Oecologia (2014) 176:207–224
DOI 10.1007/s00442-014-3014-7

COMMUNITY ECOLOGY - ORIGINAL RESEARCH

Habitat fragmentation, tree diversity, and plant invasion interact to structure forest caterpillar communities

John O. Stireman III · Hilary Devlin · Annie L. Doyle

Received: 7 August 2013 / Accepted: 25 June 2014 / Published online: 12 July 2014

Abstract Habitat fragmentation and invasive species are two of the most prominent threats to terrestrial ecosystems. Few studies have examined how these factors interact to influence the diversity of natural communities, particularly primary consumers. Here, we examined the effects of forest fragmentation and invasion of exotic honeysuckle (*Lonicera maackii*, Caprifoliaceae) on the abundance and diversity of the dominant forest herbivores: woody plant-feeding Lepidoptera. We systematically surveyed understory caterpillars along transects in 19 forest fragments over multiple years in southwestern Ohio and evaluated how fragment area, isolation, tree diversity, invasion by honeysuckle and interactions among these factors influence species richness, diversity and abundance. We found strong seasonal variation in caterpillar communities, which responded differently to fragmentation and invasion. Abundance and richness increased with fragment area, but these effects were mitigated by high levels of honeysuckle, tree diversity, landscape forest cover, and large recent changes in area. Honeysuckle infestation was generally associated with decreased caterpillar abundance and diversity, but these effects were strongly dependent on other fragment traits. Effects of honeysuckle on abundance were moderated when fragment area, landscape forest cover and tree diversity were high. In contrast, negative effects of honeysuckle invasion on caterpillar diversity were most pronounced in fragments with high tree diversity and large recent increases in area. Our results illustrate the complex interdependencies of habitat fragmentation, plant diversity and plant invasion in their effects on primary consumers and emphasize the need to consider these processes in concert to understand the consequences of anthropogenic habitat change for biodiversity.

Keywords Forest fragmentation · Lepidoptera · *Lonicera* · Insect diversity · Interaction modification

Introduction

Terrestrial landscapes are increasingly becoming altered by human activities. It is estimated that approximately 20 % of the Earth's land surface is dominated by human use and 39–50 % has been substantially anthropogenically transformed or degraded (Vitousek et al. 1997; Haberl et al. 2007). Even where the human footprint is not immediately apparent, indirect effects of humans such as global climate change, airborne pollutants, and introduced species are quietly modifying the structure and function of terrestrial ecosystems—often in ways that we are unaware of or do not completely understand. Two of the greatest environmental threats that natural ecological communities face are fragmentation of suitable habitat and displacement or destruction by invasive species (Wilcove et al. 1998; Sala et al. 2000). Here, we seek to understand how these two factors interact to influence forest Lepidoptera communities.

Communicated by Konrad Fiedler.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-014-3014-7) contains supplementary material, which is available to authorized users.

J. O. Stireman III (✉) · H. Devlin · A. L. Doyle
Department of Biological Sciences, Wright State University,
3640 N. Colonel Glenn Hwy., Dayton, OH 45435, USA
e-mail: john.stireman@wright.edu

H. Devlin
e-mail: hilary.cerny@gmail.com

A. L. Doyle
e-mail: annie.Doyle@sinclair.edu

Impacts of forest fragmentation

Habitat fragmentation can affect ecological communities through a variety of mechanisms. Most generally, as fragmentation divides continuous habitat into a series of "islands," the habitat-dependent communities contained therein may behave according to the general dynamics and equilibria predicted for oceanic islands (i.e., Island Biogeography; MacArthur and Wilson 1967). Although there are limitations in applying MacArthur and Wilson's theory of Island Biogeography to fragmented habitats (Laurance 2008), the basic predictions that smaller, more isolated fragments should retain fewer species than larger, more connected ones, is well supported (Watling and Donnelly 2006; Prugh et al. 2008). This reduction in diversity may be due to stochastic local extinctions of populations combined with limited dispersal among fragments and/or to a lower diversity of discrete habitats in smaller fragments. In addition, fragmentation leads to an increase in edge habitat, altering the physical and biotic environment of forest fragments (Ries et al. 2004). The matrix surrounding habitat fragments can also strongly influence the extent of species loss and community dynamics (Ricketts et al. 2001), a topic not fully considered in basic island biogeography theory (Cook et al. 2002; Laurance 2008). The most dramatic consequences of habitat fragmentation may not be reductions in population size or the loss of particular species, but alteration in the structure of ecological communities and their temporal dynamics. For example, the loss of top predators from fragments can cause drastic changes in the diversity and dynamics of underlying trophic levels, ramifying down to the primary producers in a trophic cascade (Laurance et al. 2002). Furthermore, because of their size, fragments are expected to be more vulnerable to stochastic population fluctuations and experience more extreme dynamics than larger scale systems (Laurance 2008).

Recent research on the effects of habitat fragmentation has focused on tropical forests due to the high levels of biodiversity at stake and high rates of habitat loss (e.g., Didham 1997, Didham et al. 1998; Laurance and Berregaard 1997; Hill et al. 2011), but the extent of forest fragmentation is extreme in many temperate regions (Potapov et al. 2008), particularly in the Midwest United States (Iverson et al. 1994). This region has experienced some of the most intense deforestation in the United States, with some areas having lost more than 80 % of their originally extensive forested habitat (Curtis 1956; Iverson 1988). Even with this great loss, forest cover in many parts of the Midwest, including Ohio, has substantially increased as a result of agricultural abandonment in the past 90 years (Smith et al. 1993; Brown 2003). However, most forest fragments in the eastern United States are less than 100 acres (~40.5 ha) in size, consist of highly fragmented secondary forest, and are either poorly protected or managed for timber production (Norton 1996).

Forests support a great diversity of insect species, many of which are dependent on these habitats (Schowalter et al. 1986) and play crucial ecological roles as pollinators (Didham et al. 1996), seed dispersers (Zelikova et al. 2008), nutrient recyclers (Andresen 2003), herbivores (Schowalter et al. 1986), prey, and predators (Janzen 1988; Price 1997). Despite these critical relationships between insects and forests, most studies of forest fragmentation have concentrated on vertebrates and higher plants (Warburton 1997), with few studies focusing on the diverse communities of forest insects.

Fragmentation and invasion

The introduction and proliferation of invasive species into novel habitats rivals habitat loss and fragmentation in its influence on terrestrial ecological communities (Pimentel et al. 2000). Invasive species can decimate native populations through direct consumption (e.g., Salo et al. 2007, Smitley et al. 2008); or they can displace native species by outcompeting them (e.g., Porter and Sagivnano 1990). Of particular concern is the introduction and invasion of plant species that can displace native competitors and dominate entire floral communities (Crooks 2002), with cascading effects on communities of primary and secondary consumers (Vitousek et al. 1997; McKinney and Lockwood 1999; Crooks 2002).

As with other major drivers of global change (e.g., climate change, pollution, nutrient deposition), there is growing appreciation that invasion of alien species and habitat fragmentation are interconnected processes that interact both linearly and non-linearly to disrupt and reshape ecological communities (Didham et al. 2007; Montero-Castaño and Vilà 2012). Habitat loss can have numerically mediated (interaction-chain) effects on the impacts of invasive species (e.g., linearly increasing the likelihood or magnitude of invasion), and it can have functionally moderated ("interaction modification") effects where habitat loss influences the per capita effect of invasive species (or vice versa; Didham et al. 2007). For example, habitat fragmentation can create pathways for invasion and provide abundant edge habitats conducive for establishment of invasive organisms (Cronk and Fuller 1995). Once such invasive organisms become established, they may switch from being "passengers" to "drivers" of ecological change, altering the environment in which they grow and facilitating expansion into less disturbed areas (Didham et al. 2005). These two processes, habitat fragmentation and species invasion, are so often found acting in concert that it can be difficult to separate their effects (Didham et al. 2007; Tylianakis et al. 2008).

One apparent consequence of forest fragmentation in the Midwestern US is the invasion of Amur honeysuckle, *Lonicera maackii* (Caprifoliaceae; hereafter as “honeysuckle”). Honeysuckle was introduced to the United States from northeast Asia in 1898 as an ornamental shrub (Luken and Thieret 1996) and has since become naturalized in at least 26 states in the eastern US (Trisel 1997, USDA Plant Database 2012). Honeysuckle invasion is more extensive in regions where forest fragments are disturbed and more connected to one another than in isolated forest fragments (Hutchinson and Vankat 1997). It can dominate forest under stories to the point where it forms dense monocultures (Deering and Vankat1999). Invasion of *Lonicera* reduces survival and fecundity of native herbs and forest perennials (Gould and Gorchov 2000, Hartman and McCarthy 2008), and may inhibit germination and growth of tree seedlings (Gorchov and Trisel 2003). It has been shown to disrupt competitive relationships in fragmented forest under stories (Hartman and McCarthy 2008) and reduce species richness of native herb and tree seedlings (Collier et al. 2002). Despite considerable research on honeysuckle invasion, there has been little investigation of its effects on insect communities (though see Loomis and Cameron 2014).

Objectives

Our goal was to examine how forest fragmentation, plant invasion, and their interactions affect tree and shrub feeding forest Lepidoptera. Such interactive effects of plant invasion and fragmentation on insect herbivore communities have not been examined previously in any system that we are aware of. Due to their integral role as both consumers and prey in forest systems, understanding how these pervasive drivers of global change affect caterpillars is likely to provide insight into more general impacts on the ecological structure of forest communities. We predicted that caterpillar abundance and diversity (richness) should decline with decreasing area and increasing isolation due to local loss of forest dependent species, in accordance with Island Biogeography theory. Because edges and open areas provide avenues for honeysuckle invasion, we expected that effects of fragmentation should be exacerbated by honeysuckle infestation in a relatively linear, numerically mediated process. Richness and abundance of caterpillars should decline with increasing levels of invasive honeysuckle due to the replacement of native saplings with unpalatable honeysuckle, effectively reducing the size (resources) of forest fragments. Honeysuckle invasion and fragmentation may also interact synergistically if honeysuckle prevents tree recruitment and reduces the effective size of fragments. Alternatively, negative impacts of fragmentation on natural enemies (parasitoids and predators) could result in increased overall abundance of caterpillars—at least habitat generalists.

