Title: Underrepresentation of dietary-specialist larval Lepidoptera in small forest fragments: testing alternative mechanisms

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Abstract

1. Growing evidence suggests that organisms with narrow niche requirements are particularly disadvantaged in small habitat patches, typical of fragmented landscapes. However, the mechanisms behind this relationship remain unclear. Dietary specialists may be particularly constrained by the availability of their food resources as habitat area shrinks. For herbivorous insects, host plants may be filtered out of small habitat fragments by neutral sampling processes and deterministic plant community shifts due to altered microclimates, edge effects, and browsing by ungulates.
2. We examined the relationship between forest fragment area and the abundance of dietary-specialist and dietary-generalist larval Lepidoptera (caterpillars) and their host plants in the northeastern USA. We surveyed caterpillars and their host plants over three years in equal-sized plots within 32 forest fragments varying in area between 3 and 1014 ha. We tested whether the abundances and species richness of dietary specialists increased more than those of dietary generalists with increasing fragment area, and, if so, whether the difference could be explained by reduced host plant availability or increased browsing by white-tailed deer (*Odocoileus virginianus*).
3. The overall abundance of dietary specialists was positively related to fragment area; the relationship was substantially weaker for dietary generalists. There was notable variation among species within diet breadth groups, however. There was no effect of fragment area on the diversity of dietary-specialist or dietary-generalist caterpillars. Deer activity was not related to the abundances of either dietary-generalist or dietary-specialist caterpillars.
4. Plant community composition was strongly associated with fragment area. Larger fragments were more likely to include host plants for both dietary-specialist and dietary-generalist

caterpillars. Deer activity was correlated with decreased host plant availability for both groups, with a slightly stronger impact on host plants of dietary specialists. Although dietary specialists were more likely to lack host plants in fragments, the relationship between fragment area and host availability did not depend on caterpillar diet breadth.

5. This study provides further evidence that decreasing patch area disproportionately impacts specialist consumers. Because this relationship was derived from equal-sized plots, it is robust to some criticisms levelled at fragmentation research. The mechanisms for specialist consumer declines, however, remain elusive.

Introduction

The role of habitat fragmentation in driving biodiversity declines is controversial (Fahrig, 2017; Haddad et al., 2015, 2017; Riva et al., 2024; Watling et al., 2020). Theory on this topic began with applications of island biogeography theory (MacArthur & Wilson, 1967), drawing parallels between oceanic islands and habitat fragments remaining after habitat loss (Preston, 1962). In practice, the term "habitat fragmentation" is often used to refer to several simultaneous changes to the landscape including habitat loss, edge creation, matrix degradation, and area effects (Didham et al., 2012; Ries et al., 2004; Riva et al., 2024). It is particularly important to separate habitat loss from the spatial configuration of remaining habitat (fragmentation *per se*), especially given that these two aspects of change often covary. Furthermore, the effects of habitat fragmentation often vary by taxon, guild, and life history (Damschen et al., 2008; Fischer & Lindenmayer, 2006; Martinson & Fagan, 2014; Öckinger et al., 2010; Rossetti et al., 2017). The direct effects of fragmentation on individual species may be modified by altered interactions with resources, mutualists, competitors, and enemies (Aizen & Feinsinger, 1994a; Cordeiro & Howe, 2003; Laurance, 2008; Magrach et al., 2014), with the impact of these indirect effects sometimes exceeding those of direct effects (Feeley & Terborgh, 2008). These multifaceted consequences of fragmentation cannot be captured by island biogeography theory, which assumes species equivalency, ignores species interactions, and treats all habitat patches as equally suitable. Such oversimplification has led to criticisms of fragmentation research, and calls for refinement (Didham et al., 2012; Fischer & Lindenmayer, 2006; Laurance, 2008).

An important theoretical extension of island biogeography theory, trophic island biogeographic theory (Gravel et al., 2011; Holt, 1996), predicts that species' trophic position and dietary specialisation affect their sensitivity to fragment area. For a species to colonise and persist in a habitat patch, the species it consumes must also be present (Gravel et al., 2011; Holt, 1996). Simply by chance, small habitat fragments are less likely to encompass scarce resources like specific host plants (Gravel et al., 2011; Holt, 1996, 2010). Loss of host plant species from small habitat fragments through these neutral processes disproportionately affects dietary specialists because, by definition, they have fewer alternatives. In contrast, dietary generalists are likely to find at least some of their host plants in most habitat fragments. Consequently, the abundances and species richness of specialist herbivore species may decline more steeply with decreasing fragment area than the abundances and species richness of generalist species.

Plant community composition can also vary deterministically with fragment area, for instance, due to altered abundances of predators, browsing herbivores, or invasive species (Allen et al., 2013; Anderson et al., 2019; Fenoglio et al., 2012; Terborgh et al., 2001). Increased browsing by hyperabundant ungulates in small fragments may reduce food availability for insect herbivores, filter out palatable species, and alter microclimates (Alverson et al., 1988; Gorchov et al., 2021; Rooney & Waller, 2003). Even though browsing by herbivores can either increase or decrease overall plant diversity (Mortensen et al., 2018; Trepel et al., 2024), some studies suggest that browsing by deer disproportionately impacts plant species with particularly abundant and rich specialist insect-herbivore faunas (Bagchi et al., 2018; e.g., pin cherry, *Prunus pensylvanica*, in northeastern America, Wheatall et al., 2013). Again, because dietary specialists have few alternative hosts to switch to, broad-scale deer browsing is likely to have a more negative impact on dietary-specialist than dietary-generalist herbivores. Such deterministic effects of fragment area will predominantly impact herbivore species that rely on plant species that are consistently suppressed in smaller fragments (e.g., deer-sensitive plant species), with insects that consume plant species that tolerate, or thrive in, small fragments affected less, or even benefitting. In contrast, because neutral processes remove plant species at random, which herbivore species are affected will vary among fragments, but the expected effect of fragment area will be consistent among species with the same diet-breadth. Therefore, deterministic effects of fragment area should generate more variation in abundance-fragment area relationships among herbivore species within diet-breadth categories area relationships than neutral effects.

Several empirical studies, many from insect-herbivore systems, indicate that dietary-specialist, poor-dispersing, and less-fecund insect species are particularly sensitive to habitat loss, and decreases in fragment area (Martinson & Fagan, 2014; Öckinger et al., 2010; Rossetti et al., 2017). One challenge in understanding the drivers of these patterns is distinguishing how much of the changes in small fragments stem from shifts in the demography of species within them (ecosystem decay) as opposed to reductions in sample sizes in small fragments (passive sampling; Chase et al., 2020). It is also important to control for the potentially confounding effects of habitat amount at larger spatial scales (Riva et al., 2024). Existing studies examining how species traits influence the effects of fragment area on insect herbivores have not used equally sized plots (most are meta-analyses), which makes it difficult to rule out the effects of passive sampling (Chase et al., 2020). Furthermore, there is a dearth of studies that test mechanisms for trait-based variation in area sensitivity among species. For example, although the proportion of insect herbivore species with narrow diet breadth often declines with fragment area (Bagchi et al., 2018; Martinson & Fagan, 2014; Öckinger et al., 2010; Rossetti et al., 2017), few studies link those declines to reduced availability of suitable host plants in small habitat fragments (but see Cirtwill & Stouffer, 2016).

In this study, we examined whether reduced fragment area disproportionately impacted dietary-specialist lepidopteran larvae (caterpillars), and investigated the contributions of shifting plant communities and deer activity to those impacts. We predicted that as fragment area decreased, host plants required by dietary-specialist caterpillars would become less common. We hypothesised that declines in dietary specialists could result from both deterministic filtering out (e.g., by deer) of plant species favoured by specialists in small fragments or, alternatively, from a neutral sampling process where small fragments lose suitable host plant species by chance. The deterministic hypothesis additionally predicts the opposite trend for some dietary-specialist species: small fragments should contain more caterpillars that specialise on host plants that are more common in small fragments (such as exotic plants), a pattern that can be quantified by the variation among specialists in their responses to fragment area. Because smaller populations are more likely to be extirpated, we expected that species richness of dietary-specialist caterpillars would be disproportionately reduced in small fragments relative to richness of generalists (Gravel et al., 2011). We also hypothesised that increased browsing by deer, often more common in small fragments (Alverson et al., 1988), would impact dietary-specialist species more than dietary generalists. This expectation is based on the observation that some plant species preferred by deer are associated with abundant and species-rich assemblages of specialist insect herbivores (Bagchi et al., 2018; Wheatall et al., 2013). To test our hypotheses, we focussed on assemblages of forest-dwelling caterpillars feeding on woody host plants and assessed the following predictions (Figure 1):

1. The (*a*) abundance and (*b*) species richness of dietary-specialist caterpillars will be more positively correlated with forest fragment area than the abundance and species richness of dietary generalists.
2. The composition of plant communities will respond to reduced fragment area and increased deer activity with increasing abundances of exotic and deer-resistant species.

