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Tritrophic interactions in forests:

Direct and indirect interactions between birds, insect herbivores, and oaks

By

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Dissertation abstract

Insect herbivores in forest ecosystems are a phenomenally diverse group of organisms. However they face a dilemma, the so-called "trophic crunch," as they are situated between two antagonizing forces on adjacent trophic levels. The plants on which they feed possess an array of defenses and other mechanisms to reduce damage. These plant traits include chemical and physical defenses to reduce digestibility and interfere with herbivore growth and development. Insect herbivores also suffer high rates of predation from invertebrate and vertebrate predators. Insectivorous birds represent a particularly important threat because, as endotherms, they require a large amount of food to maintain their own metabolism and that of their offspring during the breeding season. Thus the abundance, diversity, and impacts of herbivore communities are influenced by both the food they eat and the predators that eat them. Using experimental and observation approaches, I examined direct and indirect interactions between avian predators, insect herbivores, and oak trees.

I used bird exclusion experiments to determine how the direct and indirect effects of bird predation vary spatially within forests. In Chapter 1 I used a randomized-block design to show that both bird and insect herbivore abundances varied through space in similar habitat. Yet the direct effects of birds on herbivores and the indirect effects on leaf damage of oaks did not vary between blocks, suggesting that the biological control services of birds are robust to variations in population abundance of both the birds and their prey.

Trophic theory predicts that the direct and indirect effects of predators on herbivores and plants, respectively, will vary with traits of the plants. Light has strong effects on leaf quality, so the impacts of predators and herbivores may differ between plants grown in sun and shade. However past experiments often have been unable to separate the effects of light environment on plant traits from effects on herbivores or predators. In Chapter 2 I used a light manipulation to produce oak saplings with different leaf quality and factorially excluded bird predators in a common light environment to measure the effects of birds and leaf quality on herbivore abundance and herbivory. Sun leaves appeared to be lower quality food, yet herbivores were significantly more abundant and caused greater leaf damage on sun-exposed trees. Bird exclusion did not change herbivore abundance, but did increase leaf damage. The effects of birds did not vary with light manipulation. The higher abundance and damage on sun trees may have been due to ovipositing females preferring hosts with greater leaf and shoot growth. Birds may have reduced leaf damage through non-consumptive effects on herbivore feeding behavior.

Because of their diversity of morphology, behavior, and host breadth, herbivore species should vary in their susceptibility to bird predation and their response to specific host plant traits. Thus the top-down impacts of birds and bottom-up effects of leaf quality variation should alter herbivore community diversity, structure, and composition. In Chapter 3 I combined a two-year bird exclusion experiment with measurement of natural variation in oak leaf quality. Although herbivore community composition varied over time, birds had little effect. Leaf quality influenced the total abundance and richness of herbivores as well as the abundance of different feeding guilds. These effects of leaf quality were strongest at the end of the growing season, when leaf quality is presumably lowest overall.

Insect herbivore abundance can be influenced by both traits of their host plants and the physical environment in which the plant grows. In Chapter 4 I studied the role of the physical light environment and foliage characteristics in determining abundance of the oak lacebug (*Corythuca arcuata* Hemiptera: Tingidae). Using an information-theoretic approach, I evaluated *a priori* hypotheses of the relationship between light, plant traits, and *C. arcuata* abundance. Abundance was best predicted by light environment and leaf carbon content. Adult *C. arcuata* prefer trees growing under an open canopy and trees with low carbon content; abundance also positively correlated with leaf water content. Although carbon and water did not vary with light in this study, low carbon and high water content are often associated with shadier conditions, suggesting that *C. arcuata* faces a trade-off between preferences for physical habitat conditions and host plant characteristics.

Insect prey abundance can also affect the distribution of avian predators. In Chapter 5 I compared the annual distribution of native cuckoos to outbreaks of invasive gypsy moths (*Lymantria dispar* Lepidoptera: Lymantriidae). Populations of cuckoos, one of the few bird species that feeds on gypsy moth caterpillars, spike within outbreaks and are significantly below average abundance for tens to hundreds of kilometers in all directions. This pattern and timing of abundance support the hypothesis that cuckoos locate concentrated food resources during a post-migratory nomadic phase and represents one of the few cases of native predator distribution being influenced by exotic prey.

These studies indicate that complex interactions exist beyond a simple, unidirectional consumption model of plants, herbivores, and avian predators. The indirect positive effect of birds on plants appears robust to variation in the abundance and

traits of the three trophic levels, but the mechanism for this effect may vary through time and space. The impact of birds, however, did not vary with plant characteristics. These characteristics, which can depend on environmental context, likely play a larger role in determining the abundance, structure, and impacts of herbivores than do insectivorous bird predators.

Acknowledgments

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McGrath and John Flunker showed me how to perform leaf analyses in the lab. The staff at Tyson Researcher Center provided great logistical support and a fun working environment, and I will miss interacting with Kevin, Travis, Beth, Megan, Pete, Steve, and the many students and postdocs that make Tyson such an important and productive field station.

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Lastly I am thankful to my family for love and support. My parents recognized the importance of an early interest in the natural world and encouraged it, even when it meant birding in subzero temperatures and visits to sewage treatment plants on family vacations. They instilled in me a love of learning that provided educational opportunities that few children are lucky enough to experience. Most importantly I thank Lacie for her love, support, and patience, and Brendan for giving me the reason and motivation to work my hardest every day.

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Chapter 1

Spatial variation in top-down direct and indirect effects on white oak (*Quercus alba* L.)

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Abstract

Recent attention has been paid to spatial variation in the direct and indirect effects of trophic interactions. Because abundances of predators and prey vary naturally through space, their interactions and the effects of these interactions may vary as well. We conducted a bird exclosure experiment on white oak (*Quercus alba* L.) using a randomized block design to assess how the direct effects of bird predation on arthropods and indirect effects of birds on plant damage and growth differ between five sites separated by 350-1,000 meters. Insect herbivore and arthropod predator abundances varied spatially but were not affected by the exclosure treatment. Bird abundance also varied among sites. Herbivore community structure (herbivore feeding guilds) differed by site as well. Bird predation significantly reduced damage to oak leaves, but this effect did not vary spatially. However, the size of this effect was positively correlated with insectivorous bird abundance. Thus despite herbivore and predator communities that varied among sites, the direct and indirect effects of bird predation appeared to be constant at the local scale at which this experiment was conducted.

Introduction

It is widely acknowledged that predation and plant characteristics act concurrently to impact herbivore populations (Matson and Hunter, 1992 and papers therein). Recent attention has focused on spatial variation in plant-herbivore-predator trophic interactions (Floyd 1996, Forkner and Hunter, 2000; Denno *et al.,* 2005; Gripenberg and Roslin, 2007). Gripenberg and Roslin (2007) pointed out that past research has usually been restricted to a single site, limiting our ability to generalize. They highlight three ubiquitous ecological phenomena that indicate top-down and bottom-up forces should vary through space: (1) landscapes are mosaics of habitats so that environmental conditions, plant quality, predation, and competition vary from one point to another; (2) herbivore populations occupying patchy habitats are themselves patchy and exhibit population dynamics that are not spatially constant; and (3) interacting species differ in their use of space (e.g. different dispersal abilities and population persistence), so the results of their interactions will vary spatially as well, leading to variation in community composition. Thus it is important to determine how top-down forces vary through space to generalize about the role of trophic control by predators.

Previous work in assessing spatial variation in predation strength on herbivores often has focused on processes in fragmented or patchy habitats (Gunnarsson and Hake, 1999; Denno *et al.,* 2002; Valladares *et al.,* 2006), although variability can exist even in continuous habitats (Maron and Harrison, 1997). The scale of these studies has varied: Brewer and Gaston (2003) quantified sources of mortality and other demographic parameters for one species of leafminer (Diptera: Agromyzidae) across its European range (thousands of kilometers), finding that bird predation was stronger in one part of the range, while parasitism was more important in another area. Valladares *et al.* (2006) found that parasitism rates increased with patch size in fragmented woodlands across a landscape at a scale of tens of kilometers. At a much smaller scale (tens to hundreds of meters), parasitism of larval *Epirrita autumnata* (Bkh.) varied among sites along an elevational gradient (Virtanen and Neuvonen, 1999).

Only two studies have included spatial variation in indirect effects of avian predators of herbivores on plant damage, and both of these were conducted at relatively large scales. Mazia *et al.* (2004) found variation in leaf damage among sites separated by tens of kilometers with different precipitation patterns, but no interaction between site and predator exclusion, indicating that predation impact did not vary among sites. Similarly Van Bael and Brawn (2005) compared effects of bird predation between two neotropical forests (70 km apart) that differed in rainfall and plant composition; birds reduced damage only at the drier site.

Here we use a bird exclusion experiment replicated at five sites across a continuous forested landscape to determine how the impact of avian predation varied at a scale of hundreds of meters. Our research was designed to answer the following questions: 1) How do the insect herbivore communities and predator communities vary spatially? 2) How does the direct effect of bird predation change herbivore community structure through space? 3) How does damage and growth on oaks, as an indirect result of the interaction between herbivores and birds, vary spatially?

Methods

We conducted this experiment at Tyson Research Center (St. Louis County, MO, USA, 90.6˚ W, 38.5˚ N), an 809 ha facility operated by Washington University. Most of Tyson is oak (*Quercus*)-hickory (*Carya*) forest, and white oak (*Quercus alba* L.) is a co-dominant canopy tree (Marquis and Whelan 1994). Sapling and mid-story white oaks are uncommon at Tyson, possibly due to browsing by white-tailed deer (*Odocoileus virginianus* Boddaert), which were overpopulated but have been controlled since the late-1990s. In recent years seedling white oaks have become more common (N. A. B., pers. obs.).

We selected five sites separated by 350-1,000 meters in early spring 2006. Sites were chosen to be as similar to each other as possible. Each site was along a single-lane, ridgeline dirt road through mature forest with an open understory. The five sites (Fig. 1) were all on similar soils and part of the same limestone bedrock formation (Criss 2001). Elevations ranged from 217-235 m above sea level, and sites were on relatively level ground or southwest-facing slopes (white oak is considerably less common on north- and east-facing slopes at Tyson). Within each site we chose six canopy or mid-story white oaks with accessible understory branches. These trees were at least 10 m off the road to minimize edge effects. We randomly assigned trees to control or exclusion treatment; thus each site was a block with treatments replicated (n = 3 trees per treatment per block). In March and April 2006 we constructed bird exclosures on exclusion branches. Exclosures consisted of a 2 cm diameter PVC pipe frame anchored with 1 cm thick rebar and covered with monofilament nylon netting with 3.8 cm holes. Because exclosures were custom built on each tree, they varied in size but were generally 1.5-2 m wide and 2-3 m tall. Netting was in place when spring leaf expansion began in late April. Exclosures were built large enough that netting did not contact foliage.

We surveyed arthropods on experimental branches in May, July, and late August to coincide with known peaks in the oak insect herbivore community in Missouri (Marquis and Whelan, 1994; Marquis and LeCorff, 1997). We inspected upper and lower surfaces of all leaves and branches and recorded the number and identity of each arthropod encountered (Forkner *et al.,* 2004). Through work with the Missouri Ozark Forest Ecosystem Project (Shifley and Kabrick, 2002), we are able to identify to species or morphospecies essentially all local leaf-chewing insect herbivores on white oak (Marquis *et al., in press*). Unidentified herbivores were collected and reared in captivity for identification. Arthropod predators were identified to order or family. We counted the number of leaves censused in each survey and standardized arthropod abundances by leaf area based on the known mean leaf size of understory white oak in Missouri (58.7 cm^2, LeCorff and Marquis, 1999). Abundances are expressed here as individuals/m^2 leaf area.

To quantify the bird community at each site we performed a timed transect survey (Bibby 2000) in each site between 0600 and 0800 hrs on three separate days in June 2006. A 100 m transect was measured along the road passing through each site. The observer (N. A. B.) slowly walked the transect for ten minutes recording all birds seen or heard within 50 m perpendicular to the transect. In this way, the bird survey included all birds within 1 ha of forest surrounding each site.

We quantified the impact of herbivores (and thus indirect effects of bird predation) on trees in three ways. First, in late May, following the first peak in herbivore abundance, 30 leaves were systematically chosen on each branch; i.e., if a branch had 300 leaves we started at the base and chose every tenth leaf. These leaves were visually categorized by percent leaf damage (1 = 0-5%, 2 = 5-25%,3 = 25-50%, 4 = 50-75%, 5 = 75-100%) but were not collected. Leaf scars (where a leaf petiole had been attached to a bundle) were classified as 100% herbivory. The mean of these 30 leaf scores estimated total spring herbivory on each branch. Second, we quantified end-of-season herbivore damage in late September before leaf senescence. Thirty leaves were systematically chosen as above and collected from each branch. These were not necessarily the same 30 leaves used in the spring herbivory measurement. Leaves were digitized in the laboratory using a computer scanner, and from these digitized images we calculated mean percent leaf area missing for each branch. Third, we determined if bird exclusion affected biomass accumulation on oaks by measuring twig expansion in summer 2007. Twig growth reflects in part the previous year's photosynthetic assimilation, so 2007 twig growth should be negatively affected by 2006 herbivory (Marquis and Whelan, 1994). We measured all new twigs on experimental branches and calculated mean twig length.