Materials and methods

Focal organisms: forest Lepidoptera

Caterpillars, larval stages of the order Lepidoptera, are an enormously diverse group (ca. 150,000 described species; Daly et al. 1998) that reach their highest levels of diversity and abundance in forested ecosystems (Summerville and Crist 2008), where they play important roles as primary consumers (Stamp and Casey 1993) and as food for vertebrate (Brook 2009) and invertebrate (Stireman and Singer 2003) taxa. Caterpillars tend to be relatively specialized on particular food plants (Dyer et al. 2007), and thus are highly sensitive to changes in plant communities (With and Crist 1995). Therefore, variation in Lepidoptera density and distribution is indicative of broader patterns of biodiversity (Kremen et al. 1993; Noss 1999; Lund and Rahbek 2002). Most analyses addressing effects of habitat fragmentation on insect populations have focused mainly on adult moths (e.g., Summerville and Crist 2004), which can be transient and might not be an accurate indicator of local forest quality. Focusing on immature stages provides a more accurate perspective of the impacts of fragmentation on Lepidoptera populations, because it indicates where reproduction and development are occurring and directly reflects the quality of the vegetation within forest fragments (Kitching et al. 2000). However, we acknowledge that focusing on the larvae may result in other sampling biases (e.g., only sampling understory caterpillars, see "Discussion").

Study sites

Forest fragments included in this study were located in southwest Ohio (39°28′ to 39°49′N; 83°47′ to 84°25′W) in the glaciated North Central Till plain region (see Summerville and Crist 2003). Fragments were chosen based on location, size, shape, and management practices, and ranged in size from 6 to 800 hectares (Table 1). Most of the fragments chosen were located within an agricultural matrix and contained trees of varying size, including some large, mature individuals (>40 cm dbh). We chose fragments that had an obvious edge and interior, avoiding fragments that were long and narrow or sparsely forested.

Fragment characteristics

Scaled images of the 19 forest fragments were downloaded and analyzed in the graphics program Image J (Rasband 1997–2012). Each fragment was outlined by hand within

Table 1 Fragments sampled during the course of this study, with number of transects sampled (# T), average honeysuckle density (HSD, shrubs per meter of transect surveyed), number of caterpillars collected (Inds.), number of caterpillar species collected (Sp.), rarefied caterpillar species numbers (Rar. Sp. measured at 100 m^2 of leaf area searched; NA sites where <100 m^2 of leaf area was searched), and species diversity (e^H)

Fragment site	Size (Ha)	# T	HSD	Inds.	Sp.	Rar. Sp.	Div.
Fife	6.2	10	3.06	252	13	12.94	2.16
Cemex 3	7.5	3	2.45	36	11	NA	2.47
Fairborn Comm. Park	14.2	9	1.06	85	31	18.86	2.65
Breeze	14.7	13	4.78	62	12	12.55	1.77
Cemex 2	15.1	2	0.94	0	0	NA	NA
Cemex 4	23.8	5	1.55	88	23	17.12	2.22
Glenn Thompson	24.2	15	2.71	71	34	12.64	3.44
Huffman MetroPark	37.0	16	0.13	154	33	28.75	4.01
Collet Woods	38.4	16	0.01	127	26	10.19	1.95
Crooked Creek	81.1	8	0.05	37	19	10.18	1.81
Wright State University Woods	82.4	20	4.85	377	41	16.82	2.90
Sara Lee Arnovitz	108.5	11	2.34	84	29	16.83	3.22
Indian Mound Reserve	117.2	11	5.33	149	33	13.99	3.93
Thompson Woodlot	118.3	15	7.88	113	30	22.32	3.77
Sycamore State Park	137.4	13	5.05	274	25	13.57	2.10
Narrows Reserve	180.5	11	1.72	94	32	15.12	2.68
Sugarcreek MetroPark	235.9	6	3.10	21	12	13.00	1.97
Germantown MetroPark	687.7	17	0.37	186	49	20.64	3.10
Glen Helen/John Bryan	802.3	18	0.96	299	53	25.01	3.87

the program in order to calculate the area, perimeter, and circularity (4π(area/perimeter^2); see Rasband (1997–2012). The amount of surrounding forest habitat within a 5-km radius centered on each fragment was also measured using Google Earth and Image J. This measure reflects the degree of the fragment's isolation within the agricultural matrix and is referred to as the landscape forest cover. Aerial photographs from 1956 and 1989, obtained from local county soil and water conservation districts, were used to estimate the historical area of each fragment and changes in area over time.

Honeysuckle density was measured along at least two of the 100 m transects used for caterpillar sampling (below) in each fragment. At each transect meter, the area up to 2 meters on either side was examined for the presence of honeysuckle. If honeysuckle was present, the number of shrubs was counted and recorded along with the height class of each shrub (<0.5, 0.5–2, >2 m). Average densities ranged from nearly zero to almost eight individuals per transect meter (Table 1). To include both effects of honeysuckle density and honeysuckle size (related to age since establishment), these data were converted into an index of honeysuckle infestation (HS) for each site as follows:

$$\mathrm{HS} = \frac{\sum(Nh \times \overline{Hc})}{M}.$$

where N_h is the number and $\overline{Hc}$ is the mean height class of honeysuckle individuals for each meter of transect and M is the total number of meters surveyed per fragment.

Tree diversity of fragments was estimated based on all trees surveyed while sampling caterpillars along transects (see "Sampling"). Since only trees with searchable foliage were surveyed, some larger trees may not have been recorded. Thus, the estimates of tree diversity reflect the diversity of foliage below ca. 2 m, rather than total canopy diversity. Nevertheless, our measures are likely to reflect the overall diversity of the forest fragments. We investigated the influence of tree diversity in models as the "effective number of species" calculated as e^H (Jost 2006; where H is the Shannon-Weiner diversity index) as well as simply as the total number of species (i.e., richness). Rarefaction indicated that tree richness quickly became asymptotic with sampling such that estimates were minimally affected by unequal sampling (e.g., the correlation between total richness and rarefied richness at 140 sampled trees was $r = 0.954$).

Sampling

Caterpillar sampling was conducted over four years, from 2006 to 2009. During the course of our sampling, we found that there were two major peaks in caterpillar abundance, occurring in spring (April to June) and summer/fall (August to October; hereafter referred to as summer). We, therefore, focused our sampling effort during these two periods. Each site included in the analysis had at least two transects sampled (Table 1) and most were surveyed during each season in multiple years. Six additional sampled fragments were excluded from analyses due to insufficient sampling.

Within each forest fragment, we sampled 100-m transects oriented roughly perpendicular to fragment edges. Transects followed an approximate straight line, starting from the fragment edge, providing a representation of the floral composition of the fragment from edge to interior. Surveying was conducted by walking along each transect and recording every tree with accessible foliage within 1 m of the transect line. Foliage, twigs, and trunks were examined from the ground level up to around 2 m (as high as can be effectively searched). For each tree, the tree species, number of leaves searched, and number of caterpillars found were recorded. Each caterpillar was given a unique number and placed in a bag along with host plant material and transported to the laboratory. We included foliage feeding sawfly (Symphyta: Hymenoptera) larvae in our study due to their frequent occurrence and ecological similarity to caterpillars, but they made up only a small fraction of the total number of species (6.9 %) and individuals (4.4 %) sampled.

The number of leaves searched for each tree sampled was estimated to quantify search effort. We digitally scanned between ten and 50 leaves for each of 38 focal tree or shrub species, selected to span a range of sizes, measured their areas in Image J, and calculated a mean leaf area for each tree species. These means were multiplied by the total number of leaves searched on each tree to estimate the total leaf area searched. For species with greater variability, we scanned more leaves. For some rarely surveyed trees, we used mean leaf areas calculated from similar, related species (e.g., we used *Acer sacharum* values for *Acer rubrum*). We avoided sampling caterpillars from honeysuckle, because very little herbivory occurs on this invasive shrub (Lieurance and Cipollini 2011) and our aim was to assess how honeysuckle affects caterpillar diversity on the native woody plant community.

Rearing and identification

Caterpillars were reared on foliage of the host species on which they were found, to confirm plant suitability and for identification. Caterpillars were reared in plastic tubs with wet paper towel and host plant material, inside an environmental chamber set to mimic day and night temperatures and light patterns for the season. Conditions were changed monthly to correspond with the changing season. Every other day during the growing season, caterpillars were checked for survival, pupation, and eclosion, and plant material was replaced. When caterpillars reached the prepupal stage, peat moss was placed in bottom of the container. Upon eclosion, adult moths were frozen. In November, the environmental chamber was set to 4 °C and total darkness for three months, according to rearing guidelines from Wagner (2005). After this period, the conditions were changed to April temperatures and light patterns and containers were checked regularly for eclosed moths.

All caterpillars collected were identified to the lowest taxonomic level possible based on morphological appearance, distribution, host plant specificity, and seasonality using Wagner (2005). Once adults emerged, specimens were spread and preserved and identified with the use of Covell (2005), Wagner (2005), Microleps.org, The North American Moth Photographer's Group (http://mothphotographersgroup.msstate.edu), and other traditional and digital resources. Some specimens were taken to the Ohio State University insect collection for comparison and identification. Some specimens that could not be identified retained morphospecies designations. Vouchers of all taxa were deposited in the Wright State University insect collection maintained by Stireman.

Analysis

Caterpillar faunas in the spring and summer seasons were highly distinct, with species overlap (Jaccard similarity indices) ranging from 0.04 to 0.21 across years. This is consistent with analyses of adult moth diversity in the same region by Summerville and Crist (2002, 2003), who found that season was the most important variable affecting community composition. Furthermore, preliminary analyses suggested that these distinct communities respond differently to forest fragment characteristics. For these reasons, we analyzed each community separately. However, we also performed parallel analyses with the full data set. We calculated the total number of host families, genera, and species for caterpillar species with five or more rearings to assess if the seasonal communities differed in host range.

Caterpillar abundance was measured as the total number of caterpillars sampled in each season-year per fragment (see below). In a few instances where large numbers of gregarious caterpillars were collected from the same plant (i.e., a single clutch), caterpillar densities were inflated, and we used the log of the number of caterpillars in the aggregation rather than actual counts. To estimate caterpillar species richness we estimated rarefaction curves of species against square meters of foliage searched for each fragment in each season. To control for sampling effort, we then calculated caterpillar richness estimates corresponding to 66 (spring), 54 (summer), and 100 m^2 (both seasons) leaf area, with one to three of the most poorly sampled fragments omitted (Table 1). We also examined effects of fragment variables on caterpillar diversity (e^H) per fragment.