3. Increased deer activity will decrease the abundance of dietary-specialist caterpillars more than dietary generalists.
4. The availability of host plants of dietary specialists will (*a*) increase with fragment area and (*b*) decrease with deer activity more than the availability of host plants of dietary generalists.

We evaluated these predictions at a landscape scale with a 3-year survey of caterpillar assemblages in 32 forest fragments in Connecticut, northeastern USA. We assessed effects of fragment area on dietary-specialist and dietary-generalist Lepidoptera by sampling equal areas of forest in each fragment (to identify ecosystem decay). We used spatial blocking of fragments of contrasting area to control for the confounding effects of total forest cover at large spatial scales (50 km^2).

Methods

Sampling Design

We sampled plant and caterpillar assemblages in temperate forest fragments across a 3,500 km^2 area of central and eastern Connecticut, USA (mean annual temperature 9.7ºC, mean annual precipitation 1,264 mm; US National Weather Service, 2006 – 2020). Using a 2015 forested land cover database (Arnold et al., 2020) and restricting our sample to core forest (>100 m from any edge), we selected 32 forest fragments within 13 blocks, wherein each block contained 2 – 3 neighbouring forest fragments of different area classes (<100 ha, 100-200 ha and >200 ha of core forest; Figure 2A). We calculated the area of core forest in each fragment as the number of contiguous raster cells > 100 m from the edge. Fragment areas ranged between 3 ha and 1,014 ha.

Within each forest fragment, we established three 10 × 10 m vegetation sampling plots, one at each vertex of a 25 m-sided equilateral triangle located in the fragment's interior, avoiding water-logged and open areas. We established four 5 × 5 m caterpillar sampling plots adjacent to each of the three vegetation plots, for a total of twelve caterpillar plots (300 m^2) per fragment (Figure 2B).

Vegetation Surveys

We recorded the species identity (or greatest taxonomic resolution possible) of every woody plant >1 m tall within the three vegetation plots at each fragment. We measured diameter at breast height (dbh, measured at 1.3 m above ground) for trees >1.3 m tall and height of smaller stems. Vegetation surveys were conducted only once in each fragment, during July – October of 2017 – 2019, because turnover in woody plant composition is relatively slow.

Caterpillar Sampling and Identification

During each June of 2017 – 2019, we sampled the twelve caterpillar plots in each fragment. In each plot, we sampled up to five branches 1–2 m above the ground of each woody plant species present. Host plants were identified to species when sampled.

We sampled caterpillars at least 10 mm long using a beat sheet survey (Wagner, 2005) with 1-m^2 beat sheets (ripstop nylon, Bioquip Products #2840R). Caterpillars unidentified in the field (approximately 10% of individuals, mostly early instars or visually indistinguishable taxa) were transported to the University of Connecticut and individually reared on leaves from the plant species they were collected on until they were identified or died.

Caterpillars unidentified during rearing were DNA barcoded using the cytochrome C oxidase subunit 1 gene (CO1, Hebert et al., 2003) to determine species identity. Fifty-five samples were barcoded by Barcode of Life Data (BOLD) System facility at Guelph Univeristy

(Ratnasingham & Hebert, 2007). For the remaining 247 samples, DNA was extracted using the arthropod lysis buffer (Ivanova et al., 2006), and purified with magnetic Sera-Mag™ SpeedBeads (GE Healthcare 65152105050250) on a magnetic plate (Ambion™ AM10027). Sanger sequencing was performed by Eurofins Genomics. Sequences were checked against BOLD ((Ratnasingham & Hebert, 2007) to determine species identity, and where alternatives were unlikely, identifications were extended to caterpillars the same morphotype.

Diet Breadth

To quantify diet breadth, we calculated a weighted mean of pairwise phylogenetic distance of all host plants on which a caterpillar species was found (adding records from 2015, Bagchi et al., 2018). Means were weighted by the number of records on each host to account for host preference and to down-weight sporadic erroneous host records. Phylogenetic distance was derived from an angiosperm phylogeny including all of our host species (Smith & Brown, 2018). Weighted mean phylogenetic distance was strongly bimodal, with a clear separation between dietary specialists and dietary generalists (Figure S1). Therefore, to simplify models, we used discrete diet breadth categories of "specialist" and "generalist", where generalists had a weighted mean phylogenetic distance >100 million years (Anderson et al., 2019). We used this approach for all species with at least five individuals. Species with 3 – 5 records were classified based on expert opinion (D. L. Wagner, M. S. Singer, S. Jaffe and J. Dombroskie) of whether the species has been observed feeding on a single plant family (specialists) or more families (generalists) within southern New England, USA. We excluded species with < 3 individuals because initial models suggested including them led to poor model diagnostics. Our classification of dietary specialists depended on host use across southern New England. We used this approach because, while some species we classified as dietary specialists (e.g., *Morrisonia evicta* and *Nadata* *gibbosa*) may have broader diets across their entire geographic range (Fox & Morrow, 1981), their dietary requirements in southern New England probably limit the availability of suitable host plants within the fragments that we studied.

Leaf Area

To account for differences among plots in the amount of foliage sampled per plant species, we either counted the number of leaves per branch, or measured branch length and diameter. To estimate leaf number from branch length and diameter, we recorded both leaf counts and branch measurements on the same branch for 1-73 branches per plant species for 40 species (38 species had ≥ 4 branches). We used a negative-binomial mixed model to predict the number of leaves from branch length, diameter, their interaction, and random intercepts for plant species nested within family. We also allowed the effect of branch diameter to vary among species. The family-level random effects allowed predictions of leaf number for species without sufficient data for a single-species model. We also scanned >40 leaves per plant species, measured their area using *ImageJ* (Rasband, 1997), and constructed a model predicting leaf area (cm^2) from a random effect of plant species nested within plant family. These two models (Table S1) were used to predict total leaf area (foliage) of branches.

Assessment of deer activity

Deer activity was assessed using three approaches: (1) camera trapping; (2) scat surveys; (3) deer browse surveys. Five camera traps were located within the 1-ha square surrounding the caterpillar plots at each fragment. One camera trap was located at a random location within each quarter of this area, with the fifth camera randomly located within the 1-ha area. Cameras were installed for two weeks at each fragment between 22 January and 19 March 2018, with eight fragments monitored concurrently. Fragments within a block were monitored simultaneously, with block order determined randomly. Images were independently examined by two researchers for deer, and captures occurring within 15 minutes of each other were considered the same record. Disagreements among researchers were resolved by re-examination of the image by a researcher more experienced in mammal identification. We summed the number of deer observations across camera traps within a fragment.

In May of 2017 and 2018, in the same 1 ha-square plot, we recorded deer scat density and browsing within 25 1.2 m-radius circular plots on a grid with 50 m between plots. In each plot, we counted deer scat piles found above the previous autumn's leaf layer. We summarised the number of scat piles in each fragment as the mean number of scat piles across the 25 plots and two years. In the same plots, we counted the proportion of seedlings in the genera *Acer*, *Betula*, *Fagus*, *Kalmia, Prunus*, and *Quercus* with evidence of deer browsing in 2017, and of all woody plant species with evidence of deer browsing in 2018. We converted these data into a measure of deer browsing by fitting an intercept-only binomial model of the probability of a seedling being browsed as a function of nested, normally distributed random effects for block, fragment, and survey point, and another random intercept for plant species. We used this model to predict the probability that a generic seedling would be browsed in each fragment. We scaled all deer metrics by subtracting their mean and dividing by their standard deviation. For each fragment, we calculated a combined metric of deer activity by taking the mean across the three scaled metrics. In our analyses, we also considered alternative models where each individual metric was used instead of the combined one.

Statistical Analyses

We used generalised linear mixed-effects models to evaluate our predictions that fragment area (prediction 1) and deer activity (prediction 3) would affect the abundance and species richness of dietary-specialist and dietary-generalist caterpillars differently. To address prediction 1*a*, we modelled caterpillar counts per species in each fragment and host plant species combination, assuming a negative-binomial error distribution (Table S2, Model 1*a*). As potential predictors, we included diet breadth (generalist or specialist), fragment area (centred by subtracting the midpoint value of 500 ha and dividing by the observed standard deviation), and their interaction. To control for variation in foliage sampled per plot, we added log leaf area as an offset term, thereby expressing caterpillar abundance as density (number per cm^2 of leaf area). The models for species richness (prediction 1*b*) were like the models for abundance except the response was number of species within each dietary category (Table S2, Model 1*b*). We also fitted similar models with Simpson's and Shannon-Weiner indices as a response to incorporate species evenness. All models also included categorical terms for year, normally distributed random intercepts for caterpillar species (except the species richness model), and nested random intercepts for fragment within block.