We analyzed insect herbivore and arthropod predator abundance using repeated-measures MANOVA with exclosure treatment and site as fixed factors. While sites (blocks) are often treated as random factors (Newman *et al.,* 1997), we treated site as a fixed factor because we were specifically interested in differences in the dependent variables among locations. Abundances were log-transformed to normalize residuals, and MANOVA was followed with univariate ANOVA and Tukey HSD post-hoc tests. We examined bird abundance differences using generalized linear models with a Poisson error distribution and log-link function. We included only insectivorous birds in this analysis and bird analyses discussed below.

To analyze effects on herbivore community structure, we divided herbivores into feeding guilds. These were free-feeders, which remain in the open on a leaf or branch; shelter-builders, which roll or tie leaves together to create structures in which they feed or are protected from predators; and miners, which feed between the upper and lower cuticle of leaves. We used repeated-measures MANOVA (von Ende, 2001) to examine abundance of these guilds, and abundances were log-transformed.

To examine herbivore damage and twig expansion, we used two-way ANOVA, again with exclosure treatment and site as fixed factors. In all analyses, a significant site effect indicates spatial variation in the insect community. A significant site × treatment effect indicates that direct or indirect effects of bird predation varied spatially.

Additionally, we compared the bird abundance in each site to the herbivore community and effects on trees. Because of limited sample size ($n = 5$ sites), we used non-parametric Spearman rank correlations. All statistical analyses were carried out using SPSS (SPSS Inc., 2004), except the bird abundance analysis, which was performed in R (R Development Core Team 2007).

Results

Herbivore and arthropod predator abundance varied by site, but not by exclosure treatment. We recorded 594 arthropods including 406 leaf-chewing herbivores (4 orders, 21 families, 55 species/morphospecies) and 188 predators (6 orders, at least 8 families). The MANOVA results for herbivore and predator abundance indicated that only site had a significant effect on abundance (Wilks's $\Lambda = 0.228$, $F_{8,38} = 5.194$, $P < 0.001$); treatment (Wilks's $\Lambda = 0.816$, $F_{2,19} = 2.146$, $P = 0.144$), census (Wilks's $\Lambda = 0.943$, $F_{4,17} = 0.256$, $P = 0.902$), and all interactions were non-significant ($P > 0.1$). Total herbivore abundance was fairly constant through time, not differing significantly by census ($F_{2,40} = 0.147$, $P = 0.864$, Fig. 2A). There was a highly significant site effect on herbivore abundance ($F_{4,20} = 10.468$, $P < 0.001$) due to site 3, which consistently had lower abundances (based on

Tukey HSD post-hoc tests). Arthropod predator abundance showed marginally significant variation among sites ($F_{4,20} = 2.578$, $P = 0.069$). While arthropod predators were more abundant within exclosures during May (univariate ANOVA treatment × census interaction $F_{2,40} = 4.853$, $P = 0.013$; Tukey HSD = 2.19, $P = 0.011$), the overall MANOVA treatment × census interaction was non-significant (Fig. 2B).

Like their potential prey, insectivorous bird abundance varied among the five sites. During bird surveys we recorded 88 individuals of 21 species. Abundance was highest in site 3 (mean number of invividuals detected $ha^{-1} \pm 1$ s.e., 12.3 ± 3.3) and significantly lower in site 5 (6.3 ± 1.5, $z = 2.361$, $P = 0.018$) and 1 (7.0 ± 1.5, $z = 2.078$, $P = 0.038$). Species richness was fairly uniform, varying from 9 (site 4) to 12 species (sites 3 and 5).

Abundances of herbivore foraging guilds varied by site and census, but were not affected by exclosure treatment. There was a significant effect of site (Wilks's $\Lambda = 0.330$, $F_{12,48} = 2.078$, $P = 0.037$) and census (Wilks's $\Lambda = 0.096$, $F_{6,15} = 23.414$, $P < 0.001$) on herbivore guilds but no treatment or interaction effects. Abundance of all three guilds (free-feeders, shelter-builders, and miners) differed among sites ($F_{4,20} = 3.424$, $P = 0.027$; $F_{4,20} = 3.124$, $P = 0.038$; $F_{4,20} = 2.727$, $P = 0.058$, respectively) and by census ($F_{2,40} = 18.172$, $P < 0.001$; $F_{2,40} = 13.610$, $P < 0.001$; $F_{2,40} = 22.794$, $P < 0.001$, respectively) (Fig. 3).

Bird exclosure affected leaf damage, but not branch growth. The effects on leaf damage were consistent through space. May leaf damage scores were marginally greater on exclosure trees ($F_{1,20} = 3.863$, $P = 0.063$). There was a highly significant site effect on May leaf damage ($F_{4,20} = 9.954$, $P < 0.001$), again driven by site 3 which experienced extremely high herbivory in May. End-of-season herbivory in October was significantly greater on exclosure trees ($F_{1,25} = 4.259$, $P = 0.050$, Fig. 4A). This leaf damage did not differ among sites ($F_{1,25} = 0.650$, $P = 0.428$), and there was no site × treatment interaction ($F_{1,25} = 0.922$, $P = 0.346$). Mean twig growth in 2007 did not differ by treatment ($F_{1,19} = 2.608$, $P = 0.123$, Fig. 4B), nor were there site ($F_{4,19} = 0.308$, $P = 0.869$) or interaction effects ($F_{4,19} = 1.547$, $P = 0.229$). One tree was excluded from fall herbivory and twig growth analyses because the experimental branch snapped in a storm. The experimental branch on three trees died between fall 2006 and summer 2007; two of these trees were exclosure trees and one was a control tree. Twig growth for these trees was considered 0; excluding these trees from the twig growth analysis did not change results. End-of-season herbivore damage effect size (the difference in mean damage between control and exclosure trees at a site) was significantly positively correlated with total bird abundance (Spearman's rho = 0.9, $P = 0.037$).

Discussion

The results of this experiment suggest that while communities of white oak herbivores and their predators vary through space at the scale examined here, the direct and indirect effects of bird predation are relatively constant. Insect herbivore abundance varied between sites; this variation was mostly due to one of the five sites (site 3), which had low abundances of both herbivores and arthropod predators throughout the experiment. Early in the experiment, the entire research area experienced an outbreak of fall cankerworm (*Alsophila pometaria* Harris), and site 3 experienced especially severe herbivory. This species peaked in abundance early so that when we conducted the May census we recorded relatively few cankerworms. Part of the reason few herbivores were found in site 3 may have been because defoliation was so severe that there was little remaining white oak foliage on the trees being studied. Many of these trees reflushed new leaves in late spring. Reflushed leaves of oaks can be a poor quality food source for the remainder of the season (Schultz and Baldwin, 1982; Hunter and Schultz, 1995; Hunter, 1987) and thus may have been avoided by herbivores. The structure of white oak herbivore communities exhibited spatial variation as well. Sites differed in abundance of the three feeding guilds we examined (Fig. 3).

Abundances of spring arthropod predators were greater within exclosures than on control branches (Fig. 2, although this effect was nonsignificant in the omnibus MANOVA). This high predator abundance disappeared later in the summer. It is possible that arthropod predators showed a strong numerical response to the cankerworm outbreak, which may have been more common within exclosures given the marginally greater spring leaf damage on exclosure trees.

Despite the observed spatial variation in abundance and community structure of herbivores, abundance of arthropod predators, and abundance of insectivorous birds, the indirect effects of bird predation on white oak were consistent spatially. The spring herbivore damage assessment conducted in May showed a significant site effect, but this was entirely due to the high defoliation levels in site 3. By the end of the season, exclosure trees had experienced significantly higher leaf damage from insect herbivores, indicating that bird predation can reduce insect damage on white oak, as has been demonstrated previously on saplings at this site (Marquis and Whelan, 1994). There were no site effects or site × treatment interactions, indicating that the indirect effect of birds on leaf damage were spatially constant at this site. Twig growth in the following year, which partly reflects the previous year's leaf damage, was lower on exclosure trees, which were more heavily damaged, but this effect was not statistically significant. Twig growth was significantly correlated with May herbivory scores ($R^2 = 0.272$, $P = 0.010$) but not end-of-season herbivore damage. Leaf damage present in May, when leaves are young, represents lost photosynthetic capacity for the remainder of the growing season, while the additional damage included in the fall damage estimate was accumulated more gradually over the preceding four months. Thus if twig growth is related to the previous year's photosynthetic assimilation, it would be expected that growth would be more strongly correlated with spring herbivory than total end-of-season herbivory. Again, however, mean twig growth did not vary across sites.

It is not entirely clear why leaf damage was greater on exclosure trees when there was no difference in herbivore abundance: we documented the indirect effect of the bird-insect-plant trophic cascade, but not the direct effect of birds on herbivores. Although we censused herbivores during known peaks in their abundance, the early cankerworm outbreak progressed so rapidly that it was largely over when we conducted the spring census. Cankerworms may have been responsible for a large proportion of the herbivory we measured.

The reduction in leaf damage on control trees was higher in sites with higher insectivorous bird abundance. Although our bird surveys took place in June, between the first and second arthropod censuses, they likely reflect local bird abundance throughout the study period. All the birds recorded breed locally and have established territories before the May arthropod census. Local bird abundance increases in late summer when offspring fledge, but this increase should be positively correlated with the abundance of nesting birds.

Our results appear to contradict the logical argument by Gripenberg and Roslin (2007) that spatial variation in the distribution of herbivores and their predators will result in spatially variable interactions. Despite the similar appearance of the five sites studied here, the composition and structure of the insect herbivore community differed spatially, but according to the ANOVA model the indirect effects of bird predation on white oak did not differ among sites. The only evidence that we found for spatial variation in interaction was a significantly positive correlation between bird abundance and effect size. These two results together suggest that differences in the impacts of birds among sites may have been real but were too weak to be detected. This study focused only on the effects of avian predators in this system. The spatial variation in abundance of herbivores and their different component guilds may be due to variation in bottom-up effects of plants, such as nutritional content, defensive compounds like tannins (Forkner *et al.,* 2004), or interactions among predator guilds, including birds, arthropod predators, and parasitoids.

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Figures

Fig. 1. Sites 1 through 5 at Tyson Research Center, St. Louis County, Missouri.

Fig. 2. Mean abundances (± 1 s.e.) on exclosure and control trees during May, July, and August censuses, pooled across all sites. (A) insect herbivores and (B) arthropod predators. Exclusion of avian predators did not affect abundance of any groups. Although predators were more abundant on exclosure trees in May, treatment effect was nonsignificant in omnibus MANOVA.

Fig. 3. Spatial variation in mean abundances (± 1 s.e.) of herbivore feeding guilds by census. (A) free feeders, (B) shelter-builders, and (C) miners.

Fig. 4. (A) Mean leaf damage (± 1 s.e.) on exclosure and control trees at the end of the growing season. Bird exclusion resulted in significantly higher leaf damage on exclosure trees. (B) Mean twig growth (± 1 s.e.) on exclosure and control trees in summer 2007. Although twig growth was lower numerically on exclosure trees, as expected, the difference was not statistically significant.