To test for effects of fragment characteristics on abundance (for each site, each season, each year it was sampled), we employed generalized linear mixed effects models (glmer) using the R package *lme4* (Bates et al. 2013), employing a Poisson error distribution, with site and year as random effects. Because models included sampling effort (leaf areas searched) as a covariate, our results reflect

Table 2 Correlation coefficients (r) among primary explanatory variables including both measures of tree diversity [e^H and richness (S)]

Variable	Area	Honeysuckle	Forest area	Tree S	Tree e^H	ΔArea56
Area						
Honeysuckle	−0.007					
Forest area	0.325	0.078				
Tree S	**0.523**	−0.156	0.039			
Tree e^H	0.158	−0.125	−0.295	0.612		
ΔArea56	0.041	**0.544**	0.177	−0.198	−0.051	
ΔArea89	−0.168	**0.403**	−0.089	**−0.483**	−0.129	**0.744**

Fragment and forest landscape areas were log-transformed, Δarea = proportional change in area since 1956 or 1989, respectively. Significant correlations ($p < 0.05$, without correction) are indicated in bold

effects on caterpillar density more than abundance; however, we use the term abundance due to convention. Linear regression models were used to assess effects of fragment characteristics on rarefaction-estimated caterpillar richness and diversity per fragment in R 2.15 (R Development Team 2012). Predictor variables were centered in model construction and variance inflation factors were calculated to assess and minimize problems of collinearity among factors.

Given weak effects of fragment shape in exploratory analyses and the relatively large number of model terms relative to data points (sites), we omitted this variable from final analyses. We used a stepwise model selection (both directions) based on AIC to select the best fitting models, starting with models with main effects and all two-way interactions, with further refinement until only terms with p values less than 0.10 remained. Main effects were retained in models if they were involved in significant interactions. Holm's correction was applied to account for multiple tests in assessing significance of terms within models.

Separate models were fit using current fragment areas, 1989 areas, and 1956 areas to assess which area measure resulted in the most likely model. Model AICc values and relative model probabilities (Akaike weights, see Burnham and Anderson 2002) were estimated with the R packages *AICcmodavg* (Mazerolle 2013) and *qpcR* (Spiess 2013). Model comparisons of the effects of change in area (proportion) since 1956 or 1989 indicated similar, but somewhat stronger, effects of more recent changes in area; therefore, we used change in area since 1989 in the models. Interactions between variables were visualized by plotting estimated model effects (linear predictors) in the R packages *effects* (Fox 2003) and *lattice* (Sarkar 2008).

Results

A total of 2,184 individuals of 201 morphologically recognizable species (Table S1) were sampled over all fragments and years from 220 sampling transects. Overall, densities of caterpillars were low (mean = 0.55/m^2 leaf area), with occasional transects recovering no caterpillars. Richness was similarly divided over the sampling seasons, with 106 species in spring (41 %) and 139 species in summer (59 %). Across all sampling years and sites, only 44 species (~22 %) were found in both seasons, and as reported above, Jaccard similarity indices ranged from 0.04 to 0.21. Fragment variables were generally not highly correlated; however, some correlations involving area or changes in area were significantly greater than zero (Table 2). In most analyses, current fragment areas resulted in the most likely models based on AIC weights relative to historical areas, but in summer models of caterpillar abundance and spring analyses of caterpillar diversity, historical fragment area provided a better fit. Across analyses, models employing tree richness frequently exhibited stronger effects and explained more variance than those employing tree diversity; however, this measure was correlated with fragment area (r = 0.52–0.58) and the models tended to exhibit higher variance inflation factors. The relative magnitudes of factor effects and their directions are similar regardless of which measure was used, and to be conservative, we focus on tree diversity.

Caterpillar abundance

Spring

There were many strong effects of explanatory variables and their interaction on caterpillar abundance in spring (Table 3), notably landscape forest area and tree diversity. Variance inflation factors (VIFs) were moderately high ($\leq$6), but this was primarily due to correlations between main effects and interactions; when only main effects were examined, VIFs were <2. There is danger in attempting to interpret main effects of factors also involved in significant interactions (i.e., the "principle of marginality"; Nelder 1977), so we focus on the strong interactions, which reveal the most interesting and important patterns in our analyses.

Table 3 Generalized linear models for caterpillar abundance (per site/year) for spring, summer, and both seasons combined

Predictor	Spring			Summer			Total		
	Est.	*z*	*p*	Est.	*z*	*p*	Est.	*z*	*p*
Leaf area	0.009	3.28	**<0.0011**	0.006	3.84	**<0.0002**	0.01	6.91	**<0.0001**
logA[a]	0.50	2.22	<0.03	0.16	0.69	<0.49	0.04	0.32	<0.75
logFA	−4.89	−4.21	**<0.0001**	−2.74	−2.81	**<0.0050**	−4.31	−5.15	**<0.0001**
HS	−0.05	−1.00	<0.32	−0.18	−2.05	<0.04	−0.16	−4.58	**<0.0001**
treeDiv	0.15	3.11	**<0.0019**	0.23	8.50	**<0.0001**	0.15	8.48	**<0.0001**
ΔArea	−0.48	−1.00	<0.32	0.80	2.08	<0.04	0.17	0.60	<0.55
logA:treeDiv				−0.30	−6.29	**<0.0001**	−0.30	−3.12	**<0.002**
logA:HS	−0.42	−3.10	**<0.002**				−0.10	−3.15	**<0.002**
logA:ΔArea	4.66	4.28	**<0.0001**				2.05	2.99	**<0.003**
logFA:HS	1.15	2.92	**<0.004**						
logFA:treeDiv	1.34	3.08	**<0.002**	1.61	7.68	**<0.0001**	1.39	9.69	**<0.0001**
logFA:ΔArea							7.68	3.91	**<0.0001**
HS: treeDiv	0.05	4.29	**<0.0001**	0.04	3.51	**<0.0005**	0.05	7.65	**<0.0001**
treeDiv:ΔArea	−0.57	−5.36	**<0.0001**	−0.41	−4.79	**<0.0001**	−0.34	−6.36	**<0.0001**

Leaf area leaf area searched; *logA* log(area); *logFA* log (landscape forest coverage); *HS* honeysuckle invasion index; *treeDiv* tree diversity; Δ*Area* change in area since 1989, see text for further explanation of variables; *Est.* parameter estimate

Significant *p* values, adjusted for multiple comparisons within models, are in bold

[a] *LogA* current area for spring and total, 1956 area for summer

The effect of fragment area is generally positive (Table 3), but high honeysuckle inhibits this effect (Fig. 1a), and substantial changes in area decrease caterpillar abundance in small fragments (area × Δarea interaction; Fig. 1b). Surprisingly, under most conditions, isolation (low landscape forest cover) is associated with greater caterpillar abundance. Isolation exposes negative effects of honeysuckle (Fig. 1c), but appears to buffer caterpillar abundance from negative effects of low tree diversity (Fig. 1d). Tree diversity has a strong positive effect on caterpillar abundance, but when change in fragment area is large, its effects are diminished (Fig. 1e), and negative effects of honeysuckle are particularly pronounced in low diversity fragments (see Fig. 2a). Analyses employing tree richness resulted in similar effects, except for the absence of a tree richness × Δarea interaction (Table S2).

Summer

As in the spring caterpillar community, effects of predictor variables were complex, and often only discernable through their interactions. Strong positive effects of tree diversity and negative effects of landscape forest cover are apparent (Table 3), but again, the interactions are more revealing. As for spring caterpillars, negative effects of honeysuckle on the summer community were strongest at low tree diversity (Fig. 2a), but the relationship between change in fragment area and tree diversity differed: abundance declined only when both were low (Fig. 2b). As fragment area increases, positive effects of tree diversity on caterpillar abundance are diminished (Fig. 2c), whereas effects of tree diversity are most apparent at high levels of forest cover (as in Spring, Fig. 1d). Analyses with tree species richness (rather than diversity) resulted in similar conclusions, although negative effects of honeysuckle are stronger both directly and through interactions with fragment area (as in Fig. 1a; Table S2).

As might be expected, model results from the combined data set (i.e., both seasons; Table 3) are a combination of effects on each seasonal community, with all significant interactions present in the seasonal models except for the absence of honeysuckle x landscape forest cover interaction (spring). Significant positive effects of tree diversity and negative effects of honeysuckle and landscape forest cover were observed, with a strong negative interaction between honeysuckle and tree diversity (Fig. 2a). An interaction between landscape forest cover and fragment area change, not found in either seasonal model, is also revealed: negative effects of forest cover are only observed when change in area is low (Fig. 2d). Again, analyses employing tree richness recovered similar effects (Table S2).

Caterpillar species richness and diversity

Spring

Results for models of species richness (rarefied) depart strongly from those found for abundance with far fewer significant terms (Table 4). Current area always provided a better fit than historical area estimates (when area had a significant effect), and change in fragment area had no significant effect, directly or via interactions. Effects of fragment variables on caterpillar richness in spring are limited to tree diversity and its interaction with honeysuckle. On its own, there is a clear positive relationship between caterpillar richness and tree diversity ($F_{1,\ 15} = 9.38$, adj.