We additionally fitted a model of the effects of diet breadth and fragment area on caterpillar abundance with a random slope for fragment area for each lepidopteran species, in addition to the random intercept (Table S2, Model 1*c*). A random slope changes the interpretation of the population-level parameter to the effect of fragment area on the average species, while reducing the influence of more abundant species. The random-intercept-only model, in contrast, controls for differences in abundances of species and quantifies the aggregated response within dietary categories. This random intercept and slope model allowed us to assess variation among species within diet categories in their responses to fragment area. We quantified variation among years and species by comparing the deviance explained by these terms to χ^2 distributions.

To test whether plant composition was associated with fragment area (prediction 2), we used non-metric multidimensional scaling (NMDS) to visualise the major axes of variation in plant composition among fragments. We pooled the plant composition data from the three vegetation plots at each fragment and filtered out plant species that occurred fewer than five times across all fragments. We applied a Wisconsin double standardisation and square-root transformation to the abundance data and computed Bray's dissimilarity between each pair of fragments. We used NMDS to find three axes that best preserved the rank order of dissimilarities among the 32 fragments using 20 random starting points. We quantified the relationship between woody plant composition and fragment area and deer activity (using the mean across the three scaled metrics of deer activity) using PERMANOVA with 999 permutations.

To examine effects of fragment area (prediction 4*a*) and deer activity (prediction 4*b*) on each lepidopteran species' host plant availability, we summed the basal areas at each fragment of plants on which that caterpillar species was observed more than once in our surveys. Stems between 1 m and 1.3 m tall were given a nominal dbh of 1 mm for the basal area calculation. We modelled the total basal area of each caterpillar species' host plants as a function of dietary specialisation and its two-way interactions with fragment area and deer activity, with random intercepts for fragment nested within block (Table S2, Model 2). We fitted this model assuming a zero-hurdle gamma distribution, which accommodated lepidopteran species without hosts in some fragments. We modelled the presence of any host plants for each lepidopteran species as a function of fragment area, deer activity and their interactions with caterpillar diet breadth. Zero-hurdle models estimate the probability of zeros in the response (i.e., absences of hosts) using a log-odds scale, so we multiplied the parameters by -1 to convert them to the probability of presences and give the presence/absence and conditional abundance parameters the same direction. If vegetation composition varied with fragment area so that dietary-specialist, but not dietary-generalist, caterpillars had more host plants in larger fragments (prediction 4), the parameters for the interaction between fragment area and diet would be positive.

Data were analysed in R (v4.2.2, R Core Team, 2022), using the `tidyverse` packages for data preparation (Wickham et al., 2019). Models were fitted using the `glmmTMB` package (Brooks et al., 2017) and ordinations performed with the `vegan` package (Oksanen et al., 2022). We used the `ape` (Paradis & Schliep, 2019), and `phytools` (Lüdecke, 2022) packages to calculate mean phylogenetic distance. Data and R code are available from online repositories (see Data Availability). All samples were collected under permits from the Connecticut Department Energy and Environmental Protection (1516006 and 1719006) and under exemption E16-008 from the University of Connecticut Institutional Animal Care and Use Committee.

Results

We sampled 9,616 branches from 53 plant species across the three years of sampling and collected 11,165 caterpillars representing 176 species, including 10,140 dietary generalists (97 species) and 810 specialists (57 species). An additional 315 caterpillars could not be reliably assigned a diet breadth because they were unidentified, their host plants were unknown, or they were from species collected only once or twice. The invasive *Lymantria dispar* (Erebidae) was the most abundant lepidopteran species by far, accounting for 7,880 individuals, the vast majority (82%) of which were sampled during a regional population outbreak in 2017 (Pasquarella et al., 2018). Model diagnostics improved when records for *L. dispar* from 2017 and species with < 3 records were removed. Excluding these records resulted in a dataset with 4,406 caterpillars including 3,634 dietary generalists (63 species) and 772 dietary specialists (27 species). We report on analyses of these data here, although patterns in the entire data set were similar.

Interactive effects of fragment area and caterpillar diet (prediction 1)

Concordant with prediction 1*a*, the overall abundance of dietary-specialist caterpillars increased with increasing fragment area ($\beta = 0.34 \pm 0.142$ SE, $P = 0.016$), with a significantly weaker relationship for dietary generalists (area × diet interaction: $\beta = -0.28 \pm 0.115$ SE, $P = 0.016$; Figure 3). Although there was substantial temporal variation in caterpillar abundance (annual variation: $\chi_2^2 = 98.60$, $P < 0.001$) and the relative abundances of specialist and generalist caterpillars among years (year × diet interaction: $\chi_2^2 = 25.46$, $P < 0.001$), the relationship between fragment area and caterpillar diet was consistent across years (year × diet × area interaction: $\chi_2^2 = 0.78$, $P = 0.675$).

Counter to prediction 1*b* the species richness of dietary-specialist caterpillars was unaffected by fragment area ($\beta = 0.18 \pm 0.117$, $P = 0.123$) with a nearly identical relationship for dietary generalists (area × diet interaction: $\beta = -0.06 \pm 0.110$, $P = 0.616$). The inverse Simpson's index, which more heavily weights the evenness of species abundances than other common diversity indices, was also unrelated to fragment area (area effect for dietary specialists: $\beta = -0.08 \pm 0.112$, $P = 0.454$; area × diet interaction: $\beta = -0.005 \pm 0.077$, $P = 0.952$; the results for the Shannon-Weiner index were similar).

Variation among caterpillar species

There was considerable variation among species in the responses of caterpillar abundance to fragment area (variance of the random slope of fragment area among species = 0.361; likelihood ratio test: $\chi_2^2 = 34.38$, $P < 0.001$; Figure 4). Adding a random slope for the fragment-area term for each caterpillar species in the model removed the observed relationship between fragment area and the abundances of both dietary specialists and dietary generalists (specialists: $\beta = 0.16 \pm 0.204$, $P = 0.44$; fragment area × diet interaction: $\beta = -0.16 \pm 0.198$, $P = 0.42$). This difference between the random intercept and random slope models indicates that while dietary-specialist caterpillars were, on average, more sensitive to fragment area than dietary generalists, this pattern was not universally true across all taxa.

Interactive effects of deer activity and caterpillar diet (prediction 3)

Caterpillar densities, both generalists and specialists, were unrelated to the average of the three measures of deer activity (specialists: $\beta = 0.04 \pm 0.151$, $P = 0.784$; deer activity × diet interaction: $\beta = 0.03 \pm 0.116$, $P = 0.766$; Figure 3B). In general, this result held when the individual measures of deer activity were used in the models instead of the average measure of deer activity (Figure S3). The correlations between fragment area and our three measures of deer activity were weak (Figure S2).

Effects of fragment area on woody plant composition (prediction 2)

Woody plant community composition varied predictably with fragment area (Figure 5). The three NMDS axes were related to fragment area ($R^2 = 0.15$, $P < 0.001$) and, to a lesser extent, deer activity ($R^2 = 0.05$, $P = 0.031$). Plant species typical of smaller fragments included several exotic species (e.g., *Berberis thunbergii* and *Rosa multiflora*), and early colonising (e.g., *Acer saccharum*) and deer-resistant (e.g., *Lindera benzoin*) native species. *Hamamelis virginiana* and *Quercus* species (e.g., *Q. rubra*) had higher densities in larger fragments. Although some of the plant species with the highest proportion of dietary-specialist caterpillars were concentrated in large fragments (e.g., *H. virginiana*, *Kalmia latifolia* and *Clethra alnifolia*), other specialist-rich plant species were more common in small fragments (e.g., *L. benzoin*).

Effects of fragment area on host availability (prediction 4)

Models of summed host plant basal area indicated that the probability that at least one host plant occurred in a fragment increased with fragment area (Figure 6A and B; negative zero-hurdle model parameters for host plants of specialists: $\beta = 0.26 \pm 0.104$, $P = 0.013$). Counter to prediction 4, however, the relationship between fragment area and host plant basal area was not significantly weaker for dietary generalists (area × diet interaction: $\beta = -0.12 \pm 0.131$, $P = 0.360$). The presence of host plants of dietary-specialist caterpillars decreased with deer activity ($\beta = -0.33 \pm 0.093$, $P < 0.001$; Figure 6C), and this pattern was slightly weaker for dietary generalists (deer activity × diet interaction: $\beta = 0.22 \pm 0.114$, $P = 0.058$). Neither fragment area nor deer activity affected the total basal area of host plants for dietary-specialist or dietary-generalist Lepidoptera once the presence of at least one host plant was accounted for (conditional density model, Figure 6C and D).

