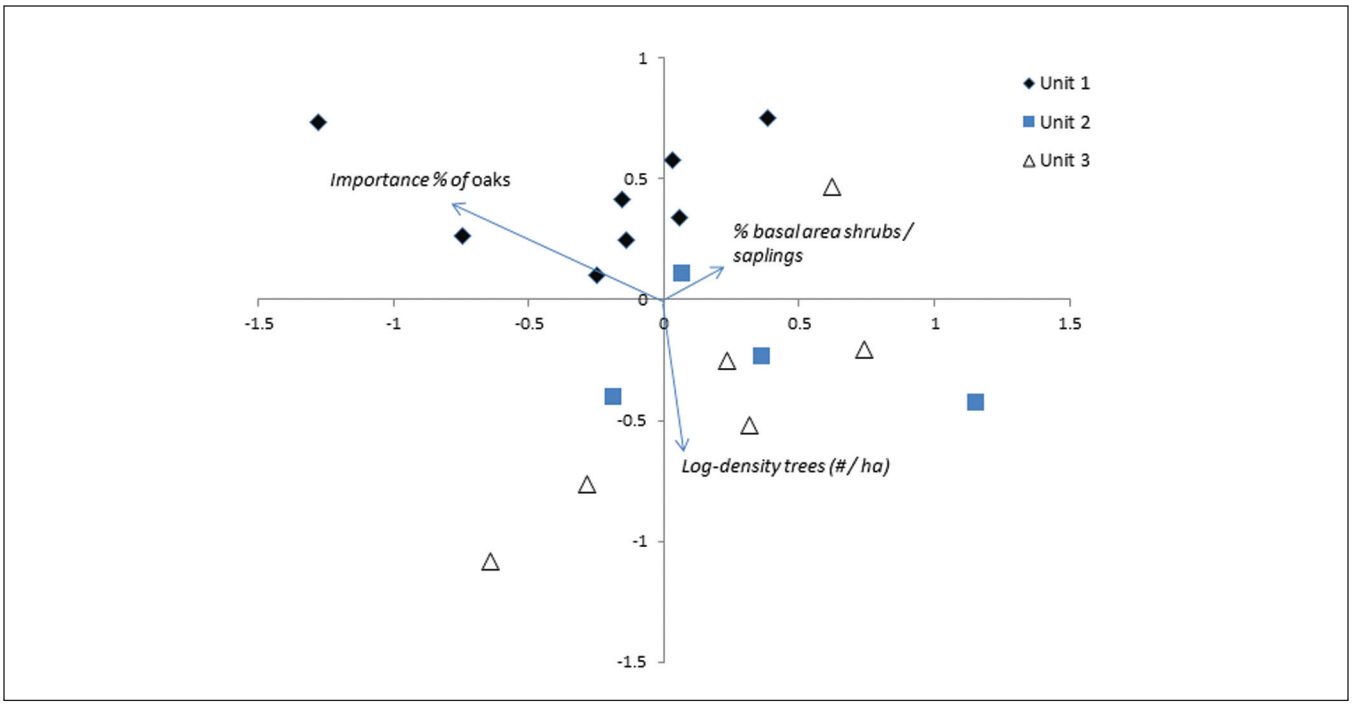

Figure 1.—Canonical correspondence analysis of 18 forest stands in MMSF and 213 moth species with total sampled abundances >2. Three environmental variables had significant r^2 values (≥0.20) with the site scores from ordination axes 1 and 2. These are depicted as joint bi-plots in ordination space.

Table 3.—Canonical coefficients derived from CCAs of all moth species with total abundance >2 sampled from Morgan-Monroe State Forest, 2007. Only the first two ordination axes were significant.

Environmental variable	Axis 1 score	Axis 2 score	Axis 3 score
% importance of oak	-0.513	0.189	0.133
% importance of sassafras	-0.002	0.151	-0.374
% basal area of shrubs and saplings	0.012	0.259	0.270
Log-tree density (# ha^{-1})	-0.258	-0.431	-0.001
Log-stand basal area (m^2 ha^{-1})	-0.270	0.040	-0.299

(Fig. 1). Species with high site scores for areas with large values of log-transformed tree density included potential management concerns such as *Malacosoma americanum* (Lasiocampidae), *Hyphantria cunea* (Erebidae), and *Datana integerrima* (Notodontidae). Sites with a high importance of oaks also tended to have a low percentage basal area of shrubs, although the partial correlation coefficient was marginal at 0.39 (Fig. 1). Several species of moths were highly correlated with sites that possessed a large value for percentage basal area in shrubs/saplings: *Digrammia ocellinata* (Geometridae), *Chlorochlamys chloroleucaria* (Geometridae), and *Hypercompe scribonia* (Erebidae). Importance of *Sassafras* and *Fraxinus* were not significant predictors of moth species composition (Table 3).