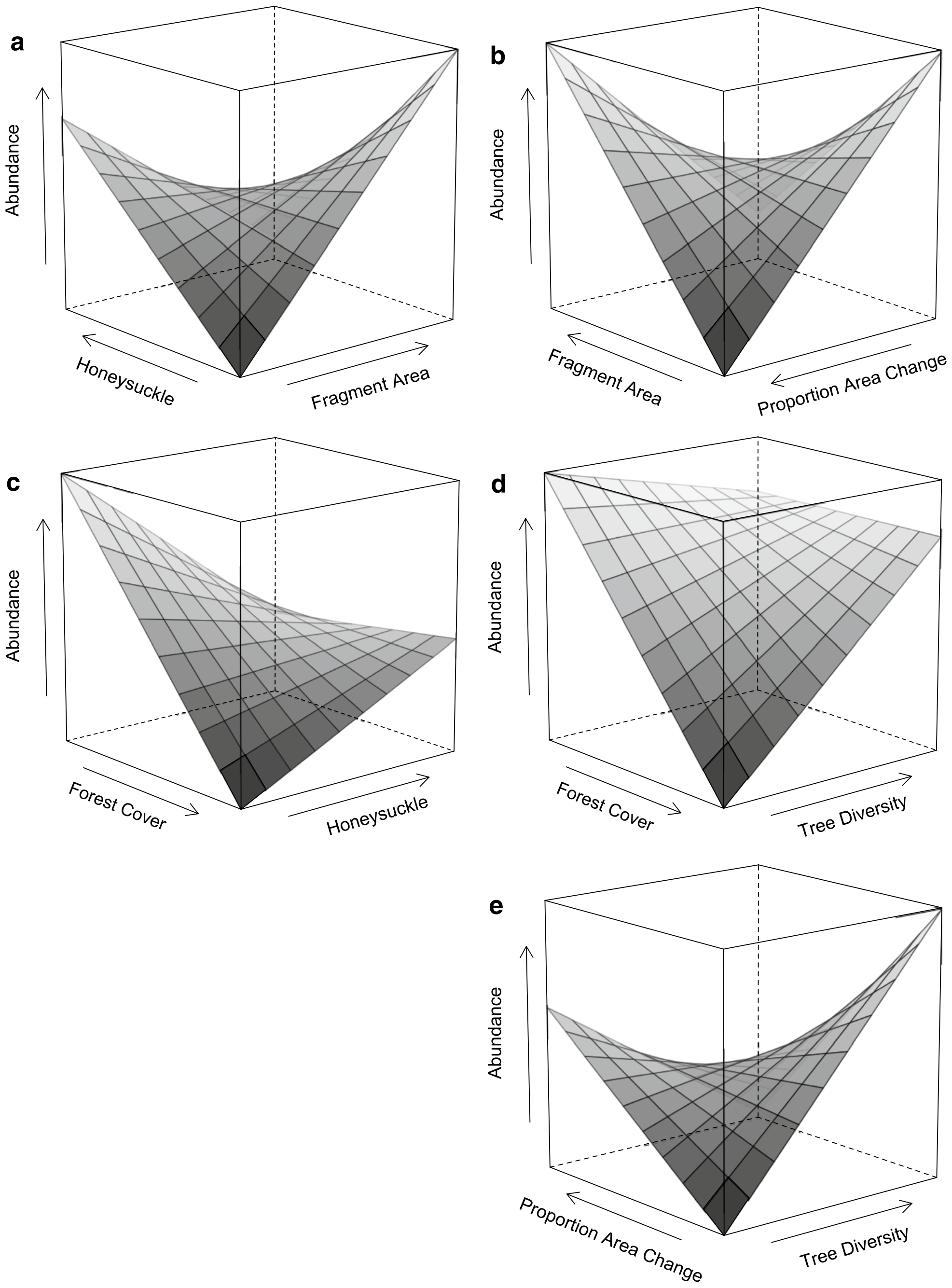


Fig. 1 Surface plots illustrating linear predictors of interaction effects on *spring* caterpillar abundance within the statistical model framework (Table 3). These plots are designed to illustrate the causes of significant interaction effects. Each numeric predictor is arbitrarily represented by 8–10 equally spaced levels. Areas are log transformed (see methods). **a** Interaction between fragment area and honeysuckle, **b** interaction between fragment area and change in fragment area (generally increase), **c** interaction between landscape forest cover and honeysuckle, **d** interaction between landscape forest cover and tree diversity, **e** interaction between change in fragment area and tree diversity. Axes are arbitrarily rotated to provide the clearest perspective of interactions. Confidence intervals are omitted for clarity and not all slopes significantly deviate from zero

$R^2 = 0.34$, $p < 0.008$) and a weak negative relationship with honeysuckle index (NS), but these effects are strongly interdependent. Strong positive effects of tree diversity on richness are dampened or even reversed when honeysuckle infestation is high, and negative effects of honeysuckle are only evident in diverse fragments (Fig. 3a). Caterpillar richness is maximized in diverse forest fragments with low levels of honeysuckle infestation. The analysis employing tree richness returned similar results, although an additional negative effect of forest cover is suggested (Table S3).

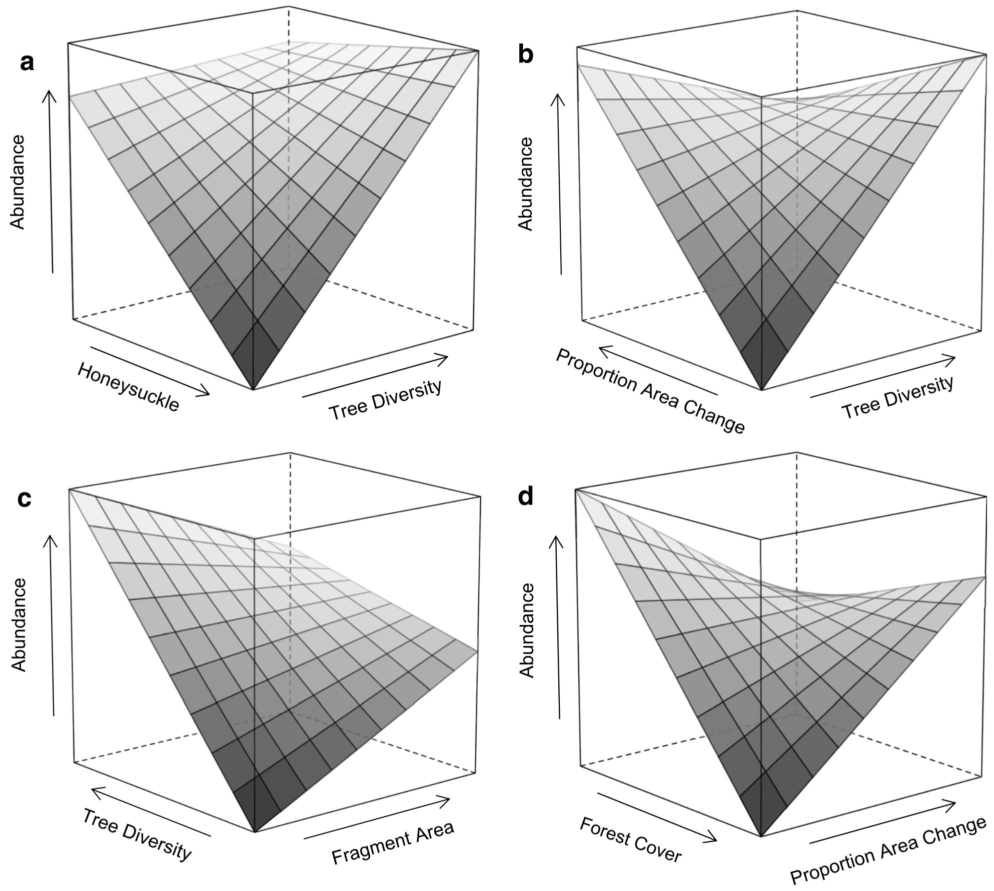


Fig. 2 Surface plots illustrating linear predictors of interaction effects on summer (and total) caterpillar abundance within the statistical model framework. **a** Interaction between honeysuckle and tree diversity, **b** interaction between tree diversity and change in fragment area, **c** interaction between area and tree diversity for all caterpillars (spring + summer), **d** interaction between landscape forest cover and change in fragment area. See Fig. 1 and the main text for details

Table 4 Multiple regression models for caterpillar species richness per fragment (based on rarefaction)

	Spring			Summer			Total		
Predictor	Est.	*t*	*p*	Est.	*t*	*p*	Est.	*t*	*p*
log*A*[a]				5.95	2.65	<0.027	0.36	2.90	**<0.013**
HS	−0.26	−1.26	<0.23	−0.05	−0.13	<0.90	−0.006	−0.30	<0.77
TreeDiv	0.72	2.88	**<0.014**	−0.05	−0.10	<0.92	0.06	2.35	<0.04
logFA				−7.54	−0.70	<0.50			
HS:treeDiv	−0.28	−3.68	**<0.003**				−0.05	−6.44	**<0.0001**
logFA:HS				8.11	2.55	<0.031			
logA:treeDiv				2.03	2.18	<0.058			

See Table 3 for explanation of terms

Significant *p* values, adjusted for multiple comparisons within models, are in bold

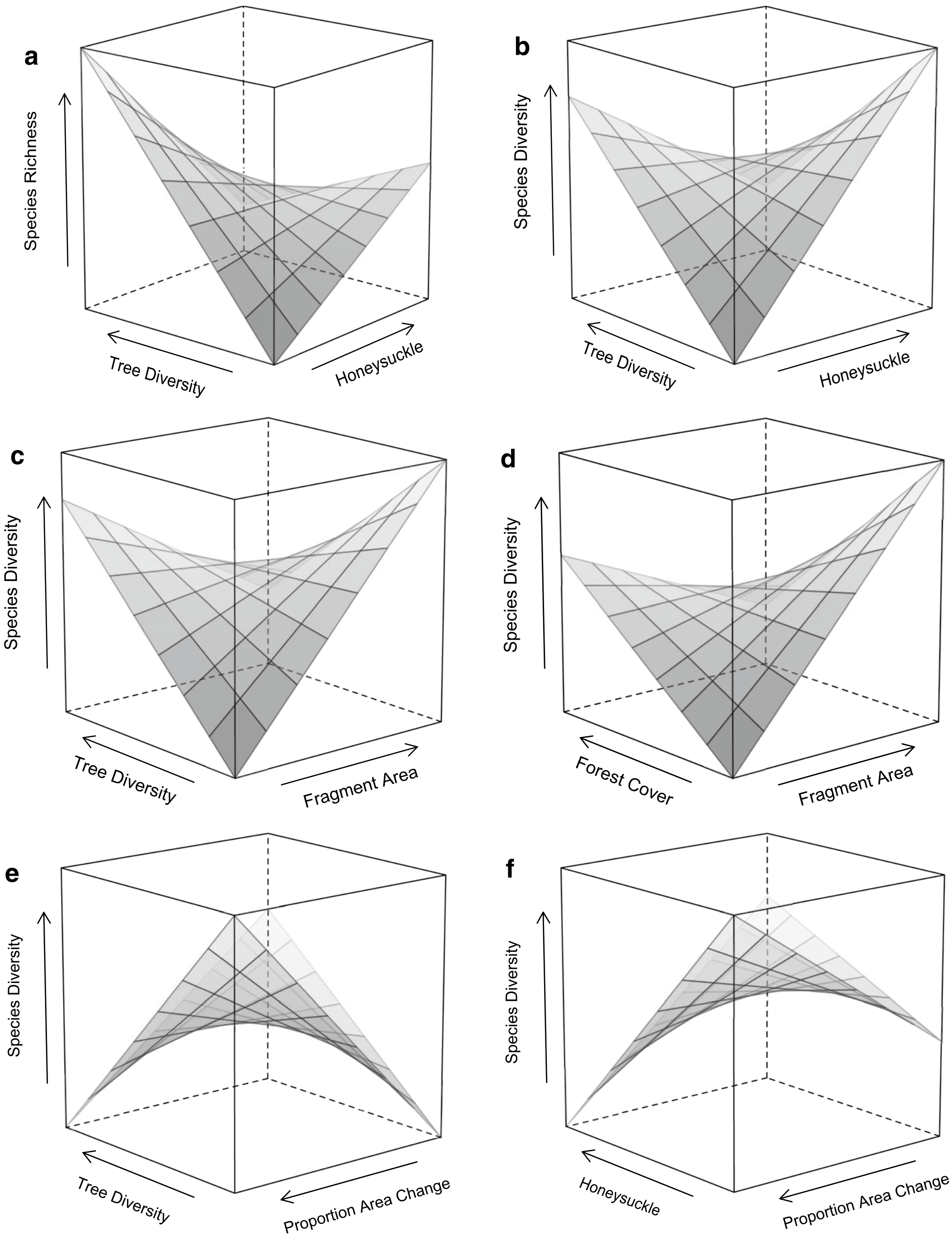
[a] Current area

Caterpillar diversity indices were more strongly affected by fragment variables (Table 5), with significant positive effects of fragment area and honeysuckle, negative effects of change in area, and interactions of both area and honeysuckle with tree diversity. High values of honeysuckle and large fragment areas dampened positive effects of tree diversity on caterpillar diversity (Fig. 3b, c). Historical area (1989) provided a marginally better fit than current area (ΔAIC = 0.23).