Fig. 1

Fig. 2

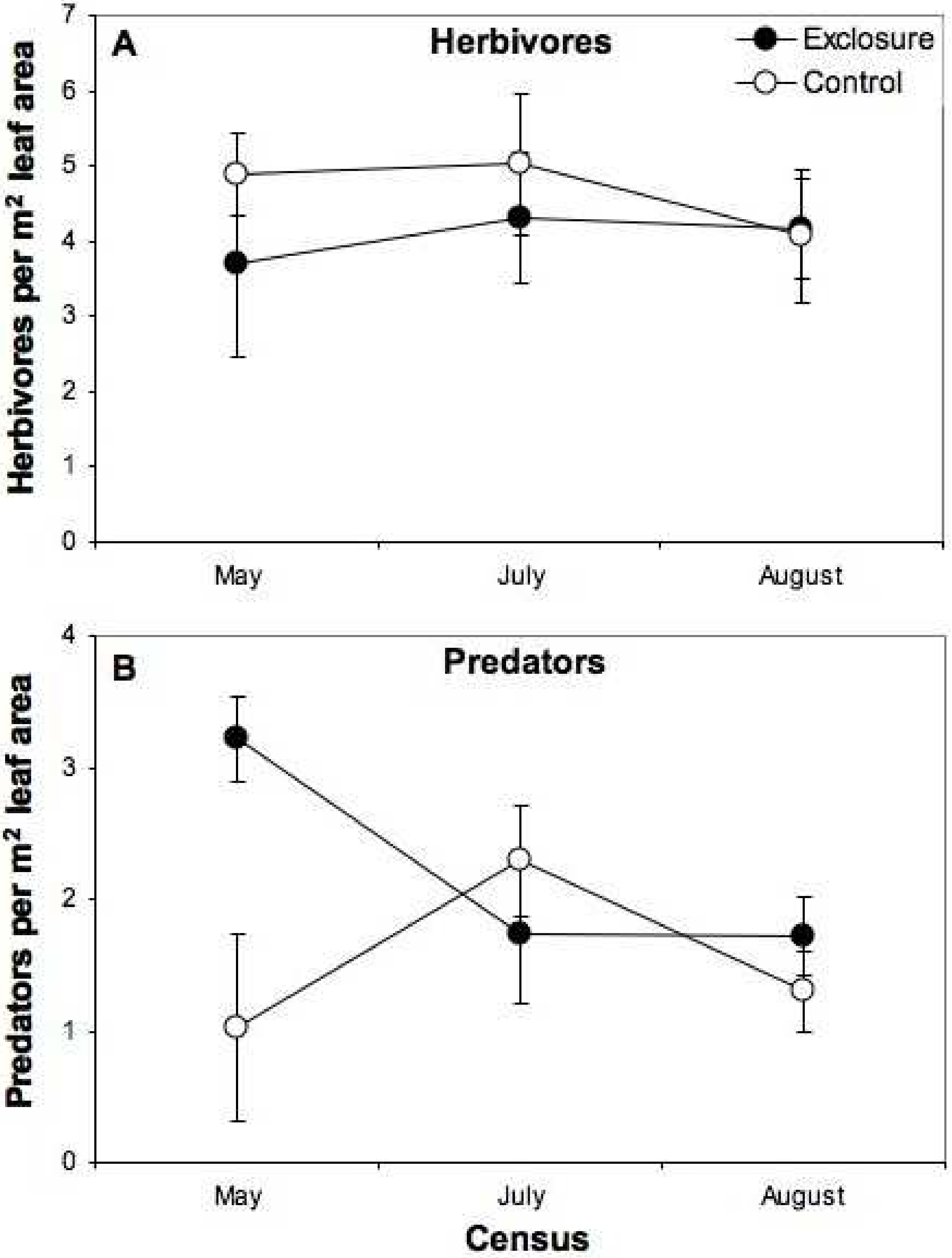

A
Herbivores
Exclosure
Control
Herbivores per m² leaf area
0
1
2
3
4
5
6
7
May
July
August
B
Predators
Predators per m² leaf area
0
1
2
3
4
May
July
August
Census

Fig. 3

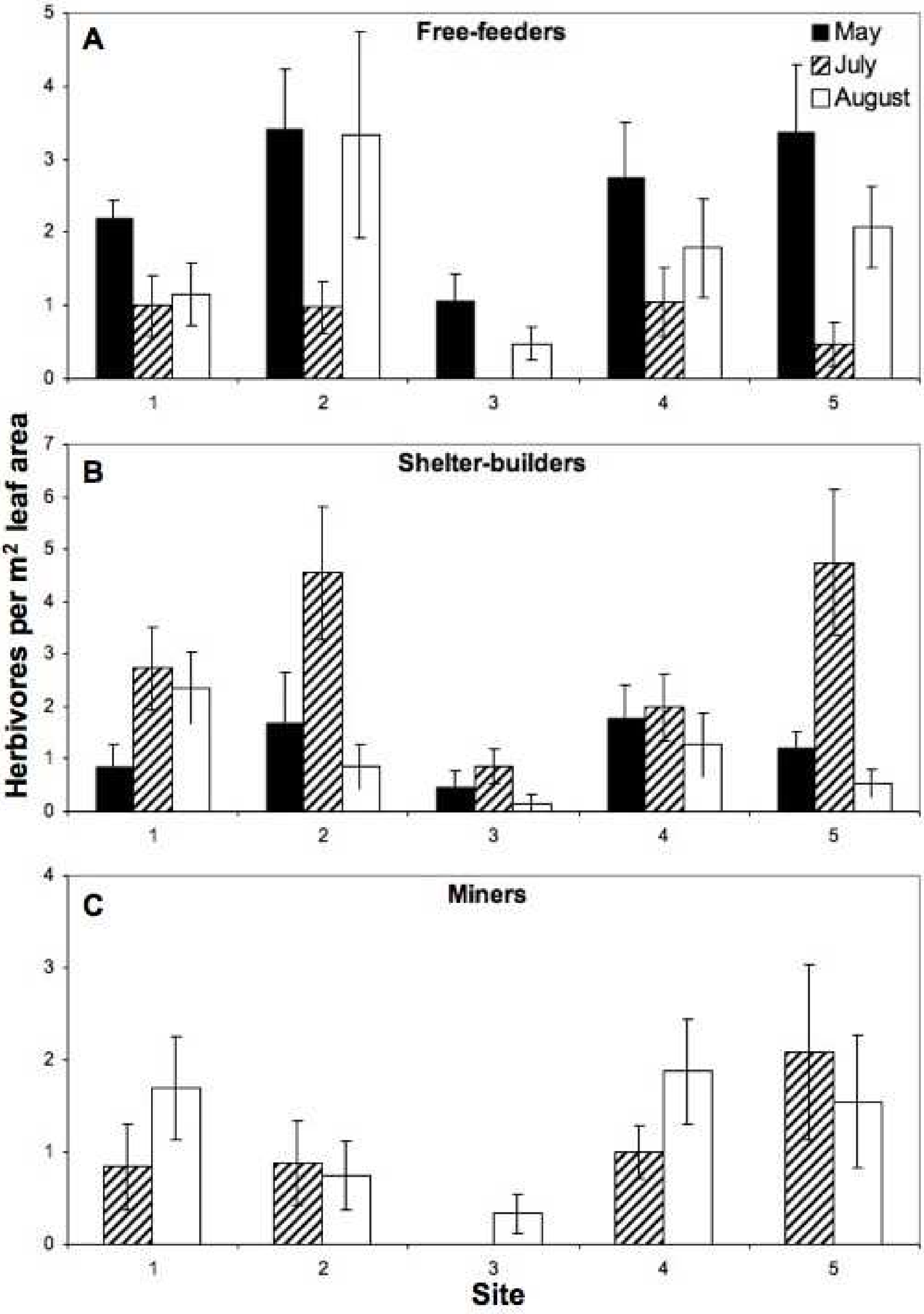
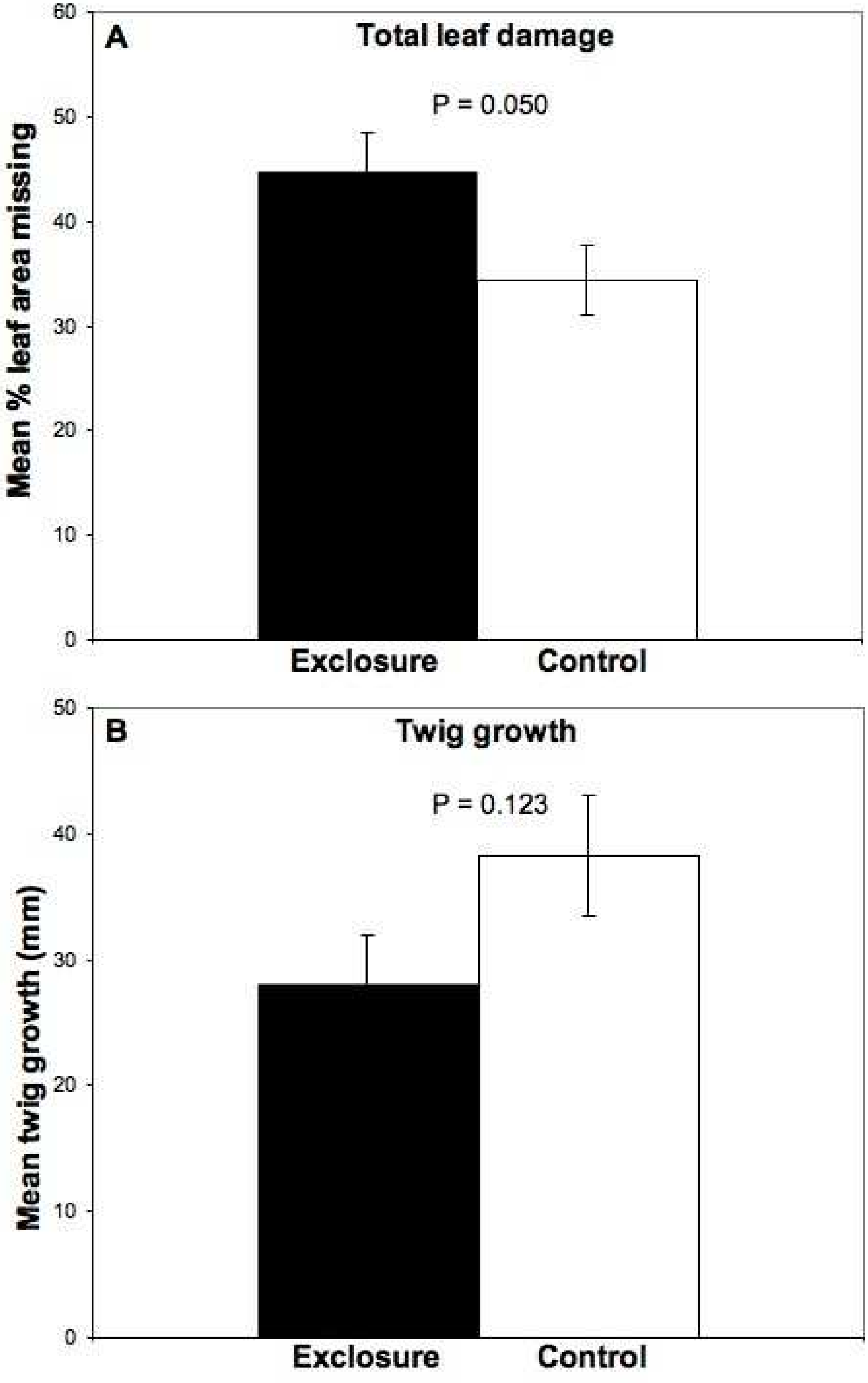

A
Free-feeders
May
July
August
B
Shelter-builders
C
Miners
Herbivores per m² leaf area
Site
0
1
2
3
4
5
6
7
1
2
3
4
5

Fig. 4


A
Total leaf damage
P = 0.050
Mean % leaf area missing
0
10
20
30
40
50
60
Exclosure
Control
B
Twig growth
P = 0.123
Mean twig growth (mm)
0
10
20
30
40
50
Exclosure
Control

Chapter 2

Impacts of foliage quality on herbivorous insect attack and bird predation

Abstract

Theory predicts that the direct and indirect effects of predators on herbivores and plants, respectively, will vary with traits of the plants. Light has strong effects on leaf quality, so the impacts of predators and herbivores may differ between plants grown in sun and shade. However past experiments have often been unable to separate the effects of light environment on plant traits and plant use by herbivores from direct effects on herbivores or predators. I used a light manipulation to produce oak saplings with different leaf quality. I then moved these plants to a common light environment where I factorially excluded bird predators and measured the effects of birds and leaf quality on herbivore abundance and herbivory. Sun leaves were presumably lower-quality food; they were thicker and tougher, had lower nitrogen and water content, and higher carbon, tannin, and phenolic content. However herbivores were significantly more abundant and caused greater leaf damage on sun-exposed trees. Bird exclusion did not change herbivore abundance, but did increase leaf damage. The effects of birds did not vary with light manipulation. The higher abundance and damage on sun trees may have been due to ovipositing females preferring hosts with greater leaf and shoot growth. Birds may have reduced leaf damage through non-consumptive effects on herbivore feeding behavior.

Key words: herbivore, top-down, bottom-up, light, leaf quality, bird predation, indirect effects, tritrophic

Introduction

Ecologists recognize that both predation pressure and food resources impact herbivore populations (Matson and Hunter 1992, Polis 1999). Food web theory predicts that systems with greater primary productivity support larger herbivore populations. As a result, the impacts of predators will increase along this gradient (Oksanen et al. 1981, Oksanen and Oksanen 2000). For this reason, the top-down vs. bottom-up paradigm in ecological research has paid particular attention to the importance of nutrient availability in evaluating food quality of foliage (e.g., Stiling and Rossi 1997, Forkner and Hunter 2000, Huberty and Denno 2006). A number of experimenters have combined fertilization treatments with manipulations of both invertebrate (Stiling and Rossi 1997, Fraser and Grime 1998, Dyer et al. 2004) and vertebrate predators (Sipura 1999, Ritchie 2000, Forkner and Hunter 2000, Gruner 2004, Strengbom et al. 2005, Boege and Marquis 2006). These studies have not produced consistent conclusions as to how the strength of predator effects varies with productivity. Similarly, an extensive meta-analysis by Borer et al. (2005) found that high system productivity is not consistently associated with stronger predator effects.