Discussion

In this large-scale analysis of the relative effects of fragment area on forest caterpillars with contrasting diets, we found robust evidence that abundances of dietary-specialist caterpillars decreased more steeply than that of dietary generalists as forest fragment area declined (prediction 1), but not from the hypothesised mechanisms (predictions 3-4). This finding offers landscape-level support that reduced fragment area is more disadvantageous to dietary-specialist than dietary-generalist species (Bagchi et al., 2018; Henle et al., 2004; Martinson & Fagan, 2014; Öckinger et al., 2010), but leaves the mechanisms unresolved. Although we found evidence of shifts in plant community composition associated with fragment area (prediction 2), these changes affected dietary-specialist and dietary-generalist caterpillars similarly, counter to prediction 4, and thus provide little support for our hypothesis that declines of dietary specialists in small fragments could be explained by a corresponding decline in their food plants.

Although the densities of specialists increased with fragment area, we did not observe a corresponding increase in species richness or evenness of either dietary specialists or generalists. Given the large number of studies that suggest a positive relationship between fragment area and species richness (Aizen & Feinsinger, 1994b; Benedick et al., 2006; Matthews et al., 2014; Chase et al., 2020), this result may seem surprising. One possible reason is that we measured caterpillar density within equally sized plots at all fragments, so any differences in species richness would have indicated change in the number of species per unit sampling effort, i.e., ecosystem decay not passive sampling (*sensu* Chase et al., 2020). The landscape of eastern Connecticut surrounding our fragments is comparatively benign, consisting of mostly forests interspersed by low-intensity agriculture, occasional residential buildings, powerline cuts, and roads. Nearly all the fragments in our study are near other forested tracts, which might have dampened differences relative to a landscape where fragments are separated by a more inhospitable matrix. The extensive forest cover around the fragments may have overwhelmed any local effects of fragment area, as might be predicted under the habitat-amount hypothesis (Fahrig, 2017; Watling et al., 2020). Furthermore, all our samples were taken within closed-canopy forests that were >100 m from edges. Consequently, many of the possible mechanisms for ecosystem decay, like edge effects (Chase et al., 2020; Ries et al., 2004) and large shifts in abiotic conditions (Ewers & Banks-Leite, 2013; Laurance et al., 2017), were probably muted at the locations we sampled. Additionally, most of the fragments were relatively old, with historical aerial photographs (https://magic.lib.uconn.edu/connecticut_data.html) indicating that about 78% of the fragments included in our study were forested in 1930. There is some evidence that the effect of forest fragment area attenuates with time (Chase et al., 2020), so the age of the fragments that we sampled may have contributed to the lack of a statistically significant relationship between species richness and fragment area.

The large variation in fragment-area dependence among dietary specialists runs counter to the expectations of neutral filtering of dietary specialists in small fragments, which should affect all specialists similarly (i.e., variation in the effects of fragment area among species should be consistent with a χ^2 distribution). Instead, the densities of a few dietary-specialist species (e.g., *Epimecis hortaria*) increased considerably in small fragments, along with their host plants (e.g., *L. benzoin*), even as others (e.g., *M. evicta*) favoured larger fragments. Some of the variation among species could be attributed to the host plants on which individual species specialised. However, we also observed situations where specialists sharing a common host had disparate relationships with fragment area. For example, the three most abundant specialists on *H. virginiana* (*Nola triquetrana*, *Pseudexentera costomaculata,* and *Pyrefera hesperidago*) had contrasting relationships with fragment area (strongly positive, weakly positive and weakly negative, respectively; Figure 4), suggesting that area relationships are heterogeneous, and that other mechanisms are undoubtedly in play. Abundances of vertebrate and invertebrate natural enemies might vary with fragment area, which could drive differential responses across their prey taxa. Life history traits such as size, flying ability and fecundity have been associated with the effects of land use change and habitat loss on lepidopteran species (Öckinger et al., 2010; Riva et al., 2023) and it might be fruitful to collect data on these traits to examine their contribution to the variation in responses observed here.

Although we found evidence that underrepresentation of dietary specialists in small fragments was not due to purely neutral mechanisms, support for the deterministic mechanisms we proposed (host plant availability, deer activity) was equivocal. Decreasing fragment area was clearly associated with shifts in plant community composition (prediction 2) and reduced the probability of caterpillars finding suitable host plants in smaller fragments, but the interaction between diet and fragment area was not statistically significant (prediction 4). While this pattern has implications for insect conservation (larger forest patches may support higher insect densities), it leaves our motivating question of why reductions in forest fragment area disproportionately reduces dietary-specialist caterpillar populations unresolved. However, interpreting interactions in binomial models (as used in the zero-hurdle component of the models here) is scale dependent because the log-odds link function often used in these models is sigmoidal (Spake et al., 2023). Specifically, because, on average, suitable hosts for generalist caterpillars occurred in most small fragments (*c*. 85%) while hosts of specialists occurred in only about half of them (Figure 6A), increasing fragment area increased the probability of specialists finding suitable hosts more than generalists. The negative diet by fragment area interaction, even if not statistically significant, reinforced this pattern so that in the largest fragments the probabilities of suitable host plants occurring for dietary-specialist and dietary-generalist caterpillars were roughly similar.

The other potential deterministic driver of change in lepidopteran assemblages we considered was deer density (Côté et al., 2004). Forest fragmentation often contributes to elevated deer densities at a landscape scale (Alverson et al., 1988; Côté et al., 2004), but we did not observe strong correlations between fragment area and deer activity (Figure S2). Deer activity was correlated with greater reductions in host-plant availability for specialist than generalist caterpillars (prediction 4*b*), but had no corresponding effect on the densities of caterpillars in the two dietary groups (prediction 1*a*). Overall, elevated deer densities could not explain the disproportionate declines of dietary-specialist caterpillars we observed in small forest fragments.

This study strengthens the evidence that dietary-specialist insects are disproportionately affected by the area of forest fragments (Martinson & Fagan, 2014; Rossetti et al., 2017; Tscharntke et al., 2002). By comparing caterpillar assemblages from equal-sized plots across a large number of fragments arranged in a blocked design over a wide geographic area, our study addresses many criticisms of previous work that confounded fragment area with sample size and environmental heterogeneity. Such declines in ecological specialists are a key element of the biotic homogenization of human-dominated landscapes (Clavel et al., 2011; McKinney & Lockwood, 1999). However, the mechanisms driving this pattern remain elusive. It is likely that decreases in fragment area impact caterpillar assemblages through multiple pathways, complicating attempts to identify individual component processes. Our analyses suggested that shifts in the plant community, towards fewer of the most caterpillar-rich species, did reduce caterpillar abundances; however, these impacts were not substantially related to dietary specialisation. Increased deer activity was also associated with changes in the plant community, but these changes did not appear to affect caterpillar assemblages consistently. Alternative explanations for the declines of specialists in small forest fragments might include altered predation and parasitism (Anderson et al., 2019; Bagchi et al., 2018; Fenoglio et al., 2012; Frost et al., 2015; Siegel et al., 2024) and dispersal patterns (Ries & Debinski, 2001; Schtickzelle & Baguette, 2003) in fragmented landscapes. Regardless of the mechanisms, however, reduced dietary specialisation of caterpillar assemblages in small habitat patches represents an important dimension of anthropogenic biodiversity change.

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Author Contributions

Bagchi, Singer, Wagner and Elphick conceived the study and obtained funding; Mickley, Singer, Wagner, Anderson, Bagchi, Brown, Pirtel, Musavi, Connors and Marren conducted fieldwork; Wagner, Singer, Mickley, Connors and Anderson identified caterpillars in the field and laboratory; Kilpatrick, Davis, Weeks, Pirtel, Musavi, Brown, Mickley and Bagchi designed and conducted deer surveys; Mickley, Singer and Bagchi drafted the paper; Mickley, LaScaleia and Bagchi analysed the data. All authors contributed to revising the manuscript and approved the submission.

Data Availability

Data available from the Dryad Digital Repository https://datadryad.org/stash/dataset/doi:10.5061/dryad.k3j9kd5k8 (Mickley et al., 2025). Code for the analyses available from https://github.com/BagchiLab-Uconn/FEN_specialization.git (Mickley & Bagchi, 2025).

Conflicts of Interest

The authors declare no conflicts of interest.