Summer

For the summer caterpillar community, we found no clear effects of fragment traits or their interactions on species

Fig. 3 Surface plots illustrating linear predictors of interaction effects on caterpillar *richness* and *diversity* within the statistical model framework. **a** Interaction between tree diversity and honeysuckle on caterpillar richness (spring), **b** interaction between tree diversity and honeysuckle on caterpillar diversity (spring), **c** interaction between tree diversity and fragment area (spring), **d** interaction between landscape forest cover and fragment area (summer), **e** interaction between tree diversity and change in fragment area (summer), **f** interaction between honeysuckle and change in fragment for all caterpillars (spring + summer)



richness (Table 4). The retained model hints at a marginally significant positive effect of area, and marginal non-significant effects of honeysuckle and its interaction with tree diversity, but the model as a whole was not significant ($F_{4,12} = 2.375$, $p > 0.110$). Analyses with tree richness recovered a weak positive effect of fragment area ($p = 0.041$; Table S3). Caterpillar diversity on the other hand revealed of number of significant relationships, including negative effects of honeysuckle and tree diversity, positive effects of area change, and interactions between fragment area and forest cover, area change and tree diversity and area change and honeysuckle (Fig. 3d–f; Table 5). In general, high landscape forest cover (greater connectance) diminished the positive effects of fragment area (Fig. 3d). Large changes in area appeared to reverse positive effects of tree diversity (Fig. 3e) and exacerbate negative effects of honeysuckle (as in Fig. 3f).

Richness of caterpillars across both seasons was positively influenced by fragment area, and honeysuckle eliminated positive effects of tree diversity (see Fig. 3a). A similar model, with tree richness rather than diversity, indicated positive effects of area and change in area, negative effects of landscape forest cover and honeysuckle, and interactions between fragment area and forest cover, tree richness and honeysuckle (as above), and tree richness and area change (Table S3). In terms of caterpillar diversity, we found

Table 5 Multiple regression models for caterpillar diversity (e^H) per fragment with tree diversity as an explanatory variable

Predictor	Spring Est.	Spring *t*	Spring *p*	Summer Est.	Summer *t*	Summer *p*	Total Est.	Total *t*	Total *p*
log*A*[a]	0.35	3.11	**<0.01**	0.45	3.89	<0.01	0.20	1.13	<0.29
HS	0.12	3.66	**<0.004**	−0.14	−4.41	**<0.007**	−0.46	−6.72	**<0.0001**
treeDiv	0.03	1.13	<0.28	−0.20	−8.08	**<0.0005**	−0.29	−4.92	**<0.0008**
logFA				−0.84	−2.35	<0.07	−0.40	−0.57	<0.58
ΔArea	−1.43	−6.26	**<0.0001**	0.97	4.58	**<0.006**	0.81	1.57	<0.15
logA:treeDiv	−0.22	−4.28	**<0.002**						
logA: logFA				−5.04	−6.60	**<0.002**	−6.06	−3.49	**<0.007**
HS:treeDiv	−0.32	−8.96	**<0.0001**	0.03	3.78	<0.013			
HS:LogFA				0.84	3.80	<0.013			
HS:ΔArea				−0.33	−6.05	**<0.002**	−1.98	−7.84	**<0.0001**
treeDiv:ΔArea				−1.14	−7.14	**<0.0008**	−0.65	−5.71	**<0.0003**
LogFA:ΔArea				−5.15	−2.64	<0.05			

See Table 3 for explanation of terms

Significant *p* values, adjusted for multiple comparisons within models, are in bold

[a] 1989 area for spring, current area for summer and total

strong negative effects of honeysuckle and tree diversity, as well as the same strong interactions between fragment area and forest cover and between change in area and honeysuckle/tree diversity observed in the summer analysis (Fig. 3d–f; Table 5).

Discussion

If there is one overarching conclusion from our results, it is that the effects of forest fragmentation, plant invasion and tree diversity on insect herbivore communities are complex and interactive. Single factors, such as fragment area or levels of honeysuckle infestation, by themselves explain little variation in most analyses. Interactions between variables are paramount, and many key relationships are only apparent when considered in the full model context, where other factors and interactions are controlled for. Indeed, in accordance with the marginality principle of statistics mentioned previously, we focus primarily on these interactions in trying to understand how habitat variables influence caterpillar communities. Our results also illustrate that diversity and species richness cannot be viewed simply as surrogates of one another, as they respond in different, sometimes contrasting ways to fragment traits. Another notable finding is the importance of recent changes in fragment area on caterpillar communities, indicating that these systems are far from "equilibrium" conditions. Finally, we found that distinct seasonal caterpillar communities respond quite differently to fragment characteristics, highlighting the importance of temporal influences on community structure. For example, invasive honeysuckle has a considerably stronger influence on the spring community than the summer, and positive relationships between caterpillar richness/diversity and tree diversity in spring are absent or reversed in summer. Although fewer caterpillars were sampled in spring, the combined season analyses generally reflect an averaging of effects on each particular season, with neither season wholly driving overall patterns. In the following discussion, we examine the major interactive effects of fragment variables on the caterpillar community and assess the resulting implications for how habitat fragmentation and plant invasion shape insect communities.

Area effects

Although significant positive effects of area on abundance and richness are present in most models, these effects are often not apparent when examining effects of area in isolation. A previous study of adult moths in Midwest US. forest fragments failed to find area effects on abundance (Summerville and Crist 2003, though see Summerville and Crist 2004); however, several tropical studies have found higher levels of insect herbivory, reflecting increased abundance, in larger fragments (Arnold and Asquith 2002; Fáveri et al. 2008; Ruiz-Guerra et al. 2010). Summerville and Crist (2003) observed that herb feeding moths in Ohio increased in richness in small fragments in the summer, leading to relative modest overall effects of area, and in England, Usher and Keiller (1998) only found significant effects of fragment area on woodland geometrid moths, but not the community as a whole. Thus, area effects can be complicated and additional variables, such as plant species composition, history, and age of the forest fragments, may obscure underlying dependence of caterpillar communities on area.

One underlying cause for a positive relationship between density of caterpillars and area would be if greater richness is maintained in larger fragments and if populations of different caterpillar species are relatively independent (e.g., they do not compete). Larger fragments may also harbor more robust populations (sources) and smaller fragments may be population sinks. Negative edge effects may be more potent in small fragments, and larger areas may be bigger targets for taxa that migrate between forest fragments (Laurance 2008). More indirect effects may also play a role. For example, variation in caterpillar density across different sized forest fragments could reflect differences in mortality due to predators, parasitoids, or disease (e.g., Ruiz-Guerra et al. 2012).

We found limited evidence of interactive effects between fragment area and invasive honeysuckle levels on abundance of caterpillars, and no evidence of such interactions on caterpillar richness. In spring, high levels of honeysuckle counteracted positive relationships between fragment area and abundance, and there was a suggestion of interaction modification, with abundance decreasing with area at the highest levels of honeysuckle. Although abundance was highest in large fragments with low honeysuckle, in small fragments honeysuckle had a marginally positive effect (Fig. 1a).

Effects of fragment area on caterpillar abundance and diversity were dependent on tree diversity (or richness), indicating that high tree diversity can compensate for small area. For the summer community, tree diversity appears to be the dominant driver of caterpillar abundance and area effects are only apparent when tree diversity is low (Fig. 2c). But, for spring caterpillar abundance and diversity, fragment area is at least as important as tree diversity, perhaps more so (Fig. 3c). These differing responses illustrate the ecological differences between these two seasonal communities, and suggest a scenario of lower migration in the spring fauna, where population sizes are dependent on local resource amounts, and greater migration of the summer fauna, where more diverse fragments may "capture" migrating adults.

Fragment area also interacted with landscape forest cover on summer (and total) caterpillar diversity: positive effects of fragment area diminish as landscape forest cover increases (Fig. 3d). This result is sensible from an island biogeographic perspective: as isolation decreases, area becomes less important as a determinant of diversity, although the suggestion that caterpillar diversity decreases with forest cover under some conditions departs from this simple theoretical perspective (see below). These results imply that there is dispersal limitation of adults (or caterpillars) among fragments, so they may indeed act as islands. However, such interactions were not observed for caterpillar abundance or richness, indicating that these effects were on the evenness of species, not necessarily their number.

Change in fragment area

Of the 19 wooded areas we examined, 18 increased in size from 1956 to the present. The average increase in area was 30 %, and some small fragments increased by nearly 100 %. Most of this increase in area represents immature forest developing on formerly agricultural land, thus change in area can be viewed as a proxy for the proportion of fragment area in early succession. This increase in wooded area is consistent with findings of other studies in southwestern Ohio (Medley et al. 1995). The young forest stands responsible for changes in area are likely to differ from mature forests in microclimate, habitat structure, and diversity, and are more likely to be heavily infested with honeysuckle (Flory and Clay 2006), such that they contribute less (or differently) to caterpillar abundance and richness. Such young, secondary growth may contribute to species richness and abundance patterns by supporting generalist or edge-associated taxa, but have little impact on taxa dependent upon mature forest.

The seasonal communities responded quite differently to recent changes in area. In spring the effect was largely negative, whereas in summer it was largely positive (Tables 3, 5). Negative effects were most evident in small and diverse fragments, whereas in large and tree-species-poor fragments, effects were absent or positive (Fig. 1b, e). For summer abundance, recent increases in area appeared to compensate for low tree diversity, but in terms of caterpillar diversity, these two factors acted antagonistically, i.e., area change increased caterpillar diversity in depauperate fragments and decreased it in diverse fragments. The young second growth forest responsible for changes in area appears to be of poor quality for the spring, forest dependent, caterpillar fauna, whereas it may represent attractive resources for the more mobile and less forest-dependent summer community. Still, diversity of the latter community suffered from interactive effects of change in area and high honeysuckle levels (Fig. 3f). It is not clear why large proportional changes in area should have more pronounced negative effects in diverse fragments, and additional studies are needed to assess the generality and causes of this pattern.