Nutrients, however, are not the only environmental variable affecting bottom-up effects of plants. Light increases plant growth, but increased light may have an opposite effect on predator impacts compared to fertilization. Light exposure can alter leaf quality, especially in plants with carbon-based defenses, resulting in plants with low nitrogen and water content and tough leaves with high phenolic content (Nichols-Orians 1991, Dudt and Shure 1994). These characteristics can make foliage unpalatable so herbivores are less likely to feed, resulting in lower herbivore abundance and lower plant damage. Lower herbivore populations reduce the foraging intensity and effects of predators, reducing the strength of indirect top-down effects, opposite the expected results in nutrient-enrichment experiments.

Higher concentrations of phenolics such as tannins in plants can have negative effects on insect herbivores. Tannins are associated with decreased growth (Kopper et al. 2002) and survivorship (Agrell et al. 2000) of herbivores and correlate negatively with leaf damage by herbivores (Bettolo et al. 1985, Dudt and Shure 1994, Sagers and Coley 1995). Thus higher-quality shade leaves should support higher abundances of insect herbivores, while well-defended sun leaves should have fewer herbivores. Because insectivorous birds preferentially forage on vegetation with higher prey densities (Smith and Dawkins 1971, Whelan 1989, Parrish 1995), bird foraging effort and predation effects should be greater on shaded plants. These patterns suggest that the strength of the trophic cascade (relative reduction in herbivores and herbivore damage due to predation) should be greater in the less-productive shaded environment. Sipura (1999) conducted a bird exclosure study on two related willow species, one with high levels of defensive chemicals and one with low levels; the direct and indirect effects of bird predation were greater on the poorly-defended trees, consistent with these predictions.

While effects of light on plant growth, physiology, and defensive chemistry are well-known, most experiments exploring effects of light on leaf quality, herbivore abundance, and herbivore impact have been unable to separate the effects of leaf quality and light *per se* on herbivore distribution. For example, Chacón and Armesto (2006), in a design similar to a number of other studies (Dudt and Shure 1994, Muth et al. 2008), planted seedlings in forest interior and canopy gaps and documented differences in herbivory levels between the two microenvironments. But in this design it is not possible to determine if these patterns are due to leaf quality differences in the two light environments or habitat preferences of the herbivores themselves (i.e., herbivores may be more abundant or ingest more leaf material in one light environment than another). Additionally, unlike nutrient effects on herbivores that are transmitted through plants, light can directly affect herbivore growth, development, and behavior by altering temperature and humidity (Stamp and Bowers 1994, Chase 1996).

In this project I used a light manipulation to produce leaves of different qualities followed by bird predator exclusion in a common light environment to control the effects of light on herbivore and predator distribution. This design also manipulates tannin content (as called for by Forkner et al. (2004)) to elucidate the role of plant defensive chemistry in a trophic cascade ("species cacade," sensu Polis 1999). I predicted that sun-exposed trees would have lower leaf quality and thus lower herbivore abundance and damage than shaded trees in the absence of avian predators. When birds are free to forage on experimental trees, this difference would be reduced (Fig. 1A), resulting in an antagonistic interaction between birds and leaf quality on herbivores (Hare 1992). Alternatively, birds may reduce herbivores and damage without interacting with leaf quality (Fig. 1B), or birds may have no impact (Fig. 1C).

Methods

Experimental Trees

In April 2007, I planted 72 *Q. alba* saplings in 19 L (5 gal) buckets with drainage holes using a common soil source (Woodland Perennial Mix, River City Landscape Supply, Inc., Sauget, IL) and placed them in a location that provided morning sun and afternoon shade. I provided water through the 2007 growing season and insulated against freeze over the winter by piling mulch around the outside of the buckets. All saplings survived the winter.

In spring 2008, I constructed a shade canopy structure and sham control ("sun canopy") structure in an open field. Structures were 5 m x 5 m in area and 1.3 m tall. The shade canopy was covered with greenhouse shade cloth (black, "90% light reduction," International Greenhouse Company, Georgetown, IL), and the sun canopy was covered in monofilament netting (2.5 cm gaps, H. Christiansen Co., Duluth, MN). The shade canopy reduced photosynthetically active radiation (PAR) by 75% (percent μmol photons m^{-2} s^{-1} reduction = 75.4% ± 0.1% based on paired measurements on three sunny days; line quantum meter LQM70-10, Apogee Instruments, Inc., Logan, UT). A mesh fence to exclude deer surrounded the canopies.

I moved all saplings to the sun canopy in early April 2008. On the first day budbreak was evident (19 April), I randomized the saplings and moved half ("shade trees," n = 36) to the shade canopy and left the remaining saplings ("sun trees," n = 36) under the sun canopy. The shade canopy did not provide complete shade at all times; in early morning and evening, the low angle of the sun resulted in some trees receiving low-intensity direct sunlight. However trees were completely shaded from mid-morning to late afternoon when sunlight was most intense. I rotated trees within each light treatment weekly to minimize light environment differences experienced by trees beneath each canopy. Although precipitation was plentiful throughout spring 2008, I provided supplemental water to all saplings in case the shade canopy reduced the rain reaching shade trees. Because the only manipulation intended by this treatment is to vary the light environment, saplings were sprayed with an organic pyrethrin-based pesticide (Spectracide Bug Stop, Spectrum Group, St. Louis, MO) weekly and following rain from late April to mid-May. This was to ensure that spring herbivores did not impose different levels of herbivory on sun and shade trees. The pesticide was not very effective, as herbivore damage and particularly aphid damage was present at some levels on most trees.

In early June I recorded the number of leaves on each tree, length of all new shoots, stem diameter at 10 cm, and tree height. I also recorded the number of leaves with >20% damage from leaf-chewers and rated aphid damage using a 0-6 scale (where 0 was no aphid damage visible, 4 was approximately half of leaves with visible aphid damage, and 6 was all leaves with visible aphid damage; damage appeared as pale speckling or blotches on upper leaf surfaces). On 11 June, shade and sun trees were randomized for bird exclosure treatment and transported to a 50 m x 50 m deer exclosure in a mature forest setting with a shaded understory. A grid of 81 points with 5 m spacing had been established within the deer exclosure. I estimated canopy cover at each point using a concave spherical densiometer. I excluded the 9 points with the least canopy cover and assigned a tree to each remaining point. Trees were assigned to points quasi-systematically allowing for the excluded points with the goal of avoiding clumping of treatment combinations. I placed bird exclosures (0.8 m x 0.8 m x 1.5 m tall, covered with the same monofilament netting as on the sun canopy) over all trees assigned to the bird-excluded treatment and fastened exclosures to the ground.

Arthropod Censuses

Herbivores and arthropod predators were censused on 3 July and 3 September 2008. Top and bottom surfaces of all leaves and branches were visually inspected, and all arthropods encountered were identified. Herbivores were identified to species or morphospecies and predators were identified to either order or family. Abundances of herbivores were expressed in m^2 leaf area based on the mean leaf size for each plant undamaged (see "Herbivory Damage," below) multiplied by the number of leaves present on the plant in each survey.

Leaf Quality

On 30-31 July, at the approximate midpoint between the two surveys, I collected three leaves from upper branches of each tree. I collected leaves haphazardly but attempted to collect leaves with minimal damage. I weighed the three leaves from each tree together and measured toughness using a penetrometer (average of three punches per leaf, nine total punches per tree, Force Dial FDK 32, Wagner Instruments, Greenwich, CT). I kept leaves chilled on ice and refrigerated between collection and measurement (elapsed time ranged 4-224 minutes, mean ± 1 s.e. = 102 ± 7 minutes). I stored leaves at -80˚ C. Prior to lyophilization, I punched one 6 mm diameter leaf disk from each leaf. Leaves and disks remained in lyophilizer for 96 hours. I then weighed the dried leaves and the leaf disks (the latter on a microbalance) and summed the weights to calculate water content (= (wet weight – dry weight) / wet weight). I calculated specific leaf area (SLA) from the disk weights and area (= dry weight / 0.283 cm^2). Neither date of collection nor time elapsed between collection and measurement affected toughness or water content (all P > 0.2).

I assayed condensed tannins, hydrolysable tannins, and total phenolics for each tree and compared them to standards purified from bulk leaf tissue pooled from all trees. Bulk tissue was washed with 95% ethanol and extracted with 70% acetone on Sephadex LH-20 in a Büchner funnel. I removed acetone with rotary evaporation and lyophilized frozen extract. Samples from each tree were rinsed with diethyl ether, and tannins were extracted in 70% acetone followed by rotary evaporation; the resulting aqueous samples were brought to common volume. I assayed condensed tannins using the acid-butanol technique (Rossiter et al. 1988, Waterman and Mole 1994), hydrolysable tannins using the potassium iodate technique (Bate-Smith 1977, Schultz and Baldwin 1982), and total phenolics with the Folin-Denis technique (Swain and Hillis 1959). Absorbances (Versamax microplate reader, Molecular Devices Corporation) of each tree were compared to a curve constructed from bulk standard samples of known concentration and expressed as percentages of starting leaf tissue mass. All assays were performed twice, on two separate samples from each tree, and the percentages were averaged; three samples were contaminated during the extraction process, so these trees are based on a single measurement. I determined carbon and nitrogen content by microcombustion (Perkin-Elmer Series II CHNS/O Analyzer 2400).

Herbivory Damage

I systematically collected 30 leaves from each tree on 3 October to measure damage from herbivores. Collected leaves were evenly spaced throughout each plant by dividing the number of leaves counted on the plant in early June by 30; for a plant with

240 leaves, I collected every eighth leaf, starting at the base of the plant. Scars where leaves had been attached in the current year but were missing during the collection were recorded as completely consumed by herbivores. I digitally scanned each leaf and measured area with a pixel-counting program (SigmaScan Pro 5.0). I imported these scans into a paint program, filled in areas of each leaf eaten by herbivores, and remeasured the leaves to estimate the original undamaged leaf area. For leaves that were completely consumed or so severely damaged that estimating original leaf area was not possible, I assigned the mean undamaged leaf area for all measurable leaves on that plant. This mean value was the leaf size used to express abundance of herbivores (see "Arthropod Censuses," above). Total herbivore damage was calculated as the sum of the area of damaged leaves divided by the sum of the original undamaged areas, subtracted from 1. Per capita consumption for each tree was calculated as damage divided by the summed abundance of herbivores.

Analyses

To verify light manipulation effects on leaf quality, I analyzed toughness, water content, SLA, tannins, phenolics, and C and N content using MANCOVA followed by univariate ANCOVAs with light treatment, proportion of damaged leaves in June, and aphid score as covariates. Because abundance of herbivores and arthropod predators were fairly low, and because leaf damage reflects the impacts herbivores from both censuses, I summed July and September abundances. These abundances were analyzed by ANOVA with light treatment and bird exclusion as fixed factors; transformation of variables did not improve model fit. One tree died between the censuses and was excluded from this and all other analyses. One tree was almost completely defoliated by an unknown herbivore between the censuses; it is excluded here because there was essentially no leaf area on which to survey arthropods. I used ANCOVA to determine how total herbivore damage varied with light treatment and bird exclusion and if proportion of leaves damaged in spring or spring aphid damage affected this damage. Damage, expressed as proportion leaf area lost, was arcsin-square root transformed to improve normality of model residuals. All analyses were carried out in R (R Development Core Team 2008).

Results

Leaf Quality

The MANOVA results for leaf quality characteristics indicated that only light manipulation had a significant effect but that the light effect was strong (Wilks's Λ = 0.198, $F_{8,60} = 30.358$, $P < 0.001$). Aphid damage score (Wilks's Λ = 0.934, $F_{8,60} = 0.533$, $P = 0.827$) and proportion of damaged leaves (Wilks's Λ = 0.871, $F_{8,60} = 1.109$, $P = 0.371$; on average, 12.3 ± 1.5% damaged) did not impact leaf quality. Sun trees had significantly tougher leaves than shade trees (Fig. 2A, $F_{1,67} = 9.125$, $P = 0.004$) and significantly lower water content (Fig. 2B, $F_{1,67} = 6.711$, $P = 0.012$). Date of collection and time elapsed between collection and measurement did not affect these measurements. Sun trees also had significantly lower specific leaf area (Fig. 2C, $F_{1,67} = 117.106$, $P < 0.001$). Sun trees had significantly higher concentrations of all three phenolic measurements: condensed tannins increased by 225% ($F_{1,67} = 105.850$, $P < 0.001$), hydrolyzable tannins by 34% ($F_{1,67} = 64.929$, $P < 0.001$), and total phenolics by 51%

($F_{1,67} = 59.684$, $P < 0.001$) (Fig. 3). Sun trees had lower N (Fig. 4A, $F_{1,67} = 42.016$, $P < 0.001$) and higher C (Fig. 4B, $F_{1,67} = 24.014$, $P < 0.001$).

