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## Contrasting effects of habitat quantity and quality on moth communities in fragmented landscapes

Keith S. Summerville and Thomas O. Crist

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Habitat loss is commonly identified as a major threat to the loss of global biodiversity. In this study, we expand on our previous work by addressing the question of how lepidopteran species richness and composition vary among remnants of North American eastern deciduous forest located within agricultural or pastoral landscapes. Specifically, we tested the relative roles of habitat quantity (measured as stand area and percent forest in the greater landscape) and habitat quality (measured as tree species diversity) as determinants of moth species richness. We sampled > 19 000 individuals comprising 493 moth species from 21 forest sites in two forested ecoregions. In the unglaciated Western Allegheny Plateau, the species richness of moths with woody host plants diminished as forest stand size and percent forest in the landscape decreased, but the total species richness and abundance of moths were unaffected by stand size, percent forest in the landscape, or tree species diversity. In contrast, the overall species richness and abundance of moths in the glaciated North Central Tillplain were affected primarily by tree species diversity and secondarily by forest size. Higher tree species diversity may reduce species loss from smaller forest stands, suggesting that small, diverse forests can support comparable numbers of species to those in less diverse, large stands. Smaller forests, however, contained a disproportionate number of moth species that possess larvae known to feed on herbaceous vegetation. Thus, although woody plant feeding moths are lost from forests with changes in stand area, new species appear capable of recolonizing smaller fragments from the surrounding habitat matrix. Our study further suggests that when species replacement occurs, local patch size and habitat quality may be more important than landscape context in determining the community structure of forest Lepidoptera.

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Habitat loss is widely regarded as the single greatest threat facing forest plant and animal communities worldwide (Ehrlich 1988, Fahrig 2001). Indeed, the effects of forest loss on population structure have been documented for many species (e.g. Powell and Powell 1987, Klein 1989, Laurance et al. 2002). Field experiments, however, have suggested that the responses of some insect communities to habitat loss may be idiosyncratic (Robinson et al. 1992, Debinski and Holt 2000). The lack of predictable community responses to habitat

loss may be partly attributable the fine spatial scale and short duration of field experiments, which fail to capture the complex interactions that occur when a large patch of habitat is broken into smaller units (Harrison et al. 1995). As habitat is lost from a forested landscape, a number of variables likely influence whether insect species are gained or lost from a community, including the total habitat area, isolation, floristic heterogeneity, and the structure of the intervening matrix (Holt 1993, Wiens 1994, Collinge 1996, Gibbs and Stanton 2001).

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Historically, the dominant theoretical approach for predicting the numbers of species found in habitat patches differing in size relied on the theory of island biogeography. Island biogeographic theory predicts that species occurrences within patches are regulated by extinction-colonization dynamics (MacArthur and Wilson 1967). Several studies have provided evidence that the size of forest "islands" within an agricultural or pasture matrix is correlated with both extinction probabilities and emigration rates of many taxa (Thomas et al. 1998). The most commonly observed patterns are that smaller patches of forest habitat meet the minimum area requirements of fewer species, or that individuals emigrate from smaller forest patches more frequently than larger ones (e.g. Usher and Keiller 1998). The utility of the island biogeographic approach to predicting the effects of habitat loss on insect communities may be limited, however, because it fails to directly acknowledge the role of the surrounding matrix in influencing dispersal probabilities or contributing new species to the focal community (Holt 1993, Hanski and Simberloff 1997).

Development of metapopulation theory and landscape ecology greatly enhanced our appreciation for the role of matrix habitat as a determinant of population and community structure among multiple habitat patches (Wiens 1997, Luoto et al. 2001). For forest insects, changes in species richness and community structure may be partly buffered following habitat loss if the proportion of suitable habitat within the surrounding landscape remains high or species are highly vagile (Ricketts et al. 2001, Tscharntke et al. 2002). Furthermore, overall insect species diversity within a patch may increase or be unaffected following habitat loss if opportunistic plant species and their associated herbivores colonize a focal patch from the surrounding matrix (i.e. species replacement; cf. Summerville and Crist 2003). The current literature, however, remains divided regarding the relative influence of landscape structure in determining insect species richness or community composition at large spatial scales (e.g. Atauri and de Lucio 2001, Bailey et al. 2002, Tscharntke et al. 2002).