Tree diversity

Our measure of tree diversity is imperfect in that it only includes those woody plants with understory foliage available for searching. However, this diversity measure may be the most relevant, given that we were unable to survey the canopy (see below). Interestingly, tree diversity was not closely related to fragment area, whereas tree richness was (Table 2; richness: $F_{1,19} = 8.246$, adj. $R^2 = 0.266$, $p < 0.01$). Consistent with previous studies (e.g., Summerville and Crist 2004), tree diversity was among the most important factors influencing caterpillar abundance and richness, largely through interactions with other variables. Substantial beta diversity of caterpillar species among host trees from which greater than ten taxa were reared (Sørenson dissimilarity; mean 0.851, range 0.29–1.0) suggests that this effect is due, at least in part, to differences in the caterpillar communities hosted by specific tree species, although few sampled caterpillar species appeared to be specialists. The absence of major positive effects of tree diversity on summer caterpillar richness or diversity supports that the summer fauna we sampled is less dependent on forest-specific woody plants per se (as in Summerville and Crist 2003).

Effects of tree diversity on caterpillar abundance were dependent on every other variable examined: it was most beneficial in small fragments, those in more highly forested landscapes, those with high levels of honeysuckle infestation, and those that experienced little recent change in area. In general, it appears to insulate or "rescue" caterpillar abundance from negative effects of other fragment traits, and when fragments are large or honeysuckle is low, diversity has little effect (see Fig. 2a, c). This pattern suggests that fragments can support high caterpillar densities if there is sufficient diversity of native woody-plant species, despite honeysuckle invasion. However, caterpillar richness (and diversity) is most adversely affected by honeysuckle in more diverse fragments (Fig. 3a). Thus, honeysuckle invasion appears to cause high diversity fragments to behave, in terms of caterpillar richness, as though they are low diversity fragments. This pattern, driven by the spring caterpillar fauna, may reflect direct interference of honeysuckle on host location or performance (see below). Although it is tempting to interpret effects of tree diversity on caterpillar communities as direct effects, tree diversity is also likely to be correlated with other fragment characteristics, including the age and successional stage of the forest stands, degree of disturbance, and topographic heterogeneity.

It is unclear why summer caterpillar diversity should decline with tree diversity and why tree diversity should interact with the degree of change in area (Fig. 3e). There appear to be two ways for forest fragments to maintain high caterpillar diversity: either to have high tree diversity and little change in area, which may support forest dependent taxa, or to have low tree diversity and much change in area, which may provide early successional habitat that supports generalist herb and woody plant feeders and edge-associated taxa.

Honeysuckle invasion

Overall, abundance and richness of caterpillars suffers from honeysuckle invasion, but this relationship is modified by other fragment traits. The more dramatic impact of honeysuckle on abundance in more isolated fragments (spring; Fig. 1c) supports a view of limited dispersal of spring caterpillars. Similar interactions with tree diversity highlight the differences in how honeysuckle affects abundance versus richness. Abundance is only dampened by honeysuckle in fragments where tree diversity is low, possibly reflecting the development of a honeysuckle monoculture, whereas honeysuckle limits the ability of caterpillar richness to respond to tree diversity (Fig. 3a; see above). An apparent increase in spring caterpillar diversity with greater honeysuckle infestation in low tree diversity fragments is counterintuitive (Fig. 3a, b). This could result from honeysuckle invasion limiting persistence of rare taxa and encouraging a more equitable distribution of tolerant species. However, as mentioned previously, the combination of high honeysuckle and large changes in fragment area, representing early successional forest, is particularly devastating for caterpillar diversity (Fig. 3f). These interactions indicate that plant invasion in this system has the potential to alter not just the magnitude, but the direction of relationships (i.e., interaction modification) between caterpillar abundance/richness and other fragment traits.

Potentially, the most dramatic effects of honeysuckle on caterpillar communities are hidden from our analyses because we did not search for caterpillars on honeysuckle and did not include honeysuckle in our estimates of sampling effort (see above). If leaf area of honeysuckle was considered, caterpillar density and richness estimates would be lower for sites with extensive honeysuckle (because caterpillars are rarely found on this invasive shrub), resulting in more detrimental effects of honeysuckle. That we can discern strong negative effects of honeysuckle while only considering native plants and their caterpillars, suggests that the effects of this invasive plant go beyond simple replacement of native hosts.

As alluded to previously, honeysuckle invasion may influence caterpillar communities through a variety of mechanisms. It may directly limit recruitment and growth of native woody plant species (Hartman and McCarthy 2008), reducing resource abundance and diversity for forest herbivores. It may also interfere with host finding or selection more directly by reducing host plant apparency in the understory (e.g., Severns 2008), or it may acts as a population sink for generalist herbivores that accept it as a host but perform poorly on it (McEwan et al. 2009; Lieurance and Cipollini 2013). Honeysuckle has recently been shown to have a positive effect on overall arthropod diversity due to increased structural diversity (although not Lepidoptera specifically; Loomis and Cameron 2014), and this could translate into indirect effects by enhancing predation. Finally, other unmeasured variables associated with honeysuckle may have effects on caterpillar communities. For example, honeysuckle tends to be more abundant in younger, more open forest stands (Flory and Clay 2006), which may be characterized by increased sunlight, high plant growth rates and potentially greater predation pressure.

Landscape forest cover and isolation

In our analyses, the amount of forest cover around forest fragments (5-km radius) represents the relative isolation of forest fragments. However, the permeability of the non-forest matrix to migrating adults or wind born larvae may be high. The matrix surrounding focal fragments was primarily low density suburban residential areas and agricultural land (row crops, pasture, old fields). The former may provide habitat for woody plant feeding caterpillars and the latter may not present a formidable barrier to flying adults. Wooded fence rows and stream edges may also provide corridors for dispersal. Although high landscape forest cover appeared to mitigate the effects of small area on caterpillar diversity (as mentioned previously), it was associated with lower caterpillar abundance in both seasons. These negative effects were most apparent when honeysuckle levels, tree diversity and changes in fragment area were low (see Figs. 1c, d, 2d). These results contradict expectation, as greater connectivity should enhance caterpillar abundance, but they may be due to indirect effects. Greater landscape forest cover and connectance among fragments may, for example, sustain larger populations of enemies resulting in higher risk of predation or parasitism, especially in simplified (low diversity) habitats. Another possibility is that in less forested landscapes, there is a resource concentration effect in which abundances are elevated due to absence of nearby suitable habitat, but it is unclear why this should be most pronounced where tree diversity and honeysuckle is low.

Seasonal community responses

Why do spring and summer caterpillar communities respond differently to forest fragment traits? It is clear from measures of similarity and overlap that these phenological communities are distinct, as has been found in other studies of forest Lepidoptera (Summerville and Crist 2002, 2003; Hirao et al. 2007; Murakami et al. 2008; Sigmon and Lill 2013). However, variation in host specificity cannot account for differing responses of seasonal caterpillar communities as no differences were observed in host ranges relative to season (mean host families: spring: 3.76, summer: 3.54), and the proportion of generalist species (>2 host families) was actually higher in spring (0.46) than in summer (0.40). Even when considering abundance, the average caterpillar in spring was no more polyphagous than that in summer (4.14 families versus 4.11 families, respectively; $F_{1,\ 1975} = 0.054$, $p = 0.816$). One possible reason for the different responses of these seasonal communities suggested by our results is that the early season caterpillar community consists predominantly of forest habitat specialists. Early season caterpillars tend to depend on new leaves of deciduous trees that are softer and have higher nitrogen content than mature leaves (Hunter 1991; Murakami et al. 2005, 2008). Many spring caterpillar species are also univoltine, with most of the life cycle being spent in a quiescent stage in forest leaf litter and soils. Particular environmental conditions of undisturbed forest soils may be necessary for survival through the ensuing summer, fall, and winter. A number of spring moths are relatively weak fliers (Usher and Keiller 1998), which may limit their dispersal among fragments and make them more susceptible to local extinction. In fact, females of several common spring taxa including *Alsophila pometaria*, *Psyche casta* and *Orgyia definata* have completely lost the ability to fly. In contrast, the summer community is comprised of more habitat generalist species and taxa that may feed on both woody and herbaceous plants (e.g., some arctiines). The most commonly collected species in this season, *Hyphantria cunea*, is a highly polyphagous woody-plant feeder that is found almost exclusively in edge habitats (Mason et al. 2011), and the second most abundant caterpillar, *Atteva aurea*, is locally specialized on the invasive tree *Ailanthus altissima* (“Tree of Heaven”), which is also primarily found around woodland edges (McDonald and Urban 2006; Espenschied-Reilly and Runkle 2008). Differing responses of these seasonal faunas to fragmentation and invasive honeysuckle can obscure effects of fragment variables when they are considered as a group (e.g., see Cook et al. 2002; Lövei et al. 2006).

The canopy caveat

All of the results presented here must be tempered by the fact that we only surveyed caterpillars in the forest understory, and our ability to extrapolate to the canopy is unclear. Although one would expect the understory fauna to be reflective of the whole caterpillar community, densities of caterpillars can be high in canopies (Wagner et al. 1995; Le Corff and Marquis 1999), and species composition can exhibit appreciable stratification due to a variety of factors including foliage nutritional and defensive characteristics (Le Corff and Marquis 1999; Murakami et al. 2005; Hirao et al. 2009). Sampling may have also been biased towards taxa that use saplings or shrubs, which may be more characteristic of younger, more disturbed forest habitats (e.g., canopy gaps, second growth). For example, some mature forest stands had relatively little woody-plant foliage in the understory, which may bias estimates of abundance. All of the fragments examined here are probably suffering some degree of recruitment limitation from canopy trees due to high deer density, lack of fire, competition with invasive plants and other sources (e.g., Côté et al. 2004; Thompson et al. 2013), and this may have a significant impact on the caterpillar fauna found in the understory (e.g., lower diversity, more polyphagous). The extent of recruitment limitation may vary with area, with more pronounced effects expected in smaller and more isolated wood lots (Rogers et al. 2009).

Ideally, future studies would sample both in the understory and canopy and examine the extent of recruitment limitation, but such standardized canopy sampling across sites presents formidable logistical challenges. We also note that there was great variability in caterpillar abundance from year to year that could influence the results of our analyses, despite our inclusion of year as a random effect. Longer term data sets are necessary to account for year-to-year variation and to understand how this variation itself depends on fragment characteristics.