Sun trees produced more leaves (mean ± 1 s.e.: sun, 196.7 ± 8.5; shade, 160.4 ± 7.3; $t_{70} = 3.24$, $P = 0.002$) and more shoots (sun, 31.2 ± 1.2; shade, 26.1 ± 1.3; $t_{70} = 2.94$, $P = 0.004$) than shade trees. However leaves on sun trees were on average smaller than those on shade trees (sun, 61.6 ± 2.6 cm^2; shade, 77.5 ± 3.5 cm^2; $t_{69} = 3.63$, $P < 0.001$), so total leaf area did not differ with light treatment (sun, 1.17 ± 0.06 m^2; shade, 1.24 ± 0.07 m^2; $t_{69} = 0.76$, $P = 0.450$).

Arthropods

The July census recorded 114 herbivores of 23 species (1.34 herbivores/m^2 leaf area) and 44 arthropod predators, of which ants (30%) and spiders (48%) were most common. In the September census 80 herbivores of 32 species (1.02 herbivores/m^2) and 47 predators (96% spiders) were present. Herbivores were significantly more abundant on sun trees compared to shade trees. Bird exclusion did not affect herbivore abundance, and there was no significant interaction between light and bird treatments (Table 1, Fig. 5A). The proportion of damaged leaves in spring and aphid damage score did not affect herbivore abundance; as a result both effects were removed from the model. Neither treatment significantly affected arthropod predator abundance, nor was their interaction significant (Table 1, Fig. 5B).

Herbivory damage

Both light treatment and bird exclusion had a marginally significant effect on total leaf damage. Proportion of leaves damaged in spring and aphid damage score did not affect end-of-season damage and were removed from the model. On average sun trees lost 41.7% more leaf area than shade trees, and trees with birds excluded suffered 41.6% greater leaf area loss than control trees (Table 2, Fig. 6). Per capita consumption did not differ with light treatment ($t_{65} = 0.38$, $P = 0.707$) but was marginally significantly greater within bird exclosures compared to control trees ($t_{65} = 1.70$, $P = 0.094$)

Discussion

I found no evidence that the effects of bird predation on density or impacts of insect herbivores varied with leaf quality. Surprisingly, herbivores were significantly more abundant and inflicted marginally significant greater damage on sun trees. While bird exclusion did not change the abundance of insect herbivores recorded in censuses, caged trees did suffer greater herbivore damage than control trees as predicted.

Sunlight manipulation had the intended effect of changing leaf quality. Sun trees produced harder leaves with less water, lower N content, and higher phenolics and tannins. Our current understanding of the effects of leaf quality traits on herbivore fitness would consider that sun leaves would be lower in quality than shade leaves (Mattson 1980, Scriber and Slansky 1981, Coley et al. 2006, Kitamura et al. 2007). These leaf differences caused by sun exposure in spring lasted through the growing season: measurements were based on leaves collected 7 weeks after plants were moved to a common shady light environment in the forest interior.

Despite their low-quality foliage, sun trees hosted higher abundances of herbivores, contrary to my expectations. This may be due to oviposition preferences of adult female herbivores. Most of the herbivores recorded were Lepidoptera larvae, and for many caterpillars, host plant selection is left largely up to their egg-laying mothers.

Finding a new host plant may be very difficult and energetically expensive for a caterpillar, especially on understory plants as opposed to canopy-feeding herbivores which can easily drop to lower plants. In this case plants were also planted in plastic buckets into which caterpillars may have been unwilling to climb. Thus, the observed differences among sun/shade treatments may have been due to oviposition choices by gravid females. The observed pattern of greater abundance on sun trees is consistent with the plant vigor hypothesis (Price 1991), in which herbivores prefer host plants that are growing or have grown larger than other “less-vigorous” plants. Sun trees produced more leaves and shoots than shade trees, so if ovipositing female moths do prefer more vigorous-growing host plants, then abundance of herbivores may be expected to be greater on sun trees as observed in this experiment. However the smaller size of sun leaves resulted in similar total leaf area between sun and shade trees

Because herbivores were more abundant on sun trees, it is not surprising that the amount of leaf area lost to herbivory was also greater. However it is possible that this leaf damage was also greater on sun trees because of the low nutritional quality of the foliage. Because of the low nitrogen content and higher concentration of phenolic compounds that may interfere with digestion, an herbivore may need to consume a greater amount of leaf tissue on sun trees to obtain the same nutritional and energetic benefit as on shade trees where nitrogen is more concentrated and phenolics content is lower. This compensatory feeding by herbivores on plants of poor nutritional value is widespread (Simpson and Simpson 1990). If this were the case in this experiment, I would expect per capita consumption to be higher on sun trees. Per capita leaf consumption was the same for sun and shade trees, so herbivores did not appear to engage in compensatory feeding on low-nutritional plants.

The lack of an effect of bird predation on insect herbivore abundance and arthropod predator abundance is surprising given the strong effects documented by Marquis and Whelan (1994) at a nearby site on the same host plant. Many other researchers have increased arthropod abundances on plants by excluding birds (Holmes et al. 1979, Floyd 1996, Sipura 1999, Strong et al. 2000, Van Bael et al. 2003). Insectivorous birds may have been less abundant at my site than the nearby site used by Marquis and Whelan (1994). They also studied larger plants, which may have supported higher densities of herbivores per leaf area that would have made patterns of abundance more apparent (Feeny 1976). Increased abundance of, and predation by, arthropod predators in the absence of vertebrates can also mask predation effects ("compensatory predation," Pacala and Roughgarden 1984). I observed no difference in arthropod predator abundance between cage and control trees, which suggests that this did not occur in this experiment.

Per capita feeding was marginally greater within bird exclosures, which may in part explain why leaf damage was greater on plants from which birds were excluded even though this did not result in differences in herbivore abundance. Physical disturbance of plants may cause herbivores to cease feeding or other activity, or may prompt them to drop off of the host plant to escape possible predation (pers. obs.). There is evidence that Lepidopteran larvae even reduce feeding activity in response to disturbance by nearby flying insects, perhaps as a precaution against parasitoids (Tautz and Rostás 2008). Caged plants in this experiment may have experienced less physical perturbations because of the absence of foraging birds; herbivores on these plants would be disturbed less while feeding, resulting in greater damage to caged plants.

A number of studies have shown that herbivore damage is lower in forest edge, gap, and other sunny microhabitats (Dudt and Shure 1994, Muth et al. 2008). A sample of *Q. alba* leaves from edge and interior habitats at this field site agrees with this (unpubl. data). Contrary to these other studies, the results of this experiment suggest that reduced damage on sun-exposed edge leaves is not due to leaf quality, as sun trees received greater damage than shaded trees. Three possible explanations (not mutually exclusive) may explain the edge-interior leaf damage pattern. Predation on herbivores, either by vertebrate or invertebrate predators, may be greater along edges. This is supported by studies using both artificial (Richards and Coley 2007, Skoczylas et al. 2007) and live caterpillars (Richards and Coley 2008), which found bird attacks on artificial caterpillars were more frequent in forest edges. Second, adult females may avoid edges when ovipositing. Selection for this avoidance may be due in part to higher predation rates on larvae. Lastly, herbivores growing along forest edges may develop more quickly on warm sun-exposed leaves and so do not consume as much leaf tissue as in cooler interior habitats (Joos et al. 1988)

In conclusion, birds had no effect on herbivore abundance, but may have had a behavioral effect on feeding as evidenced by per capita herbivore consumption rates. The effects of bird predation did not differ with leaf quality. Herbivores were more abundant on sun plants, opposite my prediction, and this resulted in greater damage. Thus results supported a mirror-image of the hypotheses presented in Fig. 1 in which sun and shade trees should be switched. Herbivore abundance patterns then were most similar to hypothesis C in Fig. 1, while leaf damage results supported hypothesis B.

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Table 1. Herbivore and arthropod predator abundance ANOVAs.

Source	df	*F*	*P*
Herbivores			
Light	1,66	6.363	**0.014**
Birds	1,66	0.007	0.932
Light x Birds	1,66	0.688	0.410
Arthropod predators			
Light	1,66	2.217	0.287
Birds	1,66	2.484	0.260
Light x Birds	1,66	4.559	0.129

Table 2. Total leaf area lost to herbivores ANOVA.

Source	df	*F*	*P*
Total herbivore damage			
Light	1,66	2.840	*0.097*
Birds	1,66	3.443	*0.068*
Light x Birds	1,66	0.111	0.740

Figures

Fig. 1. Hypothetical impacts of birds and leaf quality on herbivore abundance and leaf damage. Dashed line indicates results within bird exclosures, and solid lines are uncaged control trees. (A) Bird predation may increase with herbivore abundance, resulting in a greater relative reduction on shade trees relative to sun trees. (B) Birds may reduce herbivores and damage, but the impact may be simply additive if the reduction does not differ with herbivore abundance (and light treatment). (C) Birds may have no impact on herbivore abundance or herbivory.

Fig. 2. Effects of light treatment on leaf characteristics. (A) toughness, (B) percent water content, (C) specific leaf area. ***, $P < 0.001$.

Fig. 3. Effects of light treatment on phenolic and tannin chemistry. ***, $P < 0.001$.

Fig. 4. Effects of light treatment on (A) N content and (B) C content. ***, $P < 0.001$.

Fig. 5. Effects of light manipulation and bird exclusion on (A) herbivore abundance and (B) arthropod predator abundance. Values are mean abundance per m^2 leaf area ± 1 s.e. Dashed lines indicate bird exclusion trees, and solid lines are control trees. Herbivores were significantly more abundant on sun trees, but bird exclusion did not affect herbivore abundance. Neither light nor bird exclusion treatments affected predator abundance. *, $P < 0.05$.

Fig. 6. Effects of light manipulation and bird exclusion on mean percent leaf area consumed by herbivores ± 1 s.e. Dashed line indicates bird exclusion trees, and solid line is control trees. Damage was marginally significantly greater on sun trees and within bird exclosures.

Fig. 1.

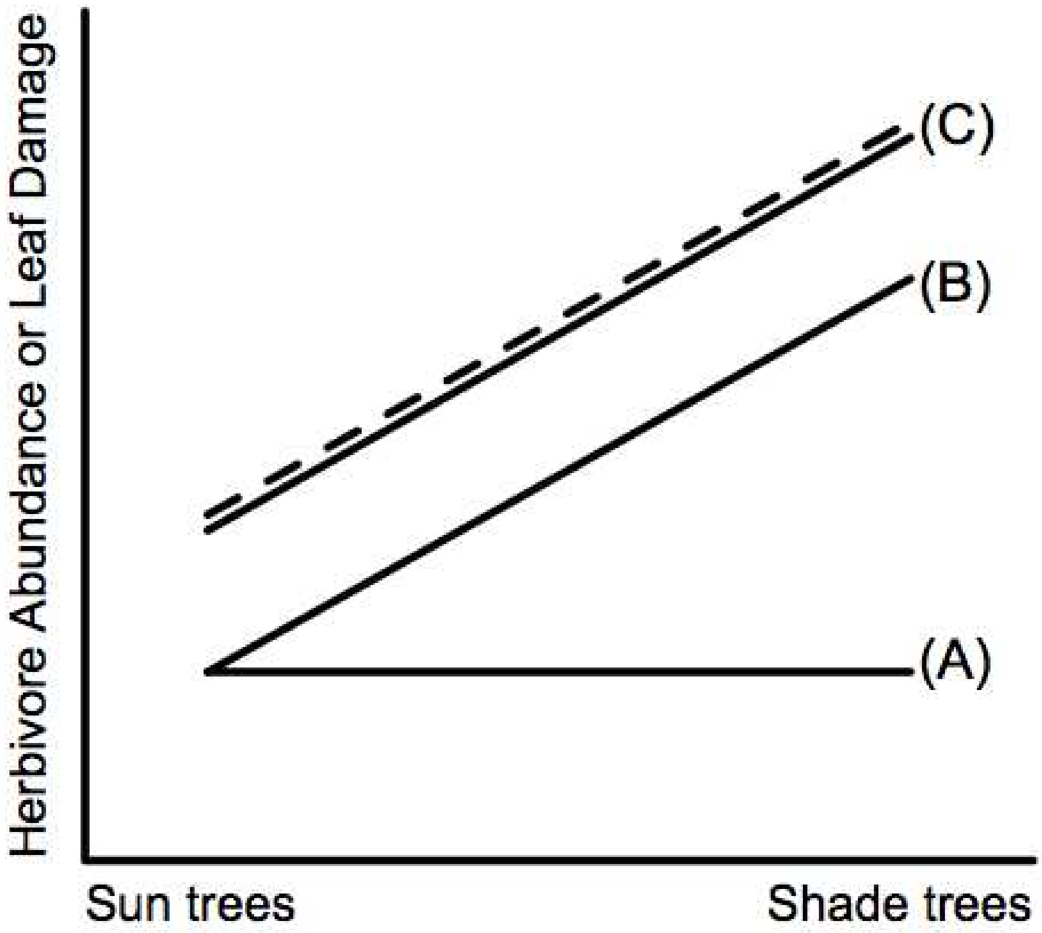

Herbivore Abundance or Leaf Damage
(C)
(B)
(A)
Sun trees
Shade trees

Fig. 2.