Significant effects of either the area of forest habitat patches or the proportion of forest habitat within the greater landscape would provide evidence for the importance of habitat quantity on insect community structure, albeit at different spatial scales. Summerville and Crist (2003) previously demonstrated that large patches of forest support a slightly greater number of moth species, but our previous study considered only a small range of forest sizes and did not directly consider how landscape structure affects change in forest moth communities. Habitat quality, however, may be as important as habitat quantity in predicting insect community structure (Thomas and Kunin 1999, Summerville and Crist 2001, Fleishman et al. 2002), but "quality" has

proven difficult for ecologists to objectively quantify in the field (Moilanen and Hanski 1998). For phytophagous forest insect communities, habitat quality may be estimated by the composition or diversity of plants occurring within a given patch (Fleishman et al. 2002). In forests, variation in plant diversity is correlated with changes in both insect diversity and community composition (Southwood et al. 1979, Summerville and Crist 2002). The role of forest habitat quality in ameliorating negative effects of habitat loss is an important and unanswered question, particularly if improvements in the habitat quality of smaller woodlots render them functionally equivalent to large forest tracts for the preservation of species diversity.

In this study, we expand on Summerville and Crist (2003) by more specifically examining how habitat loss affects lepidopteran species richness and community structure in eastern deciduous forests of North America. The Lepidoptera is among the most speciose and taxonomically tractable groups of forest insects, and have important functional roles as selective herbivores, pollinators, detritivores, and prey for migratorial passerines. Therefore, the Lepidoptera comprise an important fauna for understanding how changes in forest quantity and quality interact to influence species richness and community structure. We tested for the relative importance forest stand size, percent forest in the greater landscape, and tree species diversity as predictors of moth species richness sampled from 21 forest stands in two ecoregions. We expected to find a significant effect of forest stand area if moths respond primarily to local habitat loss as predicted by the species-area relationship. A significant and positive effect of habitat quantity in the surrounding landscape on forest moth diversity would suggest that the effects of local habitat loss on moth communities could be ameliorated by recolonization from surrounding forest patches. Finally, a positive effect of tree species diversity on moth communities would suggest that changes in habitat quality following habitat loss are important for predicting lepidopteran species richness and composition in fragmented landscapes.

## Methods

### Site descriptions

This study was conducted from May to August 2001 in two of Ohio's largest ecoregions: the Western Allegheny Plateau (WAP) and the North-Central Till Plain (NCT) (Fig. 1). The boundaries of these two ecoregions roughly correspond to the Pleistocene glacial boundaries in Ohio. The WAP largely escaped Pleistocene glaciation while the NCT was exposed to significant glacial scouring (Anon. 1999b). Forests in the unglaciated

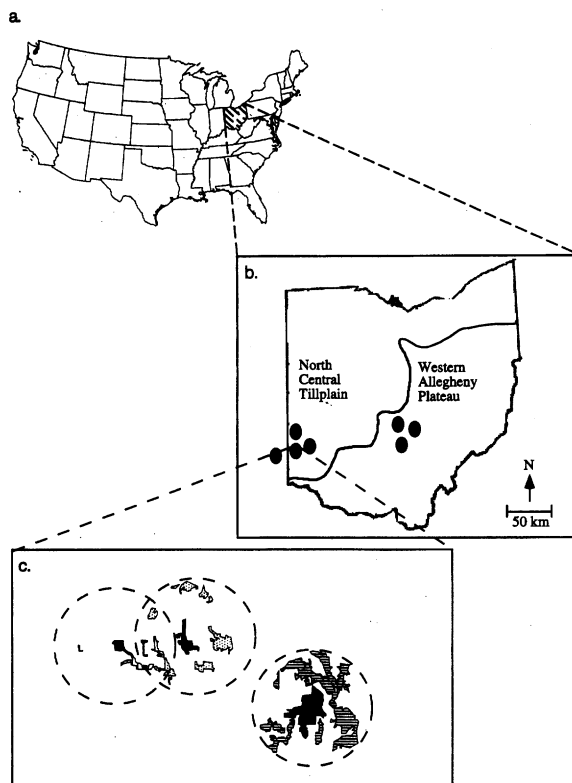


Fig. 1. a) Map of United States of America. Ohio is shown with cross-hatching. b) Moth sampling was conducted in two ecoregions within Ohio, the unglaciated Western Allegheny Plateau (WAP) and the historically glaciated North Central Tillplain (NCT). The line demarcates the approximate boundary of Pleistocene glaciation. Within both ecoregions, each ● represents one cluster of a small-, medium-, and large-sized forest site. WAP sites are centered on 39°35.4'N, 82°36.9'W, NCT sites are centered on 39°30.8'N, 84°42.6'W. c) Detail of a single cluster of forest fragments in the NCT as analyzed in ArcView GIS. Forest patches in which moths were sampled are shown in black. The amount and spatial arrangement of additional forest habitat in the surrounding landscape (1 km dashed circle around each forest stand) is also shown.