Conclusions

Despite potentially confounding factors and differing responses of seasonal assemblages, we found clear and often strong effects of fragmentation and plant invasion on forest Lepidoptera communities. Overall, caterpillar abundance and diversity was higher in larger fragments and isolation modified this effect, indicating that there is some value to applying an island-biogeographic perspective to understanding effects of forest fragmentation on insect herbivore communities. However, these are not necessarily the most important fragment traits in structuring the communities we examined, and major modifying factors are necessary. In particular, tree diversity and its interactions with invasive honeysuckle, forest fragmentation, and change in fragment area were among the most important determinants of abundance and diversity for this ecological guild. This is not surprising, given previous research on insect herbivores in fragmented landscapes (e.g., Summerville and Crist 2003), and the expectation that habitat diversity should, in general, promote greater richness (Ricklefs and Lovette 1999). Given that substantial beta diversity in caterpillar fauna may exist between individuals of the same tree species (Summerville et al. 2003), within-host species "habitat diversity" may also contribute to area effects on richness. More diverse fragments may also maintain more robust populations of more species or be more likely to attract adults moving across the landscape.

Our prediction of interactive effects (either numerically mediated or functionally moderated) between fragment area and honeysuckle was upheld for caterpillar abundance in spring, but not for other measures of caterpillar abundance or diversity. This general weak effect may be due in part to the relatively stronger effects of tree diversity than area on caterpillar abundance and richness in most circumstances. We did find evidence of interaction modification effects of honeysuckle with other fragment variables. Honeysuckle fundamentally alters the influence of isolation on caterpillar abundance (in spring), eliminating apparent benefits associated with isolation (e.g., reduced predation), and it transforms potential positive effects of changes in fragment area to severe negative ones. Honeysuckle also changes the nature of the relationship between tree diversity and caterpillar abundance and richness. In the former case, it appears to create the relationship (i.e., tree diversity has no effect at low honeysuckle levels), and in the latter case, it appears to destroy it, or even reverse it. These effects of honeysuckle invasion would clearly not be apparent without considering interactions with other fragment traits.

Relationships between fragment traits and species richness or diversity may be misleading from a conservation perspective. Local richness (alpha diversity) may peak in the transitional habitats of edges or early successional forest, but as more and more habitat becomes edge-like, beta and gamma diversity may decrease and forest-dependent species may decline. As an analogy, the United States undoubtedly contains more plant species now than when first colonized by Europeans; however, a growing proportion of the flora is non-native (an estimated 25,000 alien plant species naturalized in the United States; Pimentel et al. 2005), resulting in biotic homogenization at a global scale. Similar biotic homogenization may be occurring on a much smaller scale with the caterpillar fauna of fragmented forests in southwestern Ohio (Summerville and Crist 2003). Additional, longer term studies of caterpillars and other insect herbivores are needed to understand the complicated responses of primary consumers to fragmentation, plant invasion, and other changes in the environment, and how best to maintain their diversity and that of the parasites and predators that depend on them.

Acknowledgments We thank Patrick McAfee, Nathan Sandman, Todd England, Julietta Chavez, and Brenda Wells for help in caterpillar sampling and rearing. We would also like to thank M.S. Singer for providing valuable comments on a previous draft of this manuscript and for sharing his knowledge of caterpillar biology, and Steve Passoa (USD/APHIS) for assistance in identifying 'microlepidoptera'. We would like to thank the Ohio Department of Natural Resources, Dayton Five-River Metroparks, Greene County Parks, Fairborn Parks, the Glen Helen Nature Preserve, CEMEX Inc., and private landowners Gray and Joyce Breeze, Mark and Patty Fife, and Patty and Mark Thompson. This project was supported in part by NSF grants DEB 0717092 and 1020571 to J.O.S.

References

Andresen E (2003) Effect of forest fragmentation on dung beetle communities and functional consequences for plant regeneration. Ecography 26:87–97

Arnold AE, Asquith NM (2002) Herbivory in a fragmented tropical forest: patterns from islands at Lago Gatun, Panama. Biodivers Conserv 11:1663–1680

Bates D, Maechler M, Bolker B, Walker S (2013). lme4: Linear mixed-effects models using Eigen and S4. R package version 1.0-4. http://CRAN.Rproject.org/package=lme4

Brook BW (2009) Global warming tugs at trophic interactions. J Anim Ecol 78:1–3

Brown DG (2003) Land use and forest cover on private parcels in Upper Midwest, USA 1970 to 1990. Landscape Ecol 18:777–790

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer, New York

Collier MH, Vankat JL, Hughs MR (2002) Diminished plant richness and abundance below *Lonicera maackii*, an invasive shrub. Am Midl Nat 147:60–71

Cook WM, Lane KT, Foster BL, Holt RD (2002) Island theory, matrix effects and species richness patterns in habitat fragments. Ecol Lett 5:619–623

Côté SD, Rooney TP, Tremblay J-P, Dussault C, Waller D (2004) Ecological impacts of deer overabundance. Annu Rev Ecol Evol Syst 35:113–147

Covell CV (2005) Moths of Eastern North America. Virginia Museum of Natural History, Martinsville

Cronk QC, Fuller JL (1995) Plant invaders: The threat to natural ecosystems. Chapman and Hall, London

Crooks JA (2002) Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. Oikos 97:153–166

Curtis JT (1956) The modification of mid-latitude grasslands and forest. In: Thomas WL (ed) Man's role in changing the face of the earth. University of Chicago Press, Chicago, pp 721–736

Daly HV, Doyen JT, Purcell AH III (1998) Introduction to Insect Biology and Diversity, 2nd edn. Press, New York, Oxford U

Deering RH, Vankat JL (1999) Forest colonization and developmental growth of the invasive shrub *Lonicera maackii*. Am Midl Nat 141:43–50

Didham RK (1997) An overview of invertebrate responses to forest fragmentation. In: Watt AD, Stork NE, Hunter MD (eds) Forests and insects. Chapman and Hall, London, pp 303–320

Didham RK, Ghazoul J, Stork NE, Davis AJ (1996) Insects in fragmented forests: a functional approach. Trends Ecol Evol 11:255–260

Didham RK, Hammond PM, Lawton JH, Eggleton P, Stork NE (1998) Beetle species responses to tropical forest fragmentation. Ecol Monogr 68:295–323

Didham RK, Tylianakis JM, Hutchison MA, Ewers RM, Gemmell NJ (2005) Are invasive species the drivers of ecological change? Trends Ecol Evol 20:470–474

Didham RK, Tylianakis JM, Gemmell NJ, Rand TA, Ewers RM (2007) Interactive effects of habitat modification and species invasion on native species decline. Trends Ecol Evol 22:489–496

Dyer LA, Singer MS, Lill JT, Stireman JO III, Gentry GL, Marquis RJ, Ricklefs RE, Greeney HF, Wagner DL, Morais HC, Diniz IR, Kursar TA, Coley PD (2007) Host specificity of Lepidoptera in tropical and temperate forests. Nature 448:606–700

Espenschied-Reilly AL, Runkle JR (2008) Distribution and changes in abundance of *Ailanthus altissima* (Miller) Swingle in a southwest Ohio woodlot. Ohio J Sci 108:16–22

Fáveri SB, Vasconcelos JL, Dirzo R (2008) Effects of Amazonian forest fragmentation on the interaction between plants, insect herbivores, and their natural enemies. J Trop Ecol 24:57–64

Flory SL, Clay K (2006) Invasive shrub distribution varies with distance to roads and stand age in eastern deciduous forests in Indiana, USA. Plant Ecol 184:131–141

Fox J (2003) Effect Displays in R for Generalised Linear Models. J Stat Softw 8:1–27

Gorchov DL, Trisel DE (2003) Competitive effects of the invasive shrub, *Lonicera maackii* (Rupr.) Herder (Caprifoliaceae) on the growth and survival of native tree seedlings. Plant Ecol 166:13–24

Gould AMA, Gorchov DL (2000) Effects of the exotic invasive shrub *Lonicera maackii* on the survival and fecundity of three species of native annuals. Am Midl Nat 144:36–50

Haberl H, Erb KH, Krausmann F, Gaube V, Bondeau A, Plitzar C, Gingrich S, Lucht W, Fischer-Kowalski M (2007) Quantifying and mapping the human appropriation of net primary production in earth's terrestrial ecosystems. Proc Natl Acad Soc USA 104:12942–12947

Hartman KM, McCarthy BC (2008) Changes in forest structure and species composition following invasion by a non-indigenous shrub, Amur honeysuckle (*Lonicera maackii*). J Torrey Bot Soc 135:245–259

Hill JK, Gray MA, Khen CV, Benedick S, Tawatao N, Hamer KC (2011) Ecological impacts of tropical forest fragmentation: how consistent are patterns in species richness and nestedness? Philos T R Soc B 366:3265–3276

Hirao T, Murakami M, Kashizaki A, Tanabe SI (2007) Additive apportioning of lepidopteran and coleopteran species diversity across spatial and temporal scales in a cool-temperate deciduous forest in Japan. Ecol Entomol 32:627–636

Hirao T, Murakami M, Kashizaki A (2009) Importance of the understory stratum to entomofaunal diversity in a temperate deciduous forest. Ecol Res 24:263–272

Hunter AF (1991) Traits that distinguish outbreaking and non outbreaking macrolepidoptera feeding on northern hardwood trees. Oikos 60:275–282

Hutchinson TF, Vankat JL (1997) Invasibility and effects of amur honeysuckle in Southwestern Ohio forests. Conserv Biol 11:1117–1124

Iverson LR (1988) Land use changes in Illinois, USA: the influence of landscape attributes on current and historic land use. Landscape Ecol 2:45–61

Iverson LR, Cook EA, Graham RL (1994) Regional forest cover estimation via remote-sensing—the calibration center concept. Landscape Ecol 9:159–174

Janzen DH (1988) Ecological characterization of a Costa Rican dry forest caterpillar fauna. Biotropica 20:120–135

Jost L (2006) Entropy and Diversity. Oikos 116:363–375

Kitching RL, Orr AG, Thalib L, Mitchell H, Hopkins MS, Graham AW (2000) Moth assemblages as indicators of environmental quality in remnants of upland Australian rainforest. J Appl Ecol 37:284–297

Kremen C, Colwell RK, Erwin TL, Murphy DD, Noss RF, Sanjayan MA (1993) Terrestrial arthropod assemblages: their use in conservation planning. Conserv Biol 7:796–808

Laurance WF (2008) Theory meets reality: how habitat fragmentation research has transcended island biogeographic theory. Biol Conserv 141:1731–1744

Laurance WF, Berregaard RO (1997) Tropical forest remnants: Ecology, management, and conservation of fragmented communities. University of Chicago Press, Chicago