When only oak-feeding moth species were included in the analysis, our CCA explained slightly less of the total variance in species composition (21.8 percent; see Table 2). Both ordination axes 1 and 2 were significant, and the same three environmental variables were significant predictors of moth species composition (Table 4). The same species from the prior analysis attained large abundance in sites with high importance of oak, with the notable addition of most species in genus *Acronitca* (Noctuidae). The relative importance of log-transformed tree density and percentage basal area of shrubs and saplings was reversed, however (Fig. 2). Shrub and sapling basal area seemed to differentiate a couple of stands in unit 3 and one stand in unit 1 from the others, while tree density was associated with similar moth assemblages in units 2 and 3. Oak-feeding species associated with sites possessing high trunk density included *Orgyia definita* (Erebidae), *Hyphantria cunea* (Erebidae), *Natada nasoni* (Limacodidae), and *Charadra deridens* (Noctuidae). Moths preferring stands with large values of shrub and sapling basal area included host plant generalists such as species in the genera *Baileya* (Nolidae), *Hyperstrotia* (Erebidae), and *Eupithecia* (Geometridae).

Table 4.—Canonical coefficients derived from CCAs of oak-feeding moth species sampled from Morgan-Monroe State Forest, 2007. Only the first two ordination axes were significant.

Environmental variable	Axis 1 score	Axis 2 score	Axis 3 score
% importance of oak	-0.494	-0.210	0.153
% importance of sassafras	-0.034	0.059	0.006
% basal area of shrubs and saplings	0.047	-0.361	0.294
Log-tree density (# ha^{-1})	-0.243	0.273	0.315
Log-stand basal area (m^2 ha^{-1})	-0.192	0.090	0.073