WAP occur on variable topography (steep slopes and narrow drainages) with a parent material composed of non-calcareous shales and other conglomerates (e.g. Waverly and Pottsville shales, see Boerner and Kooser 1989). In contrast, forests in the glaciated NCT developed on a more rolling topography underlain by fine glacial till and limestone bedrock. Braun (1961) described the predominant forest association of the WAP as mixed mesophytic and compared this to the less diverse beech-maple association commonly encountered in the NCT.

In 2001, we sampled Lepidoptera from 12 forest sites in the glaciated NCT and 9 forest sites in the unglaciated WAP. Forest sites were selected based on three suitability criteria: stand size, forest age, and tree composition. First, we selected sites that varied in area (range = 2–250 ha

in each ecoregion). Second, we restricted site selection to those forest tracts that contained trees > 60 yr old to minimize the effects of forest age on moth community structure (Summerville and Crist 2002). Finally, to control the effects of topographic heterogeneity on moth communities, we focused our study on upland forests within each of the two ecoregions. Forest patches in the historically glaciated NCT primarily occur in a matrix dominated by row crops (corn, soybeans), while forest patches in the unglaciated WAP tend to be interspersed in a matrix of old field and pasture habitat. Owing to its more severe topography and poor soils, the WAP also has a much higher regional forest cover, compared to the agriculturally productive NCT. Summerville and Crist (2003) provide a more thorough description of upland forest communities within each ecoregion.

## Experimental design

In the center of each forest site, we designated a 1-ha stand for moth sampling and erected a single blacklight trap station in the center of each stand. A trap station consisted of a plywood platform elevated by a 1.5-m steel pipe. We sampled Lepidoptera using 12 W universal blacklight traps powered by 12 V gel batteries. Blacklight traps are widely considered to be the standard technique for sampling moth communities, although the method is biased toward collecting phototactic species (Southwood 1978). Summerville and Crist (2002) discuss other limitations of blacklight trapping for assessing the richness of forest moth species.

We sampled Lepidoptera during June (early) and August (late) 2001 to accommodate phenological variation in moth community composition. In temperate forest systems, these months also correspond to peaks in species richness (Thomas and Thomas 1994). To standardize the hours of trap operation, a consistent sampling interval was used in both the early and late seasons (19:30–06:00 EDT). Because weather has a significant effect on moth flight behavior and light-trap efficiency, we sampled only on nights when minimum temperature was 15.5–17.5°C, there was no precipitation, and ambient moonlight was low (Yela and Holyoak 1997).

We conducted three trapping rotations within each ecoregion during both early and late seasons. Each trapping rotation consisted of a single trap night within each forest site (12 NCT sites, 9 WAP sites). On any given trap night, one cluster of three forest sites was randomly selected and one blacklight trap was placed in each. We determined clusters a priori based on the spatial proximity of the sites to one another to reduce travel time during trap set-up. Within a sampling rotation, site clusters were randomly selected, so each

cluster was only sampled once in a given rotation. Overall, a total of 126 samples were collected in early and late seasons combined, and despite the meteorological restrictions of sampling, we completed each full rotation of trapping in 7–9 d.

Collected specimens were frozen after trap processing to facilitate curation and identification. We identified individuals to species when possible, using available taxonomic keys and vouchered specimens in museum collections (see Summerville and Crist 2003 for citations of our identification literature). Recognized experts verified or performed specimen determinations of Tortricidae, Pyralidoidea, and Oecophoridae. We did not attempt to determine specimens of several poorly known microlepidopteran superfamilies [Gelechoidea (exclusive of the oecophorids), Tineoidea, Nepticuloidea, and Incurvarioidea]. We assigned moth species to three general feeding guilds based upon plant life form or other favored larval host types: 1) woody plant feeders; 2) herbaceous plant feeders, and 3) other feeders, including detritivores and fungivores (see Summerville and Crist 2002, 2003). Species lacking published life histories were excluded from guild classification.