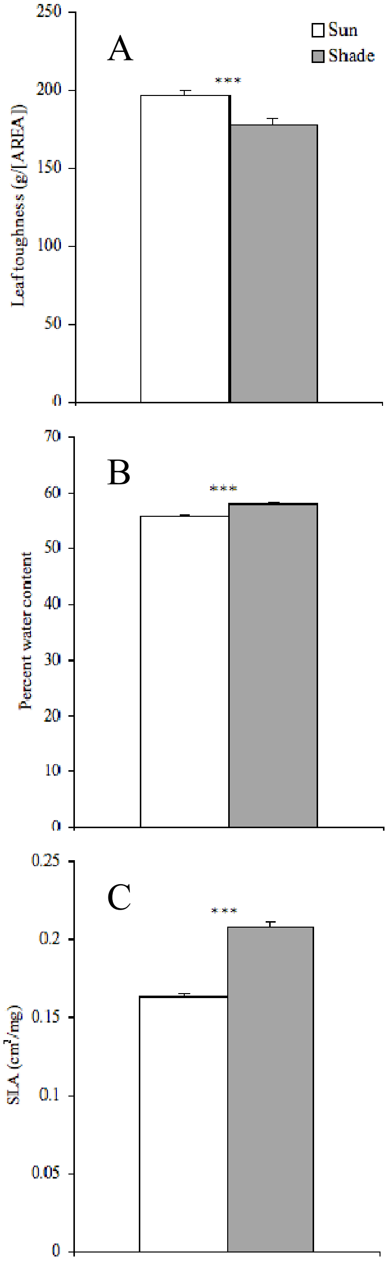

A
☐ Sun
▨ Shade
***
Leaf toughness (g/[AREA])
250
200
150
100
50
0
B
***
Percent water content
70
60
50
40
30
20
10
0
C
***
SLA (cm^2/mg)
0.25
0.2
0.15
0.1
0.05
0

Fig. 3.

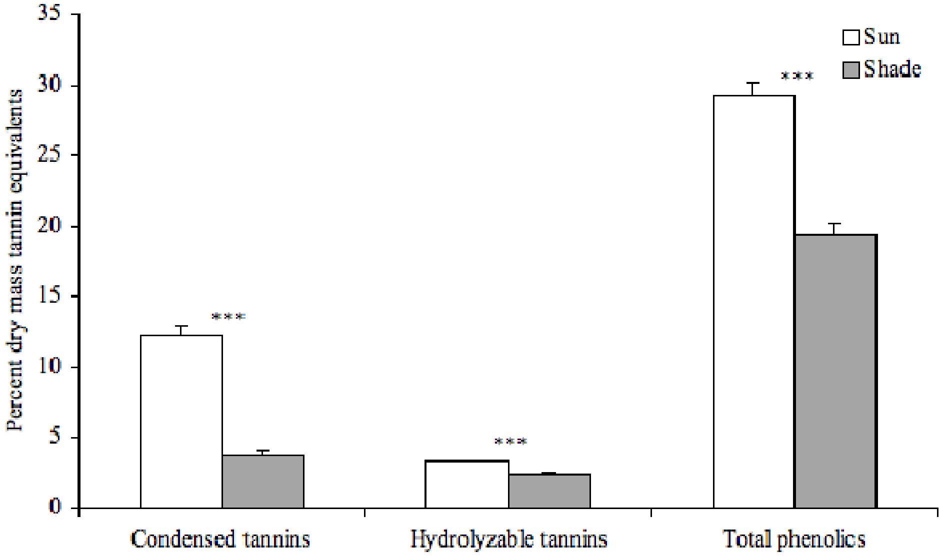

35
30
25
20
15
10
5
0
Percent dry mass tannin equivalents
□ Sun
▨ Shade
***
***
***
Condensed tannins
Hydrolyzable tannins
Total phenolics

Fig. 4.

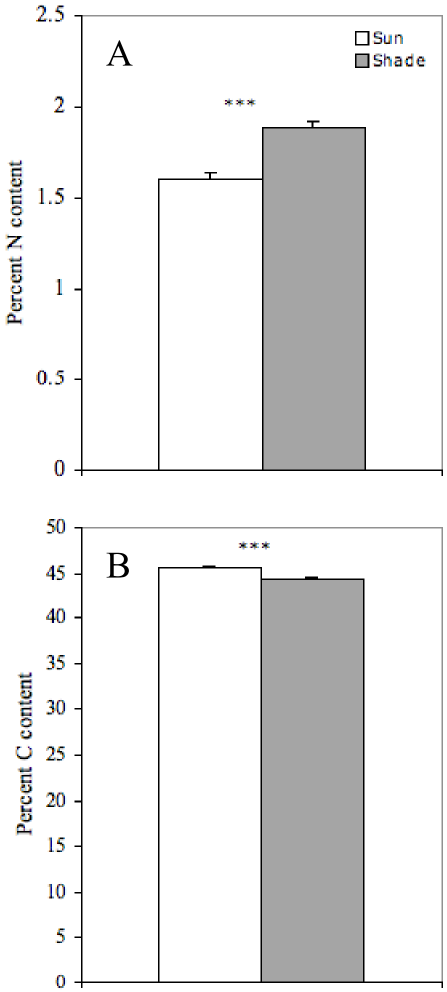

A
☐ Sun
▨ Shade
***
Percent N content
0
0.5
1
1.5
2
2.5
B
***
Percent C content
0
5
10
15
20
25
30
35
40
45
50

Fig. 5.

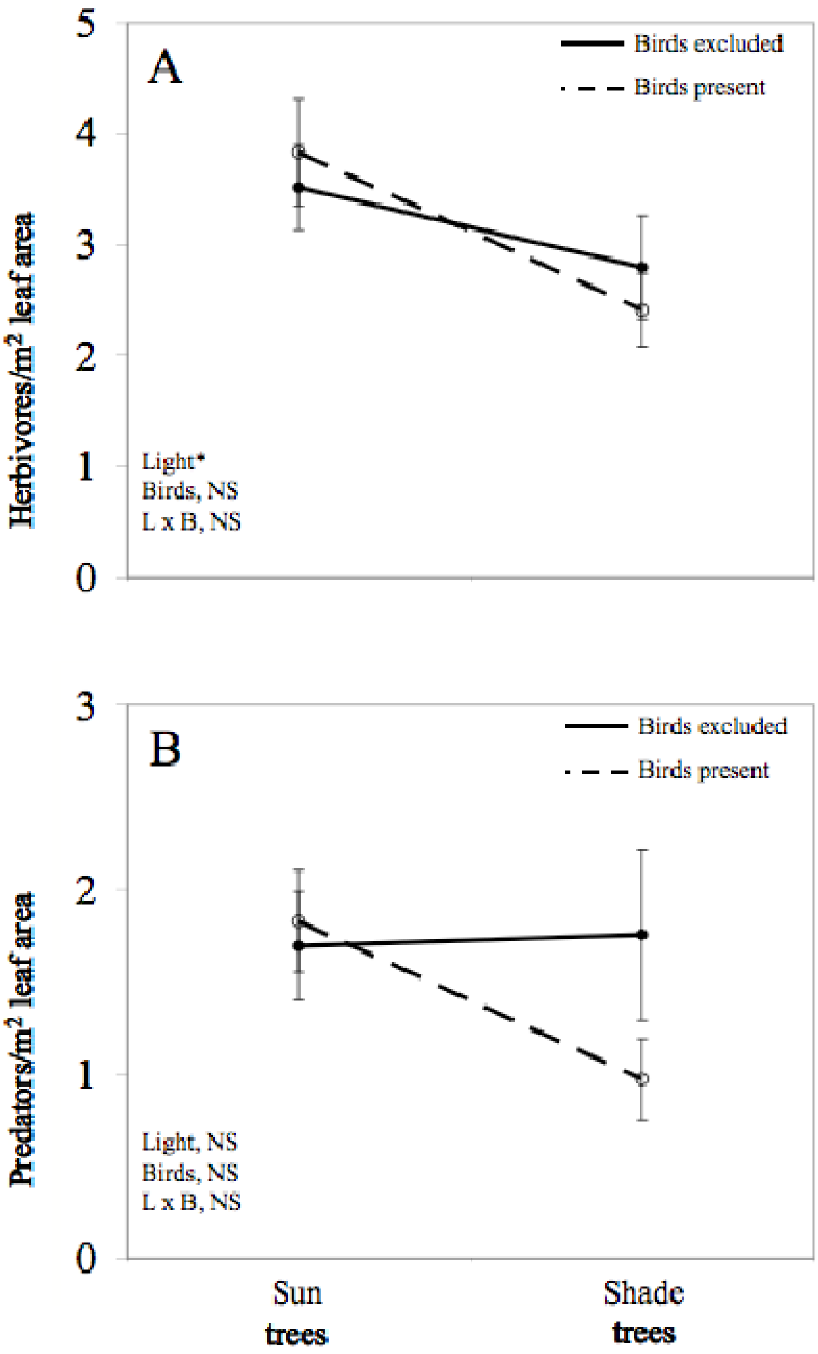
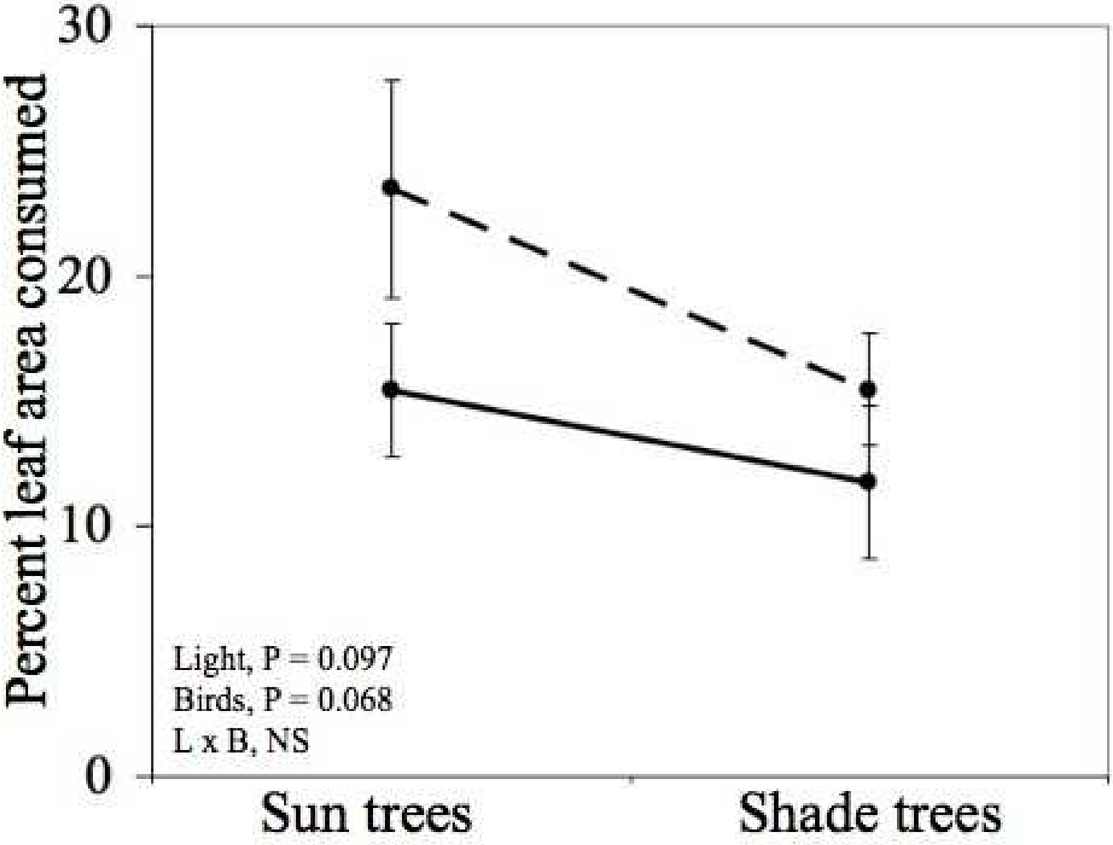

A
Birds excluded
Birds present
Herbivores/m^2 leaf area
5
4
3
2
1
0
Light*
Birds, NS
L x B, NS
B
Birds excluded
Birds present
Predators/m^2 leaf area
3
2
1
0
Light, NS
Birds, NS
L x B, NS
Sun trees
Shade trees

Fig. 6.