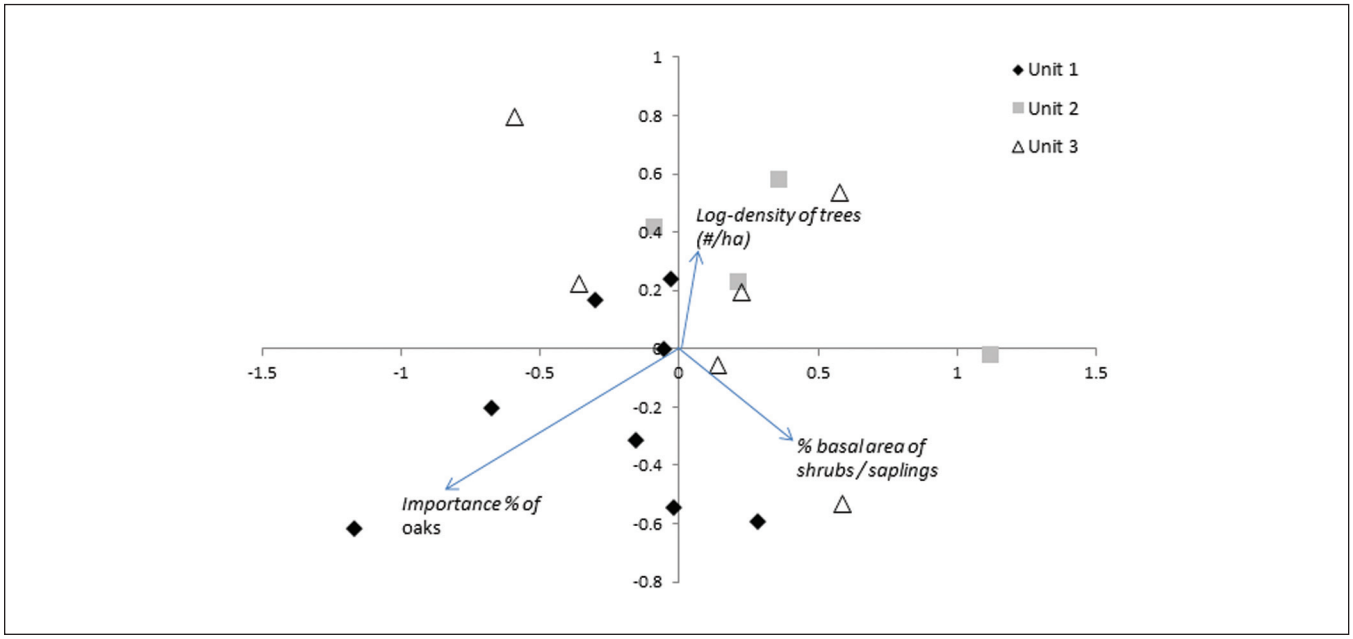

Figure 2.—Canonical correspondence analysis of 18 forest stands in MMSF and 94 oak-feeding moth species. Three environmental variables had significant r^2 values (≥0.20) with the site scores from ordination axes 1 and 2. These are depicted as joint bi-plots in ordination space.

The Mantel tests failed to detect any significant relationships between similarity in lepidopteran community composition and the linear distances between forest stands. For all moths, the relationship suggested weak spatial autocorrelation (Z = 360618, r = 0.133, P = 0.076). When the data were restricted to oak-feeders, no spatial autocorrelation was detected (Z = 318712, r = 0.098, P = 0.15). Similarly, there was no evidence of spatial dependence in the tree data from plots adjacent to moth sampling points (Z = 327654, r = 0.087, P = 0.21). Thus, spatial dependence in moth assemblages appeared less important to community structure than species sorting effects from environmental variables.

DISCUSSION

We found clear evidence that niche assembly processes are important determinants of community structure in forest macrolepidoptera. In contrast to expectation, however, the measured environmental variables explained only approximately 25 percent of the variation in species composition among the 18 forest stands. This result is very close to the variance explained using CCA to tease apart similarity in moth assemblages in the Appalachian foothills (Summerville and Crist 2002) and the Missouri oak woodlands (Forkner et al. 2006). Studies at broader spatial scales appear to have even less explanatory power (e.g., Hammond and Miller 1998). This observation prompts the question: Are niche assembly processes really minor, have studies (including this one) measured the wrong environmental variables, or are moth communities less deterministic than we assume?

Although not conducted in eastern deciduous forests of the United States, a two-decade study by Lepš et al. (1998) offers some insight into why direct effects of environmental variables on moth communities appear small. Lepš et al. demonstrated that moth communities change predictably along a seral gradient, but that turnover in species membership within a community is much more deterministic for dietary specialists. Generalist moths (i.e., those whose caterpillars feed on ≥ two plant families) have much more stochastic population fluctuations and are less predictable members of an assemblage (see Butler and Straznac 2000, Spitzer et al. 1984). Specialist moths, especially those that feed on oak, tend to form predictable assemblages in space and time (Fukumoto and Kajimara 2011, Turčáni et al. 2010). Our data from MMSF suggest that >75 percent of the species we sampled were generalists. Even within the species known to feed on oaks, 60 percent were considered generalists. Because generalist moths have larger inter-annual population fluctuations, their occurrence within a community is a product more of demographic and environmental stochasticity than of occurrence of suitable host plants (Murphy and Lill 2010, Summerville and Crist 2008).

Movement dynamics may also play a significant role in structuring moth assemblages in space, especially for microlepidoptera. In some species, dispersal assembly is a product of adult movements and mass effects (Summerville and Crist 2008), but in others it is a consequence of larval ballooning and neighborhood effects (Turčáni et al. 2010). We found little evidence of either type of dispersal assembly process for these species of macrolepidoptera.

Disturbance and environmental variables associated with disturbance are also critical determinants of moth community structure (e.g., Broome et al. 2011), and we attempted to incorporate indirect assessments of past disturbance by building Sassafras importance and tree density into our CCA. Disturbance also leaves a lasting impact on the forest understory, and some studies have suggested that forest understory vegetation is as important as overstory stand composition in generating patterns of macrolepidopteran biodiversity (Summerville and Crist 2008). Interestingly, we failed to sample many species that are restricted to woodland forbs or graminoids across MMSF, so it is possible that if these species used to be part of the forest community, they have already been lost (Holl 1996).