Measuring habitat quantity

We calculated two measures of habitat quantity for each site: total patch area and percent suitable forest habitat in the surrounding landscape using ArcView GIS 3.2 for

Windows (Anon. 1999a) and orthodigital aerial photographs (Table 1). The surrounding landscape was delimited as a 1 km radius surrounding the edge of each forest stand (Fig. 1). We selected a 1 km radius to define the “landscape” because 1) this distance may approximate an upper limit to maximum dispersal distances of many moth species (e.g. Nieminen 1986, Doak 2000, Ricketts et al. 2001), and 2) studies that model lepidopteran dispersal typically use the negative exponential function, which suggests that dispersal > 1 km is rare (Thomas et al. 1998). Some moth species, such as *Agrotis ipsilon*, have been demonstrated to fly much greater distances, so our definition of landscape will necessarily underestimate habitat quantity for highly vagile species (Showers et al. 1993 and citations within). We defined “suitable” forest cover based on coarse physiognomic similarity between a forest patch and our study sites. Thus, woodlots identified with mature or secondary successional woodland were considered similar to our study sites, but land cover such as open juniper woodland, orchards, or conifer plantations were not included. Forest cover comprised by our focal patches was also not included in estimates of percent forest cover in the greater landscape. Because a simple measure such as percent cover of forest in the landscape weights all patches of forest equally regardless of their isolation from the focal patch (Moilanen and Nieminen 2002), we also calculated availability of forest habitat in the landscape as recommended by Hanski et al. (1994), where the isolation of the focal patch is determined as  $I_i = \log_{10} \sum A_j \cdot e^{(-D_{ij})}$ . Here,  $I_i$  is the isolation of the focal

Table 1. Habitat variables associated with 21 forest sites sampled in 2001. A total of 9 sites were studied in the Western Allegheny Plateau (WAP), while 12 sites were studied in the North Central Tillplain (NCT).

Region	Site name	Area (ha)	Forest cover in landscape (%)	Tree species diversity <sup>a</sup>	Isolation <sup>b</sup>
WAP	Clear Creek MetroPark	289.0	84.9	5.59	6.89
	Crane Hollow Preserve	180.9	82.2	8.61	6.80
	Phinney Forest	93.5	84.3	6.84	6.71
	Wahkeena Nature Preserve	72.8	53.4	2.25	6.38
	Rockbridge Nature Preserve	89.8	38.3	5.09	6.34
	Klinger Woodlot	22.6	29.3	7.06	6.03
	Windy Hills Woodlot	3.8	38.5	4.97	6.00
	Ridge-Laurel Woodlot	1.7	56.2	7.69	6.20
	Fairview Farms Woodlot	6.9	12.5	3.94	5.43
NCT	Hueston Woods State Park	88.9	39.1	3.45	6.71
	Pater Lake Wildlife Area	230.6	37.1	9.01	6.21
	Brookville Reservoir Park	118.2	31.1	7.65	6.09
	Western Woods Natural Area	68.0	25.7	4.41	6.05
	Jericho Nature Preserve	11.1	4.8	7.41	5.14
	Bittner Woodlot	38.2	15.0	5.52	5.58
	McClure Woodlot	58.7	16.5	3.24	5.70
	Gregg Woodlot	29.5	10.4	3.70	5.27
	Ecology Research Center	4.6	30.5	2.88	6.00
	Herrmann Woodlot	9.6	6.3	5.70	5.12
	Drake Woodlot	1.9	10.0	3.06	3.32
	Kramer Woodlot	5.2	38.6	3.27	6.18

<sup>a</sup> calculated as Simpson’s index of diversity for trees sampled in a 50 × 50 m quadrat centered on each blacklight trap station within forest stands.

<sup>b</sup> determined as  $I_i = \log_{10} \sum A_j \cdot e^{(-D_{ij})}$  (see Hanski et al. 1994).

patch,  $A_j$  is the area of habitat patch  $j$  (in  $m^2$ ) occurring within 1-km of the study site,  $D_{ij}$  is the minimum edge-to-edge distance between the focal patch  $i$  and forest fragment  $j$ .

## Measuring habitat quality

Habitat quality has proven difficult for ecologists to quantify in the field, partly because, for many species, “quality” is subjectively assigned according to human perception (Summerville and Clappitt 1999). For phytophagous insect communities, however, habitat quality may be estimated by the diversity of host plants occurring within a given patch (Southwood et al. 1979, Summerville and Crist 2002), although questions remain regarding whether plant diversity directly determines herbivore species diversity at regional scales (Hawkins and Porter 2003). Therefore, in May and June 2001, we sampled the tree communities of all 21 forest stands using a  $50 \times 50$  m quadrat centered on the blacklight trapping station. Within the  $50 \times 50$  m quadrat, we determined the species richness and abundance of trees and saplings with a minimum diameter at breast height of 10.0 cm. Tree species diversity was determined using the Simpson index, which allowed us to measure the extent to which a given forest stand was dominated by a single species of tree (Table 1).