Percent leaf area consumed
30
20
10
0
Sun trees
Shade trees
Light, P = 0.097
Birds, P = 0.068
L x B, NS

Chapter 3

Bottom-up forces are more important than top-down in structuring a diverse oak herbivore community

Abstract

Predation and plant traits both affect the abundance of insect herbivores, but less is known about how these forces influence the structure and composition of herbivore communities. I combined a manipulation of insectivorous birds with measurements of natural variation in leaf quality characteristics of white oak (*Quercus alba*) across two growing seasons to determine top-down and bottom-up effects on herbivore richness and abundance of specific guilds. Six censuses across the two years revealed that bird effects were weak, and bird predation only reduced the abundance of one group, generalist herbivores, and only during one census. Bird predation also did not change the species composition of communities. Leaf quality affected the abundance of most guilds, and these groups were consistently more abundant on trees with high nitrogen content and low levels of hydrolysable tannins. These patterns were most apparent near the end of the growing season, when quality of foliage as food is lowest and the importance of leaf quality on host choice may be most important. Generalist herbivores, but not oak specialists, were negatively correlated with high-tannin trees, supporting the idea that specialists are adapted to variation in host plant defenses. Abundance of structure-building herbivores did not vary with leaf quality, consistent with past work on leaf-tying oak herbivores. Although predation had little effect on community structure in this system, impacts on herbivore richness and composition may be more apparent when direct effects of predators are stronger overall.

Key words: herbivore, top-down, bottom-up, leaf quality, community structure, richness

Introduction

Insect herbivore communities in forest habitats are often characterized by high species richness (Summerville and Crist 2003, Novotny et al. 2006, Dyer et al. 2007). Understanding the factors that influence diversity patterns in these communities has remained a significant challenge to ecologists (Strong et al. 1984, Lewinsohn et al. 2005). While it is widely recognized that both top-down impacts of predators and bottom-up influences of plant quality can control herbivore populations under certain conditions (Matson and Hunter 1992, Polis 1999), the roles of these forces in determining herbivore diversity and community structure area is less well understood.

Predation on herbivores by insectivorous birds can alter total insect abundance (Marquis and Whelan 1994, Strong et al. 2000, Murakami and Nakano 2000, Van Bael et al. 2003) and biomass (Mooney 2007), although these effects do not always occur (Forkner and Hunter 2000, Lichtenberg and Lichtenberg 2002, Gruner 2004). Because birds should find prey items with different feeding behaviors or appearance at different rates, bird predation effects should differ in strength among herbivore species, in turn altering herbivore community composition. Although bird exclusion studies have become common (Van Bael et al. 2008), few have reported impacts of birds on arthropod community structure (Marquis and Whelan 1994). Boege and Marquis (2006) documented an increase in herbivore richness when birds were present, but Gruner (2004) found no such effect.

Susceptibility to predation may be mediated by feeding method such that herbivores concealed within leaves or in leaf structures may be protected from predation. Structure-building herbivores seem to be unaffected by birds, except for some leaf-rolling caterpillars (Murakami 1999, Murakami and Nakano 2002). However, reported impacts of birds on leaf-miners are conflicting: although birds are known to search for and attack leaf mines (Heinrich and Collins 1983, Connor and Beck 1993, Connor et al. 1999), neither Forkner and Hunter (2000) nor Mazia et al. (2004) found changes in miner occurrence when birds were excluded. Finally Low and Connor (2003) estimated abundance of feeding guilds by measuring the area damaged by different guilds (e.g., skeletonizing, gall-forming, leaf-mining), but they found no effect of birds

Abundance of herbivore species on their host plants is also influenced by the food quality of foliage. Leaf quality is determined by various factors including nutrient content, defensive chemistry, physical characteristics (e.g., toughness, water content, specific leaf area), and the structural components that determine these physical characteristics. These characteristics covary in complex ways depending on soil conditions, light exposure, and plant genetics. The majority of research in this area has examined how herbivore communities differ between several plant species and how these differences correlate with traits of those plant species (e.g., Cornell and Kahn 1989, Murakami et al. 2008, Ricklefs 2008). Fewer ecologists have examined how intraspecific variation within a plant species relates to herbivore community structure on individual plants. In Japanese *Quercus,* richness was lower on sun-exposed oaks with leaf quality that differed from that of shaded trees; the composition of the Lepidoptera communities on these trees differed as well. Lepidoptera community structure and richness on

Quercus also varied with forest management (Forkner et al. 2006), which can alter leaf quality at a large scale (Forkner and Marquis 2004). Internal-feeding herbivores may have different leaf trait preferences compared to exposed feeders. For example, leaf-miners prefer softer leaves with higher water content (Kitamura et al. 2007, Cornelissen and Stiling 2008), but the effects of tannins and specific phenolic compounds are variable (Kitamura et al. 2007, Yarnes et al. 2008). Similarly, leaf traits are expected to interact with herbivore diet breadth to influence species' abundances. Specialist herbivores may be better adapted to plant chemical defenses so that these compounds are more effective against generalists (Dyer et al. 2004), although Forkner et al. (2004) found that defensive condensed tannins in oaks have stronger impacts on specialists.

In this study I combined a bird exclusion experiment with measurements of the natural variation in foliage characteristics in *Quercus alba* (white oak) to determine how these top-down and bottom-up forces affected the structure of a diverse insect herbivore community. Few studies have assessed the roles of both predation and leaf quality in herbivore communities, and this study is unique in that past work in the study system allows detailed categorizations of herbivores to examine the responses of particular guilds and analyses of community composition at high taxonomic resolution. I predicted that density of exposed-feeding herbivores, but not concealed guilds, would be affected by bird predation, but all guilds would vary with leaf quality. I expected leaf traits, but not birds, to differentially impact oak specialists and generalists.

Methods

This experiment took place at Tyson Research Center near Eureka, Missouri, along a southwest-facing dry slope in mature oak-hickory forest. This is roughly the same area used by Marquis and Whelan (1994) in their study of the impacts of birds on insect abundance on *Q. alba*, and encompasses sites 4 and 5 described in Barber and Marquis (*in press*).

In winter 2006-2007, I identified 60 *Q. alba* of canopy or mid-story height with accessible understory branches (< 3 m from ground) and assigned each to exclosure or control treatments. To ensure treatments were distributed evenly throughout the study area, I paired each tree with the nearest experimental tree and randomly assigned treatments. I constructed bird exclosures using pvc pipe frames covered with monofilament gill netting with 2.5 cm gaps (H. Christiansen Co., Duluth, MN). Frames were anchored by driving steel rebar into the ground and slipping the legs of each frame over these stakes. Exclosures were generally built around a single understory branch, but on some trees one or more additional branches were included to ensure a sufficient number of leaves would be enclosed. Netting was in place prior to budburst in spring 2007.

I censused arthropod communities on each tree at three points in the season when insect herbivore abundance on *Q. alba* in Missouri is known to peak. These peaks also have distinct species compositions with little or no overlap of individual herbivores from one peak to the next (Marquis and Whelan 1994, Marquis and LeCorff 1997, Forkner et al. 2004). Because herbivore phenology varies somewhat among years, herbivore populations were informally monitored to determine when populations appeared to be reaching peak abundance. In 2007, censuses took place on 11-14 May, 2-4 July, and 26-

30 August; in 2008, 9-13 May, 3-4 July, and 2-9 September. Following census protocols in Forkner et al. (2004), I searched tops and bottoms of leaves on experimental branches and identified all leaf-chewing herbivores encountered. I counted the leaves inspected and searched approximately 400 leaves per branch, although some branches did not contain this many leaves. Identification of these herbivores to species or morphospecies level is possible because of past work in the Marquis lab in conjunction with the Missouri Ozark Forest Ecosystem Project (Marquis and LeCorff 1997, Marquis et al. 2002a). I identified arthropod predators to either order or family.

Following each census, I collected three leaves from each experimental tree; I collected leaves haphazardly but chose average-sized or large leaves with minimal damage. Leaves were kept chilled on ice after collection and weighed within three hours. I measured toughness using a penetrometer (average of three punches per leaf, nine total punches per tree, Force Dial FDK 32, Wagner Instruments, Greenwich, CT). In 2008, I punched one 6 mm diameter leaf disk from each leaf. Leaves and disks were lyophilized for 72-96 hours and reweighed to obtain dry weight. I calculated water content as (wet weight – dry weight) / wet weight, and weighed leaf disks to calculate specific leaf area (SLA, dry weight / 0.283 cm^2).

I assayed condensed and hydrolyzable tannins for each tree and compared them to standards purified from bulk leaf tissue pooled from all trees. Bulk tissue was washed with 95% ethanol and extracted with 70% acetone on Sephadex LH-20 in a Büchner funnel. Samples from each tree were rinsed with diethyl ether, and tannins were extracted in 70% acetone followed by rotary evaporation; the resulting aqueous samples were brought to common volume. I assayed condensed tannins using the acid-butanol technique (Rossiter et al. 1988, Waterman and Mole 1994) and hydrolysable tannins using the potassium iodate technique (Bate-Smith 1977, Schultz and Baldwin 1982). Absorbances of each tree were compared to a curve constructed from bulk standard samples of known concentration and expressed as percentages of starting leaf tissue mass. An error in the May 2007 condensed tannin assays resulted in questionable values, so these data were discarded and excluded from analyses. I determined carbon and nitrogen content by microcombustion on a Perkin-Elmer Series II CHNS/O Analyzer 2400.

Analyses

For all analyses, abundances were divided by the total leaf area inspected per tree per census, calculated as the product of the number of leaves surveyed and the average understory leaf size for *Q. alba* reported in Le Corff and Marquis (1999), 58.7 cm^2. Thus abundances are reported as densities per m^2 leaf area.

Compositional similarity of communities was analyzed using multi-response permutation procedures (MRPP), a nonparametric method that compares distances within and between groups defined *a priori* to test the null hypothesis that distances within groups are smaller than expected by chance (McCune and Grace 2002). MRPP produces a statistic, A, that varies from $A = 1$ (all replicates within a group are identical) to $A = 0$ (heterogeneity within groups equal to that expected by chance) or $A < 0$ (more heterogeneity within groups than expected by chance). I used Sørensen distance (synonymous with Bray-Curtis distance) and natural $\log(x + 1)$-transformed abundances, following the recommendations of McCune and Grace (2002). Trees on which no herbivores were recorded (a small number in May 2007) were excluded. I first compared community similarity between the three censuses within each year and then all six censuses combined. Significant differences in composition were followed with pairwise comparisons. To test the impacts of birds on arthropod community composition, I used MRPP to compare exclosure vs. control trees in each of the six censuses individually. I presented these communities graphically using non-metric multidimensional scaling (NMS), again using Sørensen distance. I performed MRPP and NMS analyses using PC-ORD 4.25 (MjM Software, Gleneden Beach, OR).

Because leaf quality characteristics often covary, I used principal components analysis (PCA) to describe the variation in leaf traits in a smaller number of variables. Following Ricklefs (2008), I log-transformed leaf quality measurements to homogenize variances and linearize relationships between variables. I used prcomp() in the stats package of R (R Development Core Team 2007). Variables were scaled to have unit variance; thus analyses were performed on the correlation matrix. I performed six individual PCAs to describe the leaf quality in each census.

To determine how bird predation and leaf quality affect herbivore richness and density, I used MANCOVA with bird exclusion as a fixed factor and the first two leaf quality principal components (PCs) in each census as covariates. Data from repeated censuses in an experiment like this are usually analyzed using mixed models to account for lack of independence of replicates between censuses, but this was not possible since leaf quality changes from one census to the next. That is, it would not make sense to include a covariate that incorporated September leaf measurements when analyzing May herbivore density. Instead I analyzed censuses in separate MANCOVAs; this is further justified by the distinct communities in each census (see Results, below) in which few, if any, individual insects are present in more than one census. In each census I used separate MANCOVAs to analyze (1) total herbivore richness and density, (2) density of guilds (free-feeders, shelter-builders, leaf-miners, and arthropod predators), and (3) density of oak specialists (species that feed only on *Quercus* spp.) and generalists (species that feed on at least one other plant genus). Categorization of herbivores by guild and host breadth is based on information in Covell (1984), Forkner et al. (2004), and Wagner (2005). Effects of bird exclusion, leaf quality, or interactions in omnibus MANCOVAs with $P < 0.1$ were followed by examination of individual ANCOVAs.

Because high abundance of Asiatic oak weevil (*Cyrtepistomus castaneus*) in July censuses dominated the community and strongly influenced model results, I ran July models with this species excluded from total herbivore, free-feeders, and oak specialists. Weevil density was analyzed independently with separate ANCOVAs. All PCAs and MANCOVAs were carried out in R.