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Figures legends

Figure 1: Conceptual diagram of the hypothesised relationships between fragment area and the abundances of dietary-specialist and dietary-generalist caterpillars. Prediction 1(a) expects the overall relationship between fragment area and the abundance of caterpillars to be stronger for dietary-specialist species (A, B, C) than dietary-generalist species (X, Y, Z). Species richness results from the aggregated responses across species, leading to the prediction 1(b) that fragment area will affect species richness of dietary-specialist caterpillar species more than that of dietary generalists. Predictions 2 – 4 arise from the proposed mechanisms behind prediction 1. Prediction 2 depends on fragment area and deer activity influencing the species composition of host-plant assemblages. Prediction 3 suggests that deer activity influences caterpillar abundance and species richness. Prediction 4 is that fragment area and deer activity will affect the cumulative abundance of plants across a caterpillar's host species more for dietary-specialist caterpillars than dietary-generalist caterpillars.

Figure 2: (A) Location of included fragments within Connecticut, USA (modified from Anderson et al. 2019, with additional fragments). Forested areas are shaded green while white indicates all other landcover types. Core fragment area class (small: < 100 ha, medium: 100-200 ha; large: > 200 ha) is indicated by shapes and fragments in the same block are marked with the same colour. (B) Sampling design, consisting of twelve 5 × 5 m caterpillar sampling plots (blue squares) within each fragment, surrounding three 10 × 10 m vegetation plots (green squares) arranged on a 25-m sided equilateral triangle.

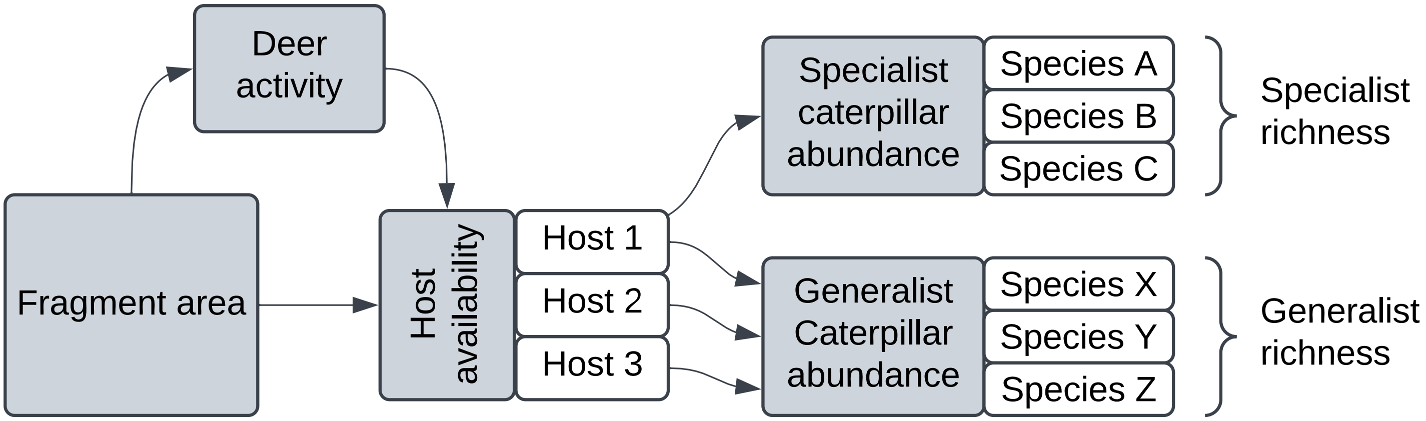
Figure 3: Effects of fragment area and deer activity on densities of caterpillars with contrasting diet breadths. (A) The density (on a log scale) of dietary-specialist, but not dietary-generalist (Diet[G]), caterpillars increased significantly with fragment area, but deer activity did not

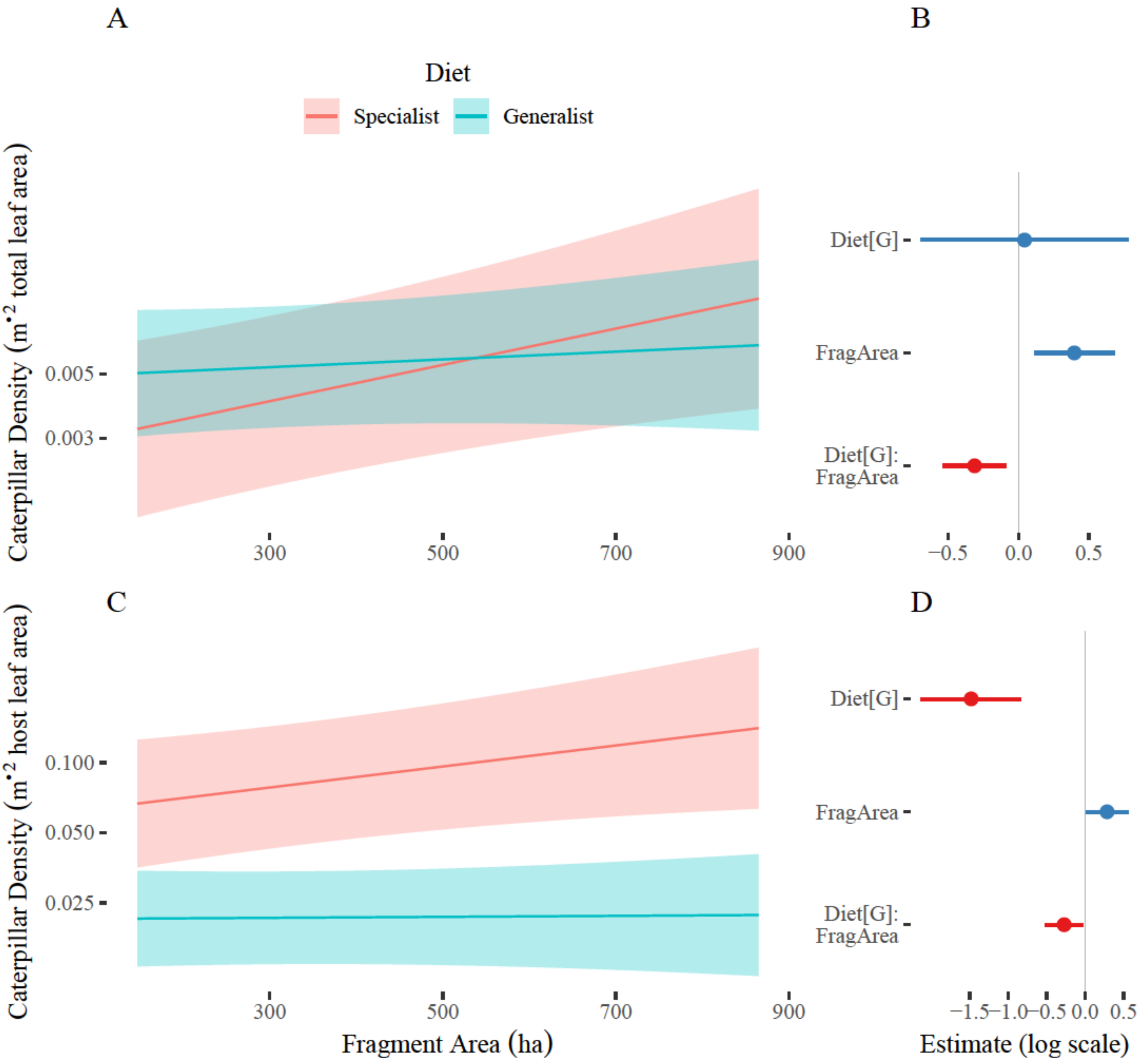
significantly affect caterpillar densities within either diet group. (B) Parameter estimates from a negative-binomial generalised linear mixed model fitted to the data. Parameters refer to dietary specialists unless they include an interaction with Diet[G], which represent differences between specialists and generalists.