## Testing for effects of habitat quantity and tree species diversity on lepidopteran species richness

We tested for the effects of forest stand area, % forest in the landscape, and tree species diversity on moth species richness and abundance using multiple regression (SAS PROC REG, Anon. 2000). Each independent variable was checked for normality prior to regression (Phillipi 1993), and forest stand area was log-transformed prior to analyses to account for problems of heteroscedasticity. We pooled species richness data between early and late seasons to produce aggregate values for total species richness and species richness of woody plant feeders. Furthermore, we screened our four independent variables for significant collinearity a priori using Pearson’s product-moment correlations (PROC CORR, Anon. 2000). Percent forest cover within 1 km of the study site and Hanski et al.’s (1994)  $I_i$  metric proved to be significantly intercorrelated ( $r = 0.62$ ,  $p < 0.05$ ). Thus, for simplicity, we used simple percent forest cover as our measure of habitat quantity at the landscape scale rather than Hanski et al.’s (1994) measure of patch isolation. Separate regressions were performed for each ecoregion using total moth species richness and species richness of moths with larvae that feed on trees (woody plant feeders) as dependent variables. In addition, for the

WAP ecoregion, forest area and percent forest cover in the landscape were significantly intercorrelated ( $r = 0.74$ ,  $p < 0.01$ ), and we ran separate regression models using either forest area or percent forest cover for this ecoregion. Results from regressions on moth data from each season treated separately were qualitatively similar to the pooled data. Furthermore, previous studies suggest that although species richness varies with season, the effect of forest patch size on moth communities was similar across seasons (Summerville and Crist 2003).

## Results

We sampled a total of 493 moth species and 19 900 individuals from the 21 forest sites in 2001 (Table 2). The four moth families with the greatest species richness were Noctuidae, Geometridae, Pyralidae, and Tortricidae, which comprised  $> 75\%$  of the diversity of forest Lepidoptera. More species occurred in forest stands of the glaciated NCT (412) compared to the unglaciated WAP (366); species richness was similar for woody-plant feeders in both ecoregions (179 in the NCT, 173 in the WAP). In terms of total abundance, the Noctuidae, Geometridae, Pyralidae, and Lasiocampidae comprised  $> 70\%$  of the individuals. Finally, a greater number of individuals was sampled from forest sites in the NCT compared to the WAP (11 902 vs 8010 respectively).

The total species richness and log-abundance of moths in the unglaciated WAP forest fragments were not significantly related to the log-area of forest fragments

Table 2. Number of species and individuals of forest Lepidoptera sampled in 21 forest fragments in two ecoregions. Families are arranged according to decreasing species richness (complete species list available from K. S. Summerville upon request).

Family	No. species	No. individuals
Noctuidae	168	4809
Geometridae	76	4775
Pyralidae	73	3698
Tortricidae	65	1087
Notodontidae	27	884
Arctiidae	26	1232
Limacodidae	14	192
Oecophoridae	13	336
Saturniidae	6	25
Sphingidae	5	24
Lymantriidae	4	100
Apotelodidae	2	10
Drepanidae	2	19
Epiplemidae	2	166
Lasiocampidae	2	2374
Megalopigidae	2	18
Sesiidae	2	3
Yponomeutidae	2	109
Mimaloniidae	1	4
Zygaenidae	1	35
Total	493	19900

Table 3. Results from multiple regression of the relationship among forest patch log-area, percent of forest in the landscape, and tree species diversity (Simpson Index) and moth community structure in the Western Allegheny Plateau ecoregion. Regressions were performed using three separate dependent variables: 1) total moth species richness, 2) species richness of woody plant feeders, and 3) log-abundance of moths.

Dependent variables	Predictor variables	DF	Partial R <sup>2</sup>	F	p	Coefficient (SE)
Moth species richness <sub>Total</sub>	Log-area	1	0.028	0.43	0.534	–
	Tree species diversity	1	0.085	2.16	0.191	–
	% forest in landscape <sup>a</sup>	1	0.067	0.32	0.592	–
Moth species richness <sub>Woody plant feeders</sub>	Log-area	1	0.611	10.26	0.019	18.86 (5.89)
	Tree species diversity	1	0.126	2.37	0.175	–
	% forest in landscape <sup>a</sup>	1	0.480	8.87	0.025	0.67 (0.23)
Log-abundance of moths	Log-area	1	0.021	0.37	0.853	–
	Tree species diversity	1	0.235	1.71	0.239	–
	% forest in landscape <sup>a</sup>	1	0.016	0.35	0.354	–

<sup>a</sup> Because forest area and % forest cover in the landscape were highly collinear in the WAP, we ran separate regression models that independently tested the effects of forest area and % cover on moth communities.