Placed within the context of current metacommunity theory, moth assemblages do appear to be far less a consequence of niche assembly processes than a function of a large number of independent, and as yet unexplained, effects. Of course, this conclusion should be placed within the context of an important caveat: the predictability of a forest moth assemblage will generally be low, except when disturbances significantly alter overstory composition. Whether as part of natural gap dynamics or due to timber extraction, forest disturbance alters forest microclimate, facilitates shifts in stand composition, and allows moth species the opportunity to colonize new habitats (Summerville et al. 2009).

If a previously oak-dominated forest is logged and recovers as mixed beech (*Fagus*)-maple, then a new assemblage lacking oak specialists will likely replace it. Because between 50 and 60 percent of oak-feeding macrolepidoptera have been documented to feed upon maple or beech, however, the mass extinction of lepidopterans may not occur. Of course, documenting that moth larvae will feed on foliage is not equivalent to demonstrating that the foliage is ultimately suitable for sustaining viable populations (see Matsuki et al. 2011). Landscape-level loss of oak from forest stands can homogenize forest moth assemblages even when species composition within individual tree crowns is the result of random ovipositions by generalist feeding species (Broome et al. 2011, Holl 1996, Summerville and Crist 2008).

Forest managers can take two main points away from our analyses here: (1) addition or subtraction of tree species from a stand will tend to add and subtract specialist macromoth species and (2) substantial losses in moth species from the regional metacommunity can largely be avoided by focusing on maintaining stand heterogeneity at the landscape level. The former point should empower the forest manager to predict how loss of tree species will impact moth species with narrow niches, and the latter suggests that stand management through timber harvesting can proceed as long as care is given to the broader forest landscape.

Ongoing recruitment challenges of oak and the continued replacement of oak and hickory with maple and beech suggest that the Central Hardwood Forest faces an extinction debt of oak-feeding lepidopterans (sensu Sang et al. 2010). The looming feedback loop between climate change on a global scale and increased irruptions of defoliating herbivores suggests that broad-scale stand homogeneity is creating a template for extreme outbreak events of some pest Lepidoptera (Clark et al. 2010, Dymond et al. 2010, Hennigar and MacLean 2010). Should crown defoliation exacerbate shifts in tree species composition away from the current pattern, loss of some lepidopteran species from all eastern deciduous forests might become troublingly easy to predict.

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APPENDIX 1.

Lepidoptera species sampled from MMSF in 2007. Species are arranged by taxonomic family. Nomenclature follows Hodges et al. (1983) with revisions to the Geometroidea after Ferguson (2008) and to the Noctuoidea following LaFontaine and Schmidt (2010).