Laurance WF, Lovejoy TE, Vasconcelos HL, Bruna EM, Didham RK, Stouffer PC, Gascon C, Bierregaard RO, Laurance SG, Sampaio E (2002) Ecosystem decay of Amazonian forest fragments: a 22-year investigation. Conserv Biol 16:605–618

Le Corff J, Marquis RJ (1999) Differences between understorey and canopy in herbivore community composition and leaf quality for two oak species in Missouri. Ecol Entomol 24:46–58

Lieurance D, Cipollini DF (2011) Damage levels from arthropod herbivores on *Lonicera maackii* suggest enemy release in its introduced range. Biol Invasions 14:863–873

Lieurance D, Cipollini DF (2013) Exotic *Lonicera* species both escape and resist specialist and generalist herbivores in the introduced range in North America. Biol Invasions 15:1713–1724

Loomis JD, Cameron GN (2014) Impact of the invasive shrub Amur honeysuckle (*Lonicera maackii*) on shrub-layer insects in a deciduous forest in the eastern United States. Biol Invasions 16:89–100

Lövei GL, Magura T, Tóthmérész B, Ködöböcz V (2006) The influence of matrix and edges on species richness patterns of ground beetles (Coleoptera, Carabidae) in habitat islands. Global Ecol Biodiv 15:283–289

Luken JO, Thieret JW (1996) Amur honeysuckle, its fall from grace. Bioscience 46:18–24

Lund MP, Rahbek C (2002) Cross-taxon congruence in complementarity and conservation of temperate biodiversity. Anim Conserv 5:163–171

MacArthur RH, Wilson EO (1967) The theory of island biogeography. Princeton University press, Princeton

Mason PA, Wilkes SR, Lill JT, Singer MS (2011) Abundance trumps quality: bi-trophic performance and parasitism risk fail to explain host use in the fall webworm. Oikos 120:1509–1518

Mazerolle MJ (2013) AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 1.27. http://CRAN.R-project.org/package=AICcmodavg

McDonald RI, Urban DL (2006) Edge effects on species composition and exotic species abundance in the North Carolina Piedmont. Biol Invasions 8:1049–1060

McEwan RW, Rieske LK, Arthur MA (2009) Potential interactions between invasive woody shrubs and the gypsy moth (*Lymantriadispar*), an invasive insect herbivore. Biol Invasions 11:1053–1058

McKinney ML, Lockwood JL (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends Ecol Evol 14:450–453

Medley KE, Okey BW, Barrett GW, Lucas MF, Renwick VM (1995) Landscape change with agricultural intensification in a rural watershed, southwestern Ohio, USA. Lands Ecol 10:161–176

Montero-Castaño A, Vilà M (2012) Impact of landscape alteration and invasions on pollinators: a meta-analysis. J Ecology 100:884–893

Murakami M, Yoshida K, Hara H, Toda MJ (2005) Spatio-temporal variation in Lepidopteran larval assemblages associated with oak, *Quercuscrispula*: the importance of leaf quality. Ecol Entomol 30:521–531

Murakami M, Ichie T, Hirao T (2008) Beta-diversity of lepidopteran larval communities in a Japanese temperate forest: effects of phenology and tree species. Ecol Res 23:179–187

Nelder JA (1977) A Reformulation of Linear Models. J Roy Stat Soc 140:48–77

Norton TW (1996) Conservation of biological diversity in temperate and boreal forests. Forest Ecol Manag 85:1–7

Noss RF (1999) Assessing and monitoring forest biodiversity: a suggested framework and indicators. Forest Ecol Manag 115:135–146

Pimentel D, Lach L, Zuniga R, Morrison D (2000) Environmental and economic costs of nonindigenous species in the United States. Bioscience 50:53–65

Pimentel D, Zuniga R, Morrison D (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecol Econ 52:273–288

Porter SD, Sagivnano DA (1990) Invasion of polygyne fire ants decimates native ants and disrupts arthropod community. Ecology 71:2095–2106

Potapov P, Yaroshenko A, Turubanova S, Dubinin M, Laestadius L, Thies C, Aksenov D, Egorov A, Yesipova Y, Glushkov I, Karpachevskiy M, Kostikova A, Manisha A, Tsybikova E, Zhuravleva I (2008) Mapping the World's Intact Forest Landscapes by Remote Sensing. Ecol Soc 13:51

Price PW (1997) Insect ecology, 3rd edn. Wiley, New York

Prugh LR, Hodges KE, Sinclair ARE, Brashares JS (2008) Effect of habitat area and isolation on fragmented animal populations. P Natl Acad Sci U SA 105:20770–20775

R Development Team (2012) R: a language and environment for statistical computing. V. 2.15.2.R Foundation for Statistical Computing. URL http://www.R-project.org

Rasband WS (1997–2011) ImageJ. US. National Institutes of Health (http://imagejnih.gov/ij/)

Ricketts TA, Daily G, Ehrlich PR, Fay JP (2001) Countryside biogeography of moths in a fragmented landscape: biodiversity in native and agricultural habitats. Conserv Biol 15:37–388

Ricklefs RE, Lovette IJ (1999) The roles of island area *per se* and habitat diversity in the species-area relationships of four Lesser Antillean faunal groups. J Anim Ecol 68:1142–1160

Ries L, Fletcher RJ Jr, Battin J, Sisk TD (2004) Ecological responses to habitat edges: mechanisms, models and variability explained. Annu Rev Ecol Evol Syst 35:491–522

Rogers DA, Rooney TP, Hawbaker TJ, Radeloff VC, Waller DM (2009) Paying the extinction debt in southern Wisconsin forest under stories. Conserv Biol 23:1497–1506

Ruiz-Guerra B, Guevara R, Mariano NA, Dirzo R (2010) Insect herbivory declines with forest fragmentation and covaries with plant regeneration mode: evidence from a Mexican tropical rain forest. Oikos 119:317–325

Ruiz-Guerra B, Renton K, Dirzo R (2012) Consequences of fragmentation of tropical moist forest for birds and their role in predation of herbivorous insects. Bio tropica 44:228–236

Sala OE, Chapin FS, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A, Leemans R, Lodge DM, Mooney HA, Oesterheld M, Poff NL, Sykes MT, Walker BH, Walker M, Wall DH (2000) Global biodiversity scenarios for the year 2100. Science 287:1770–1777

Salo P, Korpimäki E, Banks PB, Nordström M, Dickman CR (2007) Alien predators are more dangerous than native predators to prey populations. P Roy Soc B Biol Sci 274:1237–1243

Sarkar D (2008) Lattice: Multivariate Data Visualization with R. Springer, New York

Schowalter T, Crossley D Jr, Hargrove W (1986) Herbivory in forest ecosystems. Annu Rev Entomol 31:177–196

Severns PM (2008) Exotic grass invasion impacts fitness of an endangered prairie butterfly. Icariciaicarioides fender J Insect Conserv 12:651–661

Sigmon E, Lill JT (2013) Phenological variation in the composition of a temperate forest leaf tie community. Environ Entomol 42:29–37

Smith BE, Marks PL, Gardescus S (1993) Two hundred years of forest cover changes In Tompkins County, New York. B Torrey Bot Club 120:229–247

Smitley D, Davis T, Rebek E (2008) Progression of ash canopy thinning and dieback outward from the initial infestation of emerald ash borer (Coleoptera :buprestidae) in Southeastern Michigan. J Econ Entomol 101:1643–1650

Spiess, A-N (2013) qpcR: modelling and analysis of real-time PCR data. R package version 1.3-7.1. http://CRAN.R-project.org/package=qpcR

Stamp NE, Casey TM (1993) Caterpillars: Ecological and evolutionary constraints on foraging. Chapman and Hall, London

Stireman JO III, Singer MS (2003) Determinants of parasitoid-host associations: insights from a natural tachinid-lepidopteran community. Ecology 84:296–310

Summerville KS, Crist TO (2002) Effects of timber harvest on forest moths (Lepidoptera): community, guild, and species responses. Ecol Appl 12:820–835

Summerville KS, Crist TO (2003) Determinants of lepidopteran community composition and species diversity in eastern deciduous forests: roles of season, eco-region, and patch size. Oikos 100:134–148

Summerville KS, Crist TO, Kahn JK, Gering JC (2003) Community structure of arboreal caterpillars (Lepidoptera) within and among four tree species in the eastern deciduous forest. Ecol Entomol 28:747–757

Summerville KS, Crist TO (2004) Contrasting effects of habitat quantity and quality on moth communities in fragmented landscapes. Ecography 27:3–12

Summerville KS, Crist TO (2008) Structure and conservation of lepidopteran communities in managed forests of northeastern North America: a review. Can Entomol 140:475–494

Thompson JR, Carpenter DN, Cogbill CV, Foster DR (2013) Four Centuries of Change in Northeastern United States Forests. PLoS ONE 8:e72540

Trisel DE (1997) The invasive shrub, *Lonicera maackii* (Rupr.) Herder (Caprifoliaceae): Factors contributing to its success and its effect on native species. PhD Dissertation. Miami University., Oxford, Ohio

Tylianakis JM, Didham RK, Bascompte J, Wardle DA (2008) Global change and species interactions in terrestrial ecosystems. Ecol Lett 11:1351–1363

USDA Plants Database (2012) http://plants.usda.gov/. accessed June 2012

Usher MB, Keiller SWJ (1998) The Macrolepidoptera of farm woodlands: determinants of diversity and community structure. Biodivers Conserv 7:725–748

Vitousek PM, Mooney HA, Lubchenco J, Melillo JM (1997) Human Domination of Earth's Ecosystems. Science 277:494–499

Wagner DL (2005) Caterpillars of Eastern North America. Princeton university Press, Princeton

Wagner DL, Peacock JW, Carter JL, Talley S (1995) Spring caterpillar fauna of oak and blueberry in a Virginia deciduous forest. Ann Entomol Soc Am 88:416–426

Warburton NH (1997) Structure and conservation of forest avifauna in isolated rainforest remnants in tropical Australia. In: Laurence WE, Bierregaard RO (eds) Tropical forest remnants: Ecology, management, and conservation of fragmented communities. University of Chicago Press, Chicago, pp 333–345

Watling JI, Donnelly MA (2006) Fragments as islands: a synthesis of faunal responses to habitat patchiness. Conserv Biol 20:1016–1025

Wilcove DS, Rothstein D, Dubow J, Phillips A, Losos E (1998) Quantifying threats to imperiled species in the United States. Bioscience 48:607–615

With KA, Crist TO (1995) Critical thresholds in species responses to landscape structure. Ecology 76:2446–2459

Zelikova TJ, Dunn RR, Sanders NJ (2008) Variation in seed dispersal along an elevational gradient in Great Smoky Mountains National Park. Acta Oecol 34:155–162