or tree species diversity (Table 3). Model fit was not improved by substitution of % forest in the landscape for forest area. Thus, total species richness and log-abundance of forest moths did not differ among forests of differing size, % forest in the landscape, or tree species diversity. Only when the species richness of woody plant feeding moths was considered as the dependent variable did the log-area of the forest fragments significantly predict the number of species in each woodlot ( $p < 0.05$ , see Table 3). Nearly 2 times as many species of woody-plant feeders were found in large forest fragments compared to small fragments (Fig. 2). A similar model fit was obtained using % forest in the landscape as a predictor variable in place of forest log-area (Table 3).

Stand area and tree species diversity significantly influenced the number of moth species sampled from forest sites in the glaciated NCT (Table 4). Total species richness was a function of both tree diversity and forest log area ( $p < 0.05$  for both parameters), and explained

53% and 26% of the variation in moth species richness, respectively (Table 4). Thus, fragments with greater tree species diversity and a larger area contained a greater diversity of Lepidoptera (Fig. 3a, b). When the richness of moth species that feed on woody plants was considered as the dependent variable, the multiple regression analyses revealed that only forest log-area was a significant predictor of lepidopteran richness (Table 4). Forest log-area explained  $> 55\%$  of the variance in the species richness of this guild of moths, and the largest forest stands contained twice as many moth species as the smaller woodlots (Fig. 3c). Finally, tree species diversity was the sole predictor of the log-abundance of forest moths ( $p < 0.05$ , Table 4): forest sites with a greater Simpson diversity of woody plants supported a larger number of moths.

We considered the potential that forest patch area or percent cover in the landscape might also have nonlinear effects on moth species richness. Fitting nonlinear regressions that considered patch area or % forest cover in the landscape as quadratic effects, however, generally resulted in poorer model fits compared to our linear regressions. The overall  $R^2$  values for nonlinear models in both the WAP and NCT ranged between 0.18 and 0.06, and parameter estimates for quadratic effects were non-significant ( $p > 0.05$  for all tests of slope parameters). Thus, within the range of patch areas and cover values considered in this study, nonlinear effects appear less important than linear relationships when predicting the response of forest moth communities to habitat loss.

The structure of moth communities in the both the WAP and the NCT was influenced by forest stand size. Across both ecoregions, smaller forests (2–25 ha) contained, on average, 3.6 species of Notodontidae (larvae primarily restricted to tree foliage) and 16.1 species of Crambidae (grass and forb feeders), whereas moth communities in larger forests (50–250 ha) contained 12.7 and 4.8 species from each respective family. In both the WAP and the NCT, moth communities in larger forest stands contained a greater proportion of

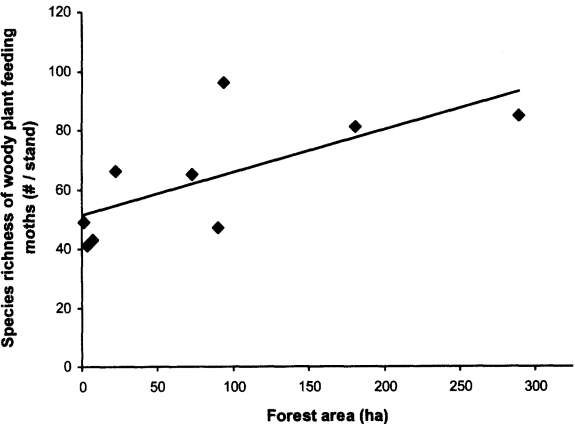


Fig. 2. Relationship between the area of forest stands in the unglaciated WAP and the species richness of woody plant feeding moths. The regression is significant ( $R^2 = 0.61$ ,  $p < 0.05$ ). Regression equations appear in Table 2.

Table 4. Results from multiple regression of the relationship among forest patch log-area, percent of forest in the landscape, and tree species diversity (Simpson Index) and moth community structure in the North Central Tillplain ecoregion. Regressions were performed using three separate dependent variables: 1) total moth species richness, 2) species richness of woody plant feeders, and 3) log-abundance of moths.