Species	Author	Family	Species	Author	Family
Apatelodes torrefacta	J.E. Smith	Apatelodidae	*Panopoda carneicosta*	Gn.	Erebidae
Ocleclostera angelica	Grt.	Apatelodidae	*Panopoda rufimargo*	Hbn.	Erebidae
Prionoxystus robiniae	Peck	Cossidae	*Parallelia bistriaris*	Hbn.	Erebidae
Oreta rosea	Wlk.	Drepanidae	*Phalaenostola larentioides*	Grt.	Erebidae
Allotria elonympha	Hbn.	Erebidae	*Plusiodonta compressipalps*	Gn.	Erebidae
Apantesis vittata	F.	Erebidae	*Pyrrharctia isabella*	J.E. Smith	Erebidae
Bleptina caradrinalis	Gn.	Erebidae	*Renia discoloralis*	Gn.	Erebidae
Caenurgina erechtea	Cram.	Erebidae	*Renia flavipunctalis*	Gey.	Erebidae
Catocala amica	Hbn.	Erebidae	*Renia sobrialis*	Wlk.	Erebidae
Catocala ilia	Cram.	Erebidae	*Scolecocapma liburna*	Gey.	Erebidae
Catocala innubens	Gn.	Erebidae	*Spilosoma latipennis*	Stretch	Erebidae
Catocala micronympha	Gn.	Erebidae	*Spilosoma virginica*	F.	Erebidae
Catocala nebulosa	Edw.	Erebidae	*Virbia opella*	Grt.	Erebidae
Catocala obscura	Stkr.	Erebidae	*Zale lunata*	Drury	Erebidae
Catocala palaeogama	Gn.	Erebidae	*Zale minerea*	Gn.	Erebidae
Catocala residua	Grt.	Erebidae	*Zanclognatha cruralis*	Gn.	Erebidae
Catocala retecta	Grt.	Erebidae	*Zanclognatha jacchusalis*	Wlk.	Erebidae
Catocala ultronia	Hbn.	Erebidae	*Zanclognatha laevigata*	Grt.	Erebidae
Catocala vidua	J.E. Smith	Erebidae	*Zanglognatha obscuripennis*	Grt.	Erebidae
Cisseps fulvicollis	Hbn.	Erebidae	*Anacamptodes defectaria*	Gn.	Geometridae
Cisthene packardii	Grt.	Erebidae	*Anacamptodes ephyraria*	Wlk.	Geometridae
Cisthene plumbea	Stretch	Erebidae	*Anacamptodes humaria*	Gn.	Geometridae
Clemensia albata	Pack	Erebidae	*Anavitrinelia pampinaria*	Gn.	Geometridae
Crambidia lithosioides	Dyar	Erebidae	*Besma quercivoraria*	Gn.	Geometridae
Crambidia pallida	Pack	Erebidae	*Biston betularia*	L.	Geometridae
Cycnia inopinatus	H. Edw.	Erebidae	*Callizzia amorata*	Pack.	Geometridae
Cycnia tenera	Hbn.	Erebidae	*Campaea perlata*	Gn.	Geometridae
Dasychira basiflava	Pack.	Erebidae	*Cepphis armataria*	H. & S.	Geometridae
Dasychira vagans	B. & McD.	Erebidae	*Cyclophora pendulinaria*	Gn.	Geometridae
Euchaetes egle	Drury	Erebidae	*Digrammia ocellinata*	Gn.	Geometridae
Grammia figurata	Drury	Erebidae	*Ectropis crepuscularia*	D. & S.	Geometridae
Grammia virgo	L.	Erebidae	*Ennomos subsignaria*	Hbn.	Geometridae
Halysidota tessellaris	J.E. Smith	Erebidae	*Epimecis hortaria*	F.	Geometridae
Haploa clymene	Brown	Erebidae	*Erastria coloraria*	F.	Geometridae
Haploa lecontei	Guér.-Méneville	Erebidae	*Eubaphe mendica*	Wlk.	Geometridae
Haploa reversa	Stretch	Erebidae	*Euchlaena amoenaria*	Gn.	Geometridae
Hypercompe scribonia	Stoll	Erebidae	*Euchlaena irraria*	B. & McD.	Geometridae
Hyperstrotia pervertens	B. & McD.	Erebidae	*Euchlaena obtusaria*	Hbn.	Geometridae
Hyphantria cunea	Drury	Erebidae	*Euchlaena pectinaria*	D. & S.	Geometridae
Hypoprepia fucosa	Hbn.	Erebidae	*Euchlaena tigrinaria*	Gn.	Geometridae
Idia aemula	Hbn.	Erebidae	*Eulithis diversilineata*	Hbn.	Geometridae
Idia americalis	Gn.	Erebidae	*Eupithecia miserulata*	Grt.	Geometridae
Idia lubricalis	Gey.	Erebidae	*Eutrapela clemataria*	J.E. Smith	Geometridae
Idia rotundalis	Wlk.	Erebidae	*Haematopis grataria*	F.	Geometridae
Lophocampa caryae	Hodges	Erebidae	*Heterophleps triguttaria*	H.-S	Geometridae
Lymantria dispar	L.	Erebidae	*Hydrelia inornata*	Hulst	Geometridae
Macrochilo absorptalis	Wlk.	Erebidae	*Hypagyrtis unipunctata*	Haw.	Geometridae
Metalectra richardsi	Hbn.	Erebidae	*Iridopsis larvaria*	Gn.	Geometridae
Orgyia definita	Pack.	Erebidae	*Itame evagaria*	Hulst	Geometridae
Orgyia leucostigma	J.E. Smith	Erebidae	*Itame pustularia*	Hulst	Geometridae
Palthis asopialis	Gn.	Erebidae	*Itame subcessaria*	Hulst	Geometridae

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APPENDIX 1 (continued).