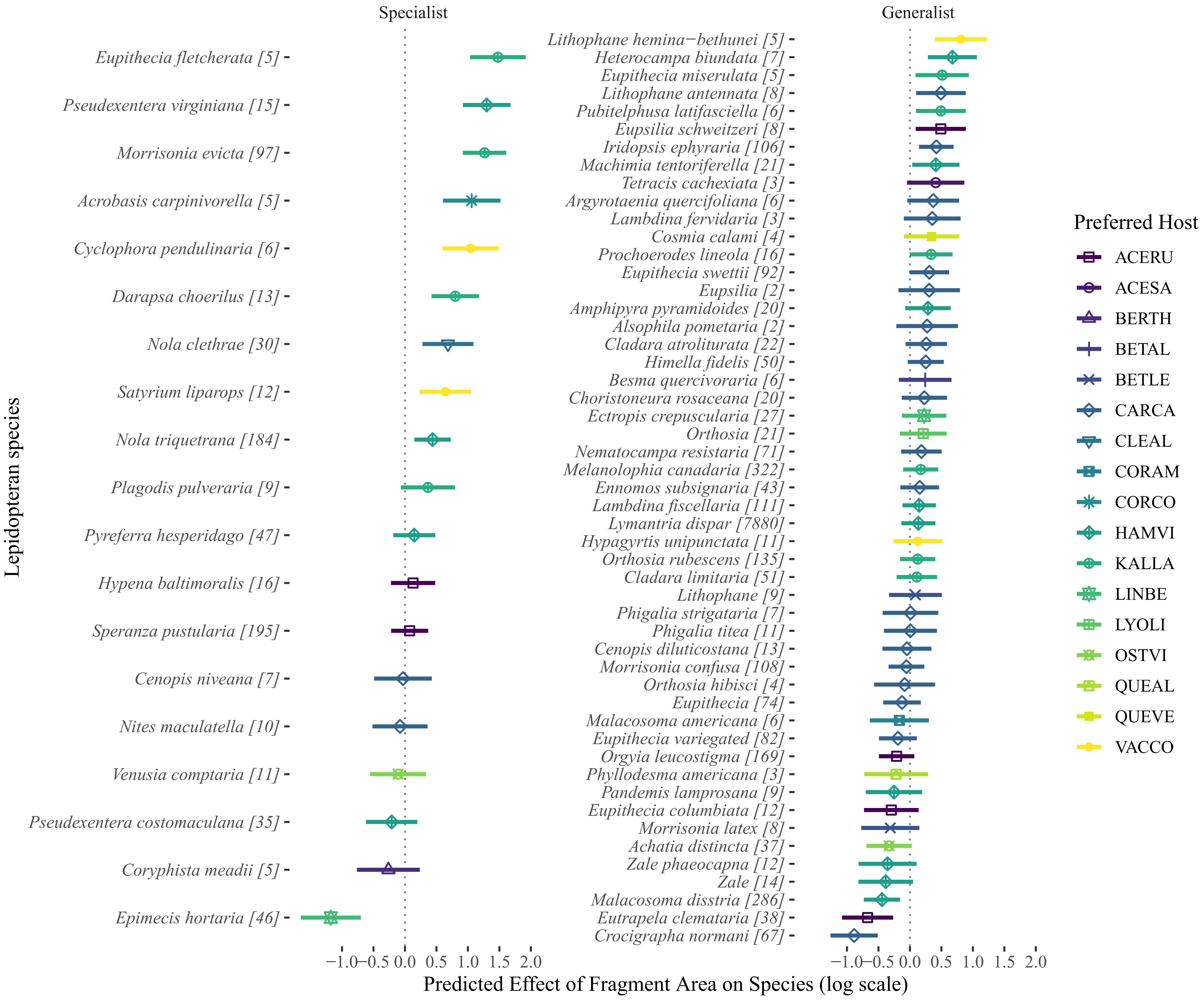
Figure 4: Predicted effects of fragment area on densities of each dietary-specialist and dietary-generalist lepidopteran species included in the models. Points represent the Best Linear Unbiased Predictor for the species added to the population estimate for the effect of fragment size on the corresponding dietary category of caterpillar, with standard errors indicated by error bars. Numbers in square brackets are the number of samples of each lepidopteran species and colours represent the plant species on which it was most frequently observed in this study, with plant species ordered by decreasing number of specialist caterpillars sampled from them (*Hamamelis virginiana* had the most).

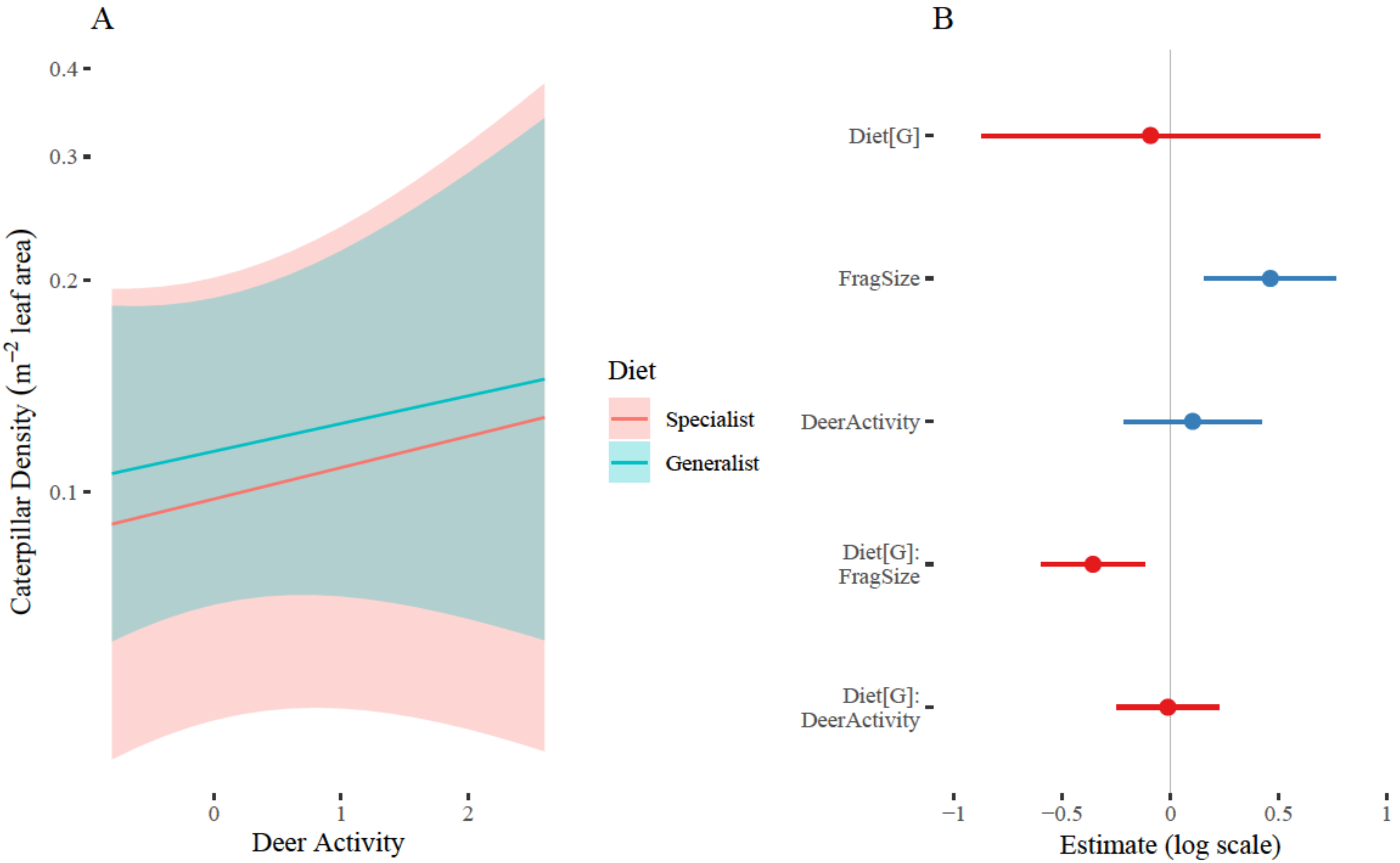
Figure 5: Variation in host plant community composition with fragment area. Plant species (see Table S3 for species codes) are plotted on the first two axes of a three-dimensional non-metric multidimensional scaling ordination of the three vegetation plots in each of the 32 fragments. Text size of the labels is proportional to the total number of caterpillars collected from the plant species (log scale) and the colour indicates the proportion of those caterpillars that were dietary specialists (square root scale; grey text indicates plant species from which no caterpillars were collected). The isoclines indicate the fragment area associated with plant species composition. Species in the lower-left corner of the figure are typical of smaller forest areas (e.g., *Berberis thunbergii,* BERTH) while species in the top-right are more abundant in larger forest areas (e.g., *Hammamelis virginiana,* HAMVI).