Dependent variables	Predictor variables	DF	Partial R <sup>2</sup>	F	p	Coefficient (SE)
Moth species richness <sub>Total</sub>	Log-area	1	0.263	5.13	0.049	16.24 (7.17)
	% forest in landscape	1	0.003	0.12	0.740	–
	Tree species diversity	1	0.526	9.13	0.016	5.98 (1.98)
Moth species richness <sub>Woody plant feeders</sub>	Log-area	1	0.561	9.37	0.016	15.6 (5.13)
	% forest in landscape	1	0.016	2.52	0.150	–
	Tree species diversity	1	0.006	1.27	0.214	–
Log-abundance of moths	Log-area	1	0.010	0.053	0.824	–
	% forest in landscape	1	0.105	3.28	0.110	–
	Tree species diversity	1	0.436	6.02	0.039	0.034 (0.014)

moth species that feed on woody plants as larvae compared to moth communities in smaller forest fragments ( $R^2 = 0.52$ ;  $p < 0.05$  for WAP;  $R^2 = 0.57$ ;  $p < 0.005$  for NCT). Because the observed richness of all moths did not vary among forest sizes in the WAP (Table 3), loss of woody-feeding moth was offset by the occurrence of a greater proportion of herbaceous feeding moth species in smaller forest stands ( $R^2 = 0.73$ ,  $p < 0.05$ ; see Fig. 4).

## Discussion

Both the species richness and composition of moth communities differed among forest stands within the two ecoregions of the eastern deciduous forest. In the unglaciated Western Allegheny Plateau, variation in the species richness of woody plant feeding moth was correlated with habitat quantity, measured at either the patch or landscape scale. Moth species richness and abundance, however, were primarily influenced by variation in tree species diversity (habitat quality) in the glaciated NCT. Forest size remained the only significant predictor of species richness for moths with larvae dependent on woody plants. Differences in forest size and percent forest in the surrounding landscape were most significant for predicting changes in the species richness of woody plant feeders, as was the case for the WAP. These results support the pattern of lower richness in smaller stands reported by Usher and Keiller (1998) for Geometridae and Summerville and Crist (2003) for all forest moths. In contrast, Ricketts et al. (2001) noted that species richness of moths in the Neotropics varied depending on the landscape context of the focal patch; richness was significantly lower in forest fragments > 1 km from continuous forest sites. These authors suggest that "halos" of relatively high species diversity will penetrate the matrix surrounding forest remnants for up to 1 km because moths are relatively vagile insect species and should be capable of colonizing moderately isolated forest remnants (Daily 1996). Not all forest

moths, however, should be expected to contribute equally to such “halos”. Some highly diverse moth families (e.g. Geometridae) are relatively sedentary and may be unable to disperse across the landscape following disturbance to their natal habitat (Thomas 2002).

Summerville and Crist (2003) presented, but did not directly test, an alternative explanation for the observation that species richness is similar across a gradient of forest sizes and isolations. They suggest that species replacement may occur: 1) when opportunistic matrix or edge species are more frequently found in smaller than in larger patches, or 2) when different assemblages of species are found in small and large patches. Species replacement thus occurs when some species are lost from forest sites (i.e., faunal relaxation) and others colonize or invade from the surrounding matrix (e.g., Brown and Hutchings 1997, Ås 1999, Harrison 1999). Our results lend some support to the species replacement explanation. In the WAP, moths that are dependent on tree foliage for larval development were lost across a gradient of forest sizes, while the richness of herbaceous feeders modestly increased. Usher and Keiller (1998) noted a similar trend for moths inhabiting woodlots in an agricultural landscape; moth communities in smaller forests more closely resembled those characteristic of the intervening matrix than forest interior habitat. Therefore, although forest size appears to be the most significant predictor of species richness within forest remnants across both ecoregions, in the WAP, landscape structure may be an important determinant of lepidopteran community composition. Because communities of larger, more vagile taxa are not necessarily contained within landscapes < 1 km in size, we note that our results are not universally applicable to all forest organisms (Atauri and de Lucio 2001).

For some lepidopterans, population dynamics are regulated more by variation in habitat quality rather than patch area or isolation (Fleishman et al. 2002, Collinge et al. 2003). Therefore, high tree species diversity may ameliorate the effects of habitat loss on moth communities, much as increasing flower availability