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Species	Author	Family	Species	Author	Family
Lambdina pellucidaria	G. & R.	Geometridae	*Acronicta americana*	Harr.	Noctuidae
Lomographa vestaliata	Gn.	Geometridae	*Acronicta exilis*	Grt.	Noctuidae
Lytrosis unitaria	H.-S.	Geometridae	*Acronicta fragilis*	Gn.	Noctuidae
Macaria aemulataria	Wlk.	Geometridae	*Acronicta grisea*	Wlk.	Noctuidae
Macaria bisignata	Wlk.	Geometridae	*Acronicta haesitata*	Grt.	Noctuidae
Macaria continuata	Wlk.	Geometridae	*Acronicta hamemelis*	Grt.	Noctuidae
Macaria promiscuata	Fgn.	Geometridae	*Acronicta hasta*	Gn.	Noctuidae
Macariamultilineata	Pack.	Geometridae	*Acronicta impleta*	Wlk.	Noctuidae
Melanolophia canadaria	Gn.	Geometridae	*Acronicta inclara*	Sm.	Noctuidae
Mellilla xanthometata	Wlk.	Geometridae	*Acronicta interrupta*	Gn.	Noctuidae
Metarranthis hypocharia	H.-S.	Geometridae	*Acronicta laetifica*	Sm.	Noctuidae
Nacophora quernaria	J.E. Smith	Geometridae	*Acronicta lithospila*	Grt.	Noctuidae
Nemoria bistriaria	Hbn.	Geometridae	*Acronicta modica*	Wlk.	Noctuidae
Orthonama centrostrigaria	Woll.	Geometridae	*Acronicta morula*	G. & R.	Noctuidae
Orthonama obstipata	F.	Geometridae	*Acronicta oblinita*	J. E. Smith	Noctuidae
Pero honestaria	Wlk.	Geometridae	*Acronicta ovata*	Grt.	Noctuidae
Plagodis alcoolaria	Gn.	Geometridae	*Acronicta retardata*	Wlk.	Noctuidae
Plagodis fervidaria	H.-S.	Geometridae	*Acronicta spinigera*	Gn.	Noctuidae
Plagodis phlogosaria	Gn.	Geometridae	*Acronicta tristis*	Sm.	Noctuidae
Plagodis serinaria	H.-S.	Geometridae	*Agrotis ipsilon*	Hufn.	Noctuidae
Probole amicaria	H.-S.	Geometridae	*Agrotis venerabilis*	Wlk.	Noctuidae
Probole nyssaria	Gn.	Geometridae	*Anagrapha falcifera*	Kby.	Noctuidae
Prochoerodes transversata	Drury	Geometridae	*Athetis tarda*	Gn.	Noctuidae
Protoboarmia porcelaria	Gn.	Geometridae	*Autographa precationis*	Gn.	Noctuidae
Scopula inductata	Gn.	Geometridae	*Balsa malana*	Fitch	Noctuidae
Scopula limboundata	Haw.	Geometridae	*Callopistria mollissima*	Gn.	Noctuidae
Sicya macularia	Harr.	Geometridae	*Cerma cerintha*	Tr.	Noctuidae
Synchlora aerate	F.	Geometridae	*Charadra deridens*	Gn.	Noctuidae
Tetracis crocallata	Gn.	Geometridae	*Chytonix palliatricula*	Gn.	Noctuidae
Trigrammia quadrinotaria	H.-S.	Geometridae	*Colocasia flavicornis*	Sm.	Noctuidae
Triphosa haesitata	Gn.	Geometridae	*Condica sutor*	Gn.	Noctuidae
Xanthorhoe ferrugata	Cl.	Geometridae	*Condica vecors*	Gn.	Noctuidae
Xanthorhoe lacustrata	Gn.	Geometridae	*Elaphria grata*	Hbn.	Noctuidae
Heteropacha rileyana	Harv.	Lasiocampidae	*Elaphria versicolor*	Grt.	Noctuidae
Malacosoma americanum	F.	Lasiocampidae	*Eudryas grata*	F.	Noctuidae
Malacosoma disstria	Hbn.	Lasiocampidae	*Euplexia benesimilis*	McD.	Noctuidae
Isa textula	H.-S.	Limacodidae	*Hypena scabra*	F.	Noctuidae
Lithacodes fasciola	H.-S.	Limacodidae	*Lacinipolia renigera*	Steph.	Noctuidae
Natada nasoni	Grt.	Limacodidae	*Marimatha nigrofimbria*	Gn.	Noctuidae
Packardia geminata	Pack.	Limacodidae	*Melanchra adjuncta*	Gn.	Noctuidae
Parasa chloris	H.-S.	Limacodidae	*Morrisonia latex*	Gn.	Noctuidae
Phyllodesma americana	Harris	Limacodidae	*Mythimna unipuncta*	Haw.	Noctuidae
Prolimacodes badia	Hbn.	Limacodidae	*Noctua pronuba*	L.	
Tortricidia flexusoa	Grt.	Limacodidae	*Noctuidae*		
Tortricidia testacea	Pack.	Limacodidae	*Ochropleura implecta*	LaFontaine	Noctuidae
Lagoa crispate	Pack.	Megalopygidae	*Ogdoconta cinereola*	Gn.	Noctuidae
Norape ovina	Sepp	Megalopygidae	*Orthodes majuscula*	Butler	Noctuidae
Lacosoma chiridota	Grt.	Mimallonidae	*Peridroma saucia*	Hbn.	Noctuidae
“Orthodes” detracta	Wlk.	Noctuidae	*Phosphila miselioides*	Hbn.	Noctuidae
Abagrotis alternata	Grote	Noctuidae	*Polygrammate hebraeicum*	Hbn.	Noctuidae
Acronicta afflicta	Grt.	Noctuidae	*Protodeltote muscosula*	Gn.	Noctuidae