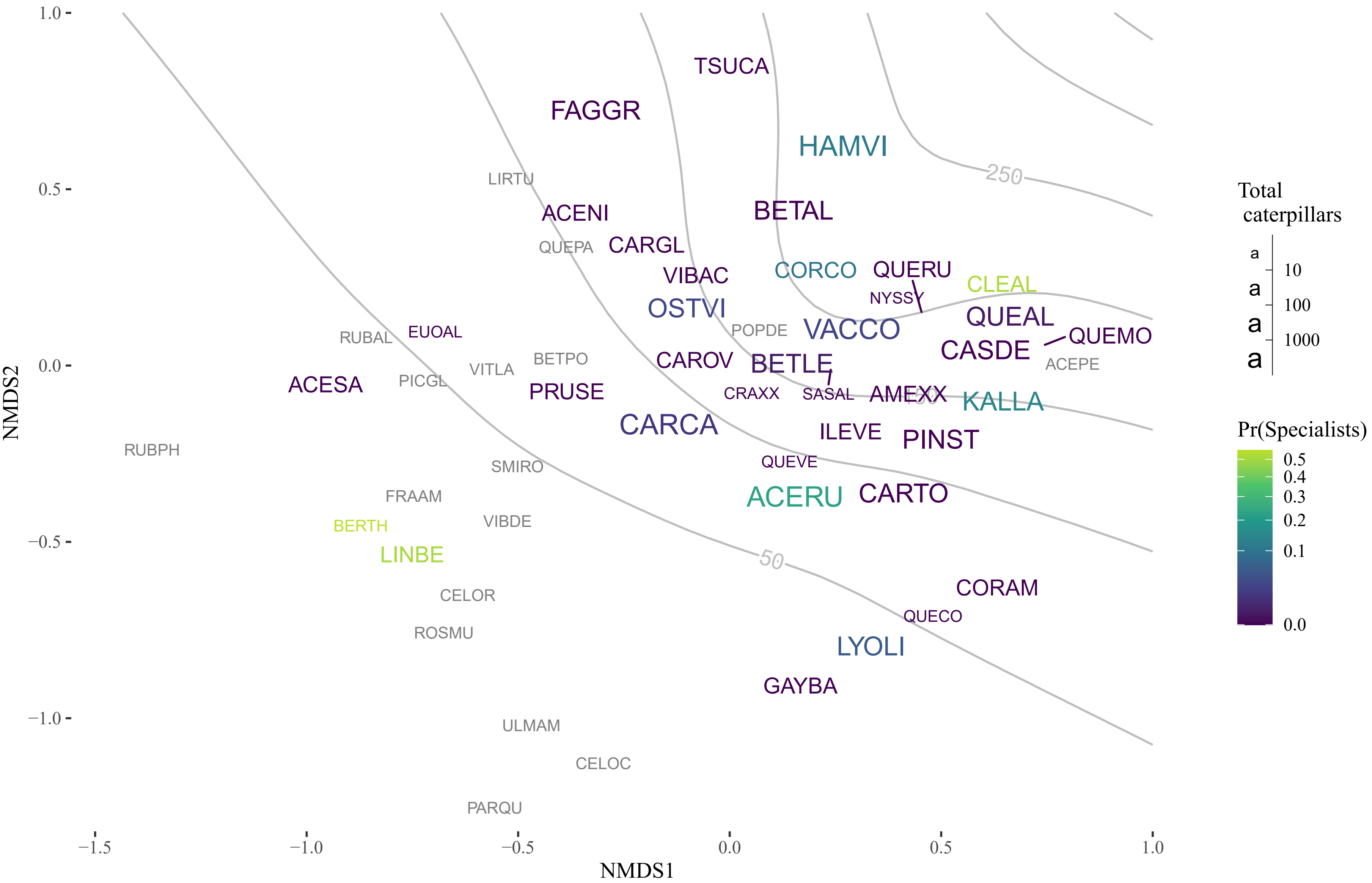
Figure 6: The effect of dietary specialisation and deer activity on the relationship between fragment area and availability of suitable host plant species within a fragment. (A) On average, the presence of caterpillar host plants was more likely in larger fragments and when deer activity was low, a pattern that was more noticeable for dietary specialists. (B) The estimates of the effect of fragment area and deer activity on the probability of at least one suitable host plant occurring in our plots. This probability increased with fragment area and decreased with deer activity for dietary specialists. The differences were smaller for dietary generalists, but not significantly so. (C) Once present, the abundance of host plants for each caterpillar species was unaffected by fragment area and deer activity with the exception that deer activity marginally reduced the abundance of host plants for generalists. (D) Parameter estimates for the effects of diet, fragment area, deer pressure and their two-way interactions on the summed basal area of host plants within a fragment, conditional on at least one host plant occurring within that fragment.

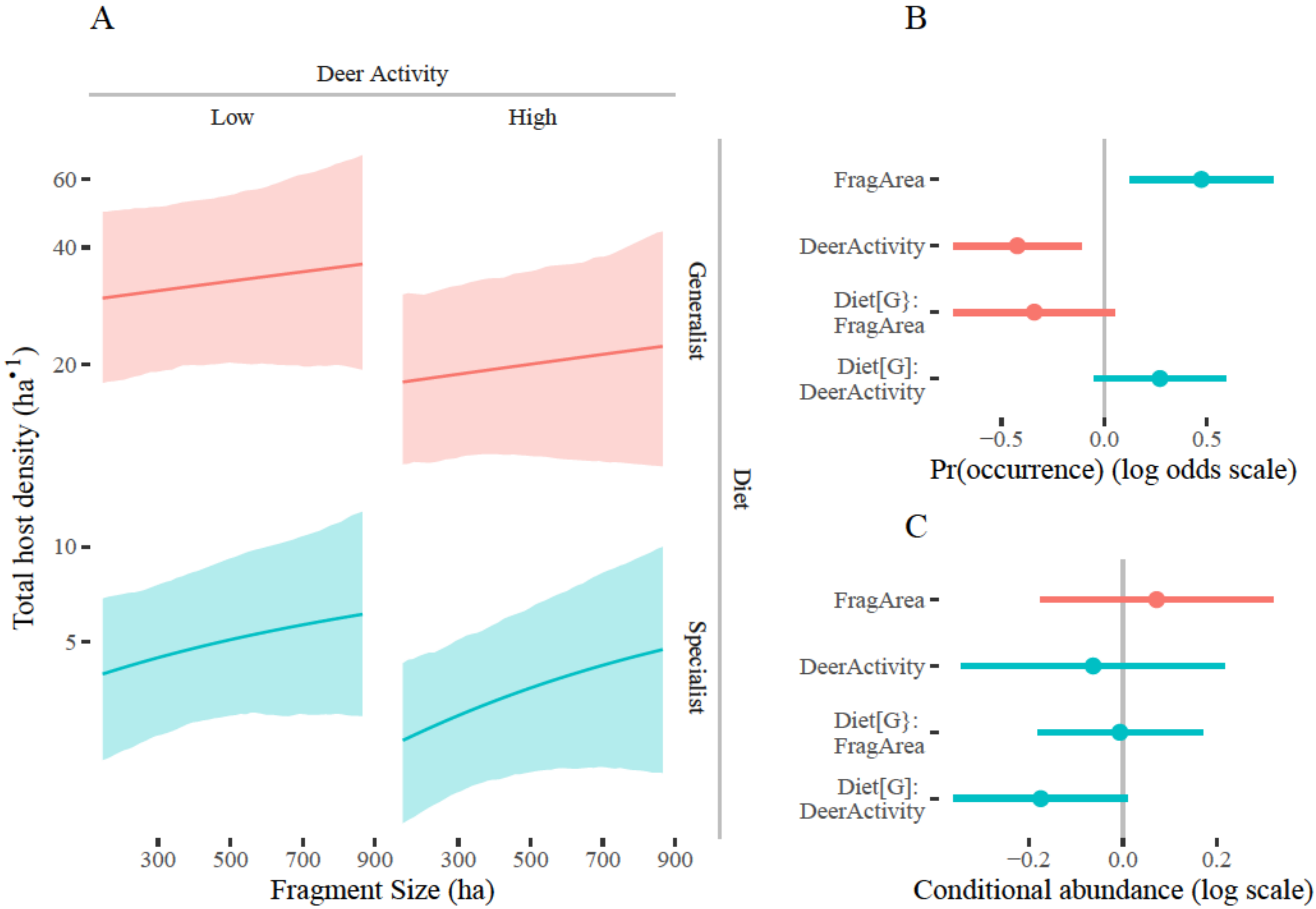

Deer activity
Fragment area
Host availability
Host 1
Host 2
Host 3
Specialist caterpillar abundance
Species A
Species B
Species C
Specialist richness
Generalist Caterpillar abundance
Species X
Species Y
Species Z
Generalist richness