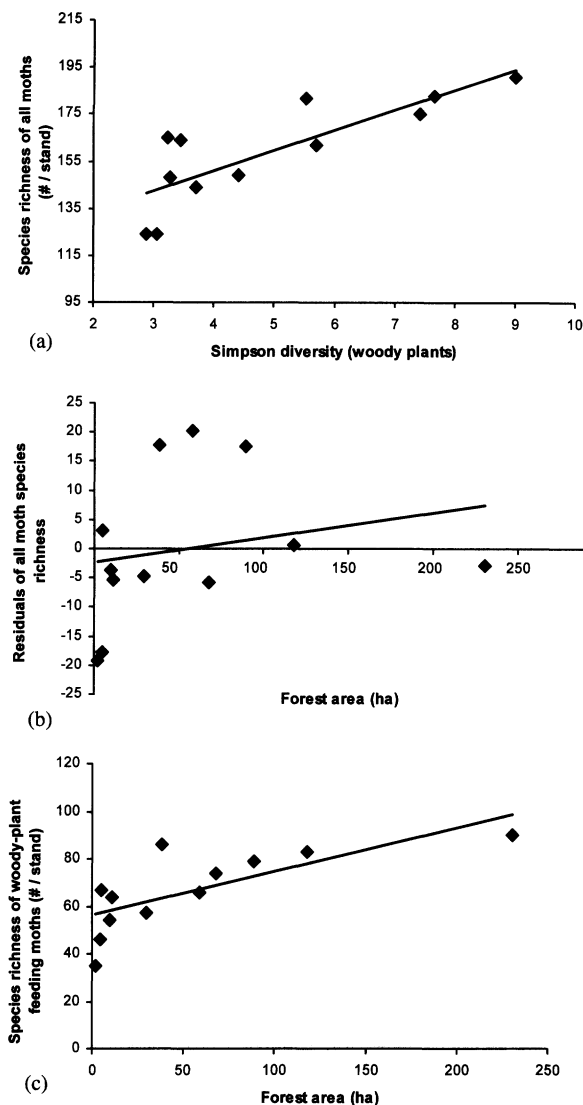


Fig. 3. The relationship between a) tree species diversity within forest stands in the glaciated NCT and the total species richness of forest moths, b) the area of forest stands in the NCT and the residuals obtained from the regression in (a), c) the area of forest stands in the NCT and the species richness of woody plant feeding moths. Regressions are statistically significant ( $p < 0.05$ , Table 3). Regression equations appear in Table 3.

reduces the magnitude of decline in butterfly diversity following fragmentation of old field habitat (Summerville and Crist 2001). The potential importance of habitat quality in maintaining lepidopteran community structure suggests that local habitat restoration may be as important for moth communities in the NCT as increasing habitat area (see also Gyllenberg and Hanski 1997). Managing for higher habitat quality in forests need not focus on practices that artificially increase the diversity of woody plants. Alternatively, discouraging the spread of non-native species such as the shrubs, *Lonicera maaackii*

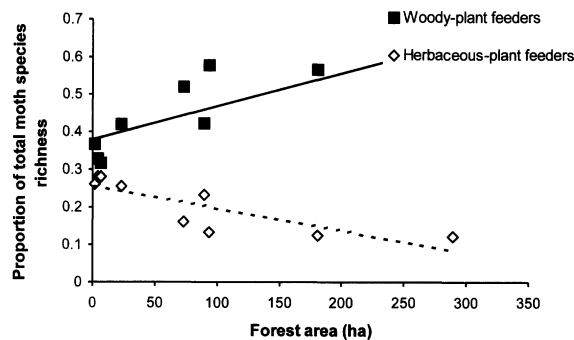


Fig. 4. Variation in the proportion of all moth species sampled in forest remnants of the WAP with larvae that feed on either woody-plants or herbaceous vegetation. Both regression relationships are significant ( $p < 0.05$ ). Regression equations are  $y = 0.0009 + 0.38$  for woody-plant feeding moths and  $y = -0.0006 + 0.26$  for herbaceous feeders. Feeding guild classification follows Summerville and Crist (2002).

and *Rosa multiflora*, or the tree, *Ailanthus altissima*, will help maintain natural floristic diversity within forest sites of differing size.

In conclusion, forest size, together with tree species diversity in the glaciated NCT, appear to be the most important site variable influencing moth species richness and community composition. Because community dynamics change significantly over both short and long temporal scales (Maurer 1999), future studies of the effects of habitat loss on lepidopteran communities should place greater emphasis on generating long-term data sets (Debinski and Holt 2000). Regardless, for the Lepidoptera it appears that understanding changes in habitat quality will be as important as modeling changes in patch area or landscape structure when predicting the effects of habitat loss. To the extent that managing the vegetation within habitat remnants will be easier to accomplish than increasing the size of forest stands in highly fragmented systems, efforts to conserve forest Lepidoptera should focus on maintaining viable populations of host species typical of undisturbed forest sites (e.g. *Quercus* spp. and associated Lepidoptera; Summerville and Crist 2002). Improving the quality of habitat in smaller fragments, especially in the North Central Tillplain, may ultimately produce forest systems that sustain levels of moth biodiversity comparable to the interiors of large forest patches in fragmented landscapes.

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