(Appendix 1 continued on next page)

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Species	Author	Family	Species	Author	Family
Protolampra brunneicollis	Grt.	Noctuidae	*Oligocentria lignicolor*	Wlk.	Notodontidae
Raphia frater	Grt.	Noctuidae	*Oligocentria semirufescens*	Wlk.	Notodontidae
Spodoptera frugiperda	J.E. Smith	Noctuidae	*Peridea angulosa*	J.E. Smith	Notodontidae
Spodoptera ornithogalli	Gn.	Noctuidae	*Peridea basitriens*	Wlk.	Notodontidae
Sympistis infixa	Grote	Noctuidae	*Pheosia rimosa*	Pack.	Notodontidae
Baileya australis	Grt.	Nolidae	*Schizura concinna*	J.E. Smith	Notodontidae
Baileya dormitans	Gn.	Nolidae	*Schizura ipomoeae*	Doubleday	Notodontidae
Baileya ophthalmica	Gn.	Nolidae	*Schizura unicornis*	J.E. Smith	Notodontidae
Meganola minuscula	Zell.	Nolidae	*Symmerista albifrons*	J.E. Smith	Notodontidae
Clostera albosigma	Fitch	Notodontidae	*Actias luna*	L.	Saturniidae
Clostera inclusa	Hbn.	Notodontidae	*Anisota stigma*	F.	Saturniidae
Dasylophia anguina	J.E. Smith	Notodontidae	*Anisota virginiensis*	Drury	Saturniidae
Dasylophia thyatiroides	Wlk.	Notodontidae	*Antheraea polyphemus*	Cram.	Saturniidae
Datana angusii	G. & R.	Notodontidae	*Automeris io*	F.	Saturniidae
Datana integerrima	G. & R.	Notodontidae	*Callosamia angulifera*	Wlk.	Saturniidae
Datana ministra	Drury	Notodontidae	*Callosamia promethea*	Drury	Saturniidae
Datana perspicua	G. & R.	Notodontidae	*Citheronia regalis*	F.	Saturniidae
Ellida caniplaga	Wlk.	Notodontidae	*Dryocampa rubicunda*	F.	Saturniidae
Gluphisia septentrionis	Wlk.	Notodontidae	*Eacles imperialis*	Drury	Saturniidae
Heterocampa guttivitta	Wlk.	Notodontidae	*Hyalophora cercropia*	L.	Saturniidae
Heterocampa obliqua	Pack.	Notodontidae	*Sphingicampa bicolor*	Harr.	Saturniidae
Heterocampa subrotata	Harv.	Notodontidae	*Ceratomia undulosa*	Wlk.	Sphingidae
Heterocampa umbrata	Wlk.	Notodontidae	*Darapsa Myron*	Cram.	Sphingidae
Hyperaeschra georgica	H.-S.	Notodontidae	*Laothoe juglandis*	F.	Sphingidae
Lochmaeus bilineata	Pack.	Notodontidae	*Pachysphinx modesta*	Harr.	Sphingidae
Macrurocampa marthesia	Cram.	Notodontidae	*Paonias excaecatus*	J.E. Smith	Sphingidae
Misogada unicolor	Pack.	Notodontidae	*Paonias myops*	J.E. Smith	Sphingidae
Nadata gibbosa	J.E. Smith	Notodontidae	*Atteva punctella*	Cram.	Yponmeutidae