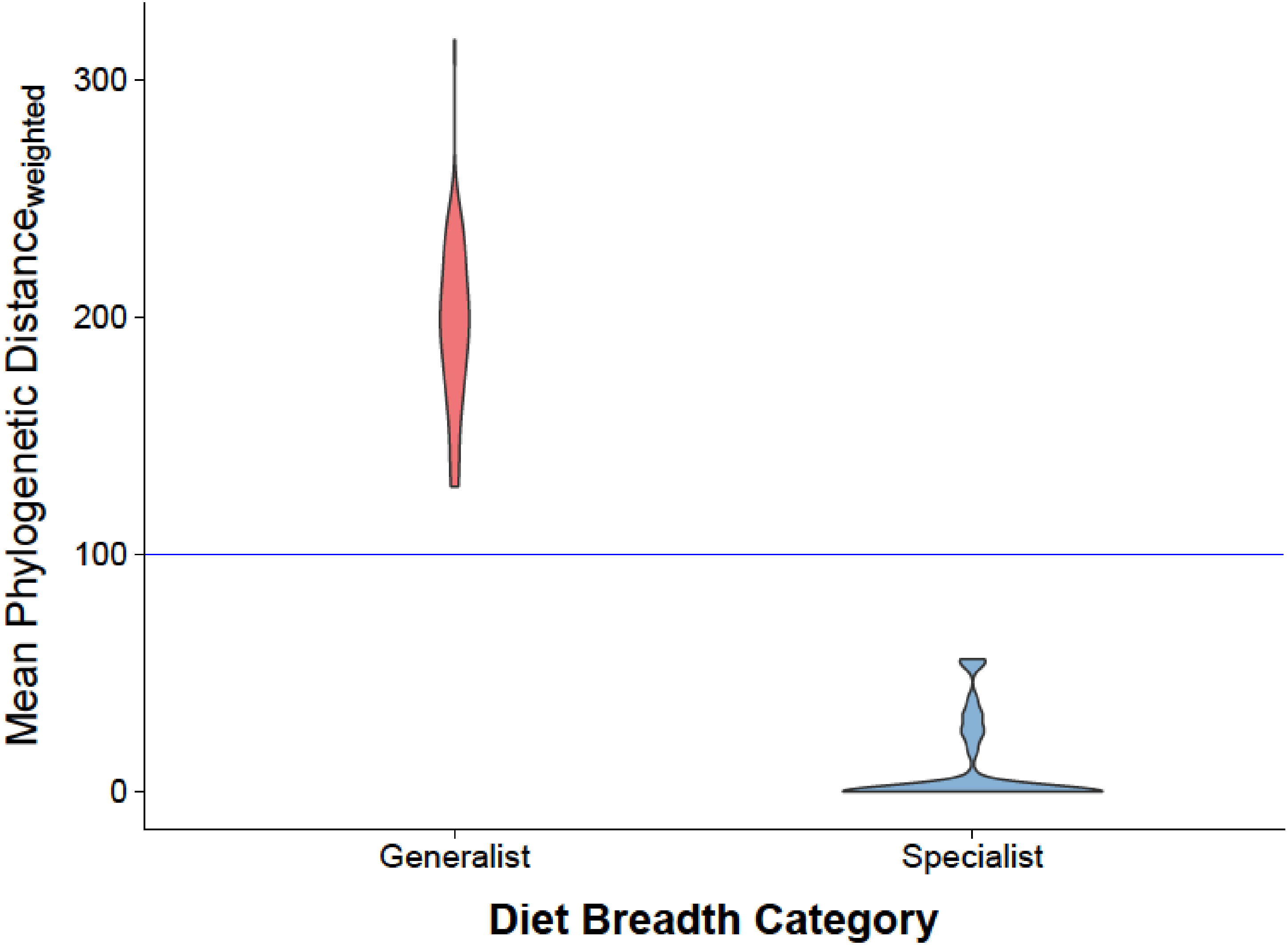

A
B
Diet
Specialist
Generalist
Caterpillar Density (m^2 total leaf area)
0.005
0.003
300
500
700
900
Diet[G]
FragArea
Diet[G]:
FragArea
−0.5
0.0
0.5
C
D
Caterpillar Density (m^2 host leaf area)
0.100
0.050
0.025
300
500
700
900
Fragment Area (ha)
Diet[G]
FragArea
Diet[G]:
FragArea
−1.5
−1.0
−0.5
0.0
0.5
Estimate (log scale)


Specialist
Generalist
Lepidopteran species
Eupithecia fletcherata [5]
Pseudexentera virginiana [15]
Morrisonia evicta [97]
Acrobasis carpinivorella [5]
Cyclophora pendulinaria [6]
Darapsa choerilus [13]
Nola clethrae [30]
Satyrium liparops [12]
Nola triquetrana [184]
Plagodis pulveraria [9]
Pyreferra hesperidago [47]
Hypena baltimoralis [16]
Speranza pustularia [195]
Cenopis niveana [7]
Nites maculatella [10]
Venusia comptaria [11]
Pseudexentera costomaculana [35]
Coryphista meadii [5]
Epimecis hortaria [46]
Lithophane hemina−bethunei [5]
Heterocampa biundata [7]
Eupithecia miserulata [5]
Lithophane antennata [8]
Pubitelphusa latifasciella [6]
Eupsilia schweitzeri [8]
Iridopsis ephyraria [106]
Machimia tentoriferella [21]
Tetracis cachexiata [3]
Argyrotaenia quercifoliana [6]
Lambdina fervidaria [3]
Cosmia calami [4]
Prochoerodes lineola [16]
Eupithecia swettii [92]
Eupsilia [2]
Amphipyra pyramidoides [20]
Alsophila pometaria [2]
Cladara atroliturata [22]
Himella fidelis [50]
Besma quercivoraria [6]
Choristoneura rosaceana [20]
Ectropis crepuscularia [27]
Orthosia [21]
Nematocampa resistaria [71]
Melanolophia canadaria [322]
Ennomos subsignaria [43]
Lambdina fiscellaria [111]
Lymantria dispar [7880]
Hypagyrtis unipunctata [11]
Orthosia rubescens [135]
Cladara limitaria [51]
Lithophane [9]
Phigalia strigataria [7]
Phigalia titea [11]
Cenopis diluticostana [13]
Morrisonia confusa [108]
Orthosia hibisci [4]
Eupithecia [74]
Malacosoma americana [6]
Eupithecia variegated [82]
Orgyia leucostigma [169]
Phyllodesma americana [3]
Pandemis lamprosana [9]
Eupithecia columbiata [12]
Morrisonia latex [8]
Achatia distincta [37]
Zale phaeocapna [12]
Zale [14]
Malacosoma disstria [286]
Eutrapela clemataria [38]
Crocigrapha normani [67]
−1.0
−0.5
0.0
0.5
1.0
1.5
2.0
−1.0
−0.5
0.0
0.5
1.0
1.5
2.0
Predicted Effect of Fragment Area on Species (log scale)
Preferred Host
ACERU
ACESA
BERTH
BETAL
BETLE
CARCA
CLEAL
CORAM
CORCO
HAMVI
KALLA
LINBE
LYOLI
OSTVI
QUEAL
QUEVE
VACCO


A
B
Caterpillar Density (m^{-2} leaf area)
0.4
0.3
0.2
0.1
0
1
2
Deer Activity
Diet
Specialist
Generalist
Diet[G]
FragSize
DeerActivity
Diet[G]:
FragSize
Diet[G]:
DeerActivity
−1
−0.5
0
0.5
1
Estimate (log scale)


NMDS2
NMDS1
1.0
0.5
0.0
−0.5
−1.0
−1.5
−1.0
−0.5
0.0
0.5
1.0
250
150
50
TSUCA
FAGGR
HAMVI
LIRTU
ACENI
BETAL
QUEPA
CARGL
VIBAC
CORCO
QUERU
CLEAL
NYSSY
OSTVI
QUEAL
RUBAL
EUOAL
POPDE
VACCO
QUEMO
BETPO
CAROV
BETLE
CASDE
VITLA
ACEPE
ACESA
PICGL
PRUSE
CRAXX
SASAL
AMEXX
KALLA
CARCA
ILEVE
PINST
RUBPH
SMIRO
QUEVE
FRAAM
ACERU
CARTO
VIBDE
BERTH
LINBE
CORAM
CELOR
QUECO
ROSMU
LYOLI
GAYBA
ULMAM
CELOC
PARQU
Total caterpillars
a
a
a
a
10
100
1000
Pr(Specialists)
0.5
0.4
0.3
0.2
0.1
0.0


A
Deer Activity
Low
High
60
40
20
10
5
Total host density (ha-1)
300
500
700
900
300
500
700
900
Fragment Size (ha)
Generalist
Specialist
Diet
B
FragArea
DeerActivity
Diet[G}:
FragArea
Diet[G]:
DeerActivity
−0.5
0.0
0.5
Pr(occurrence) (log odds scale)
C
FragArea
DeerActivity
Diet[G}:
FragArea
Diet[G]:
DeerActivity
−0.2
0.0
0.2
Conditional abundance (log scale)


Mean Phylogenetic Distance$_{\text{weighted}}$
300
200
100
0
Generalist
Specialist
Diet Breadth Category