Results

Surveys recorded 1,478 leaf-chewing herbivores of 71 species or morphospecies in 2007 and 2,415 of 77 species in 2008. 2007 herbivores densities were lower than 2008 densities (Fig. 1); in May censuses, this difference was presumably due to a late frost that occurred in early April following early warming and budbreak (Gu et al. 2008). This frost killed many early-emerging herbivores, depressing May densities and possibly densities for the later communities as well.

MRPP analyses of herbivore community composition differences among censuses were all highly significant (Appendix 1, Table 1; Fig. 2A-B), indicating strong differences between early-, mid-, and late-season herbivores. MRPP of the same censuses in different years (e.g., May 2007 vs. May 2008) were also highly significant, meaning there was variability among years as well.

Bird exclusion had few and weak effects on herbivore community composition. Differences between exclosure and control trees were marginally significant in July 2007 and May 2008 and significant in July 2008 (Appendix 1, Table 2). However $A < 0.02$ in each of these cases, suggesting weak differences, and examination of NMS ordination plots reveals no strong differences between trees with and without bird predation (Appendix 1, Figs. 1-3). Neither eliminating rare species (present on < 5% of trees) nor relativizing species abundances qualitatively changed results.

Individual PCAs for each census verified strong correlation structure within leaf quality measurements (Table 1). In five of the six censuses, the first two PCs explained > 50% of the variation in leaf quality. In July 2007 these components accounted for 48% of the variation. In July and August/September, water, hydrolyzable tannins, and nitrogen content were frequently strongly correlated; increased water tended to be correlated with high nitrogen and low hydrolysable tannins. In 2008, these trees tended to have low SLA as well. This combination of variables was represented in the first PC for all four of these censuses. High nitrogen and low hydrolysable tannins also contributed to May 2007 PC1 and May 2008 PC2. Second PCs in July and September/October represented positive correlations between condensed tannins and carbon content in 2007 but more varied relationships in 2008.

Total herbivore density and richness MANCOVAs revealed a significant impact of leaf quality in August 2007 and May and September 2008 censuses, while birds had no effects (Appendix 2, Table 1). In July 2007, the interaction between birds and PC2 was significant as well but was nonsignificant in both ANCOVAs. Density increased significantly in August 2007 ($F_{1,54} = 10.213$, $P = 0.002$) and marginally significantly in September 2008 ($F_{1,51} = 3.153$, $P = 0.082$) with PC1, which in both seasons was associated with high nitrogen and water and low tannins. Species richness decreased in May 2008 with PC2 ($F_{1,52} = 6.659$, $P = 0.013$) and increased in September 2008 with PC1 ($F_{1,51} = 11.957$, $P = 0.001$). Given the variable loadings of these PCs, this pattern is similar in both May and September: trees with high nitrogen and water content and low hydrolyzable tannins had more herbivore species (Fig. 7-8).

Feeding guild structure was influenced only by leaf quality and only in late-season censuses (August 2007 and September 2008, Appendix 2, Table 1). MANCOVAs for both of these censuses indicated a significant effect of PC1, but the groups responding were not identical in both years. Free-feeders increased with PC1 only in 2007 ($F_{1,54} = 4.377$, $P = 0.041$), while leaf-miners increased in both years (2007, $F_{1,54} = 6.481$, $P = 0.014$; 2008, $F_{1,51} = 5.341$, $P = 0.025$). Arthropod predator density was also associated with higher PC1 values in September 2008 ($F_{1,51} = 7.902$, $P = 0.007$). An interaction between bird exclusion and PC2 in September 2008 was marginally significant due to a significant interaction affecting free-feeders ($F_{1,51} = 5.277$, $P = 0.026$) and a marginally significant interaction for leaf-miners ($F_{1,51} = 3.033$, $P = 0.088$) in individual ANCOVAs. Free-feeders were negatively correlate with PC2 only on control trees; the pattern was similar but weak for leaf-miners.

Density of insect herbivores categorized by host breadth (generalist vs. specialist) was marginally significantly affected by leaf quality in May 2007 and significantly in

July and August 2007. Bird exclusion was also a significant factor in July 2007. In August 2007 and September 2008, interactions between bird exclusion and leaf quality were also identified as impacting herbivore densities (Appendix 2, Table 1). In May 2007, both oak specialists and generalists were marginally significantly positively correlated with PC2 (generalists, $F_{1,54} = 3.361$, $P = 0.062$; specialists, $F_{1,54} = 3.406$, $P = 0.070$); PC2 in May 2007 was positively correlated with both water and carbon content. Generalists in July and August 2007 were positively correlated with PC1 (July, $F_{1,52} = 5.278$, $P = 0.026$; August, $F1_{,52} = 4.570$, $P = 0.037$), indicating a preference for high-nitrogen and high-water trees with low hydrolysable tannins. Generalists were also more abundant within bird exclosures in July 2007 ($F_{1,52} = 5.837$, $P = 0.019$). Inspection of univariate ANCOVAs indicated that oak specialists in August 2007 increased with PC1 only when birds were excluded; when birds were present, specialist density was unaffected by leaf quality (exclusion x PC1, $F_{1,54} = 4.903$, $P = 0.031$). Conversely, specialist density in September 2008 was related to leaf quality when birds were present, but there was no relationship within bird exclosures (exclusion x PC2, $F_{1,51} = 5.939$, $P = 0.018$).

Asiatic oak weevil densities were not affected by birds or leaf quality in July 2007, but were positively correlated with PC1 in July 2008 ($F_{1,51} = 9.377$, $P = 0.004$), which represented trees with low water and high hydrolysable tannin content as well as high SLA.

Discussion

Overall bird exclusion had relatively weak impacts on the composition and structure of *Q. alba* herbivore communities. Leaf quality effects on herbivore richness and were much more apparent but still variable among censuses and herbivore groups. These effects were more frequent in late-season censuses and for leaf-miners and generalist herbivores.

Analyses of community composition using MRPP verified past researchers' findings that there is significant turnover in *Q. alba* herbivores during a growing season (Marquis and LeCorff 1997, Forkner et al. 2004, Forkner et al. 2006, 2008) as well as significant differences between the same time period in different years (Forkner et al. 2006, 2008). Striking differences between seasons within each year (Fig. 2A-B). It is also interesting to note that following the spring 2007 frost that killed some early-season herbivores, several species typically more abundant in mid-summer were present in the May census. As a result, the average MRPP distances between May and July censuses in 2007 was less than in 2008 (0.118 and 0.224, respectively). This is apparent in Figures 2 and 3 where trees in May 2008 are more clearly segregated.

MRPP analyses of bird exclusion effects within each census detected significant differences only in July 2008 and marginally significant differences in July 2007 and May 2008. However the very low values of the *A* statistic in all of these cases suggests negligible differences and indicates that the statistical significance may not represent biological significance: exclosure and control trees plotted in species ordination space are entirely mixed (Appendix 1, Figs. 1-3).

Excluding birds from trees did not result in higher densities of total herbivores as expected. The only group affected by birds were generalist herbivores in July 2007. This effect seems to have been driven by the three most abundant generalist lepidopterans in this census, a leaf-tier (*Psilocorsis quercicella*: Oecophoridae) and two free-feeders (*Nadata gibbosa*: Notodontidae and *Anacamptodes ephyraria*: Geometridae). Thus in this experiment, concealed feeding behavior by structure-building herbivores or leaf-miners did not confer any special protection from avian predators relative to free-feeding herbivores. The lack of bird effects on herbivore abundance is unexpected since Marquis and Whelan (1994) documented strong bird impacts at this same site. This may be due in part to changes in the local forest community including differences in vegetation structure and composition and accompanying changes in the bird and herbivore communities. For example, in the 17 years between these experiments, deer became overpopulated at the site, causing severe browsing damage, before being brought under control. Marquis and Whelan (1994) also conducted their work on saplings, while this study examined understory branches on mature trees. Oak saplings were indeed very rare during the present study, likely due to deer effects.

In some studies, vertebrate predator exclusion has caused increased abundances of intraguild arthropod predators such as spiders (Schoener and Spiller 1987, Gruner 2004), which may provide compensatory predation on herbivores in the absence of higher predators (Spiller and Schoener 1994). Although increased arthropod predator abundance in the absence of birds has been documented once in this system (Barber and Marquis *in press*), this phenomenon did not seem to occur in this experiment. Arthropod predators were not affected by bird exclusion in any census. Densities of predators were positively correlated with PC1 in September 2008, but so was total herbivore density at this time, suggesting that predators may have simply been distributed proportionally to their herbivore prey.

The impacts of leaf quality on herbivores were much more pervasive than bird exclusion. In all but the May 2008 survey, a PC that described high-nitrogen and low-hydrolyzable tannin trees influenced herbivore density. However leaf quality was clearly most influential late in the growing season: all herbivore response variables except density of structure-builders were significantly correlated with a PC in either August 2007 or September 2008 censuses. Species richness correlated with leaf quality in both May and September 2008 (Figs. 7-8). The effect of late-season leaf quality on total herbivore density as well as density of some guilds (leaf-miners in both years, free-feeders in 2007) makes sense given the season changes in *Q. alba* foliage characteristics. As a growing season progresses, carbon assimilated in photosynthesis increases and is likely incorporated into structural and defensive compounds that reduce leaf palatability to herbivores. In this study, the seasonal increase in carbon was associated with increased toughness, SLA, and condensed tannin content. Both water and nitrogen content concurrently declined, which also likely represents reduced quality of leaves, as water and nitrogen are often positively correlated with herbivore food preferences (Mattson 1980, Scriber and Slansky, Coley et al. 2006). As average leaf quality declined through the season, the effect on individual host plant choice by herbivores may have been magnified, resulting in more selective pressure on herbivores to choose high-quality hosts.

Densities of structure-building herbivores, such as leaf-rollers, -tiers, and -webbers, were affected by neither bird exclusion nor leaf quality in any census. Past work in this system has demonstrated that leaf-tying caterpillar density is strongly related to host plant architecture (Marquis et al. 2002b). Trees with leaves held close enough together so that they touch are more easily colonized by young leaf-tying caterpillars that are unable to reach and pull together leaves spaced out further because of their small size. Lill and Marquis (2001) studied *P. quercicella* on *Q. alba* and found that leaf-quality affected pupal mass, but was unrelated to development time or mortality from predators and parasitoids. This study corroborates this conclusion that leaf quality does not play a strong role in determining host choice of leaf-tiers.

Leaf quality was more important, though not consistently, to generalists than oak specialists. Generalist density was correlated with PCs throughout 2007, but no preferences were apparent in 2008. Specialist density only varied with leaf quality in May 2007, when they were marginally significantly correlated with PC2, which reflected increasing water and carbon content. The lack of a consistent effect of plant quality on specialists may support the idea that specialists are better adapted to cope with food quality variations of their hosts (Cornell and Hawkins 2003). Indeed, the Asiatic oak weevil, an exotic *Quercus* specialist, was more numerous in July 2008 on presumably poor-quality trees with low water content but high SLA and high levels of hydrolyzable tannins. These results for specialists, however, are surprising given the findings of Forkner et al. (2004), who showed that condensed tannin content, which was strongly correlated with several PCs here, was negatively correlated with abundances of several *Quercus* specialists.

In conclusion, the impacts of birds in this study were weak to nonexistent across two growing seasons. While bottom-up forces (leaf quality) may “set the stage” on which top-down forces act (Forkner & Hunter 2000), in some cases these top-down forces may not be strong enough to impact herbivores. This seems to have been the case in this study: birds did not affect the composition or species richness of herbivore communities, nor did they differentially alter the densities of particular feeding guilds. The direct effect of bird predation was weak compared to that documented by Marquis and Whelan (1994) and other bird exclusion studies (e.g., Strong et al. 2000, Murakami and Nakano 2000, Van Bael et al. 2003). It seems likely that under conditions in which direct effects of birds are stronger in general, predation may alter herbivore community composition and structure. Ecologists should focus future work on identifying which conditions are important to these trophic interactions and how they influence predation effects.

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Table 1. Leaf quality variable loadings on first and second principal components (PC1 and PC2, respectively) for each census. Condensed tannins were excluded from May 2007 because of laboratory error (see Methods). Specific leaf area was measured in 2008 but not 2007. Percent of total variance is the proportion of the total variation in leaf quality accounted for by each PC.

	May 2007		Jul 2007		Aug 2007	
Variable	PC1	PC2	PC1	PC2	PC1	PC2
Toughness	0.516	-0.072	-0.300	0.030	-0.257	0.123
Water	-0.057	0.689	0.469	-0.281	0.493	0.038
Condensed tannins	–	–	-0.362	-0.562	-0.324	0.525
Hydrolyzable tannins	0.583	0.094	-0.558	0.162	-0.564	-0.099
Carbon	0.140	0.704	-0.265	-0.672	-0.140	0.702
Nitrogen	-0.609	0.126	0.421	-0.356	0.498	0.453
% of total variance	38.2	25.3	29.6	18.4	31.8	21.2

	May 2008		Jul 2008		Sep 2008	
Variable	PC1	PC2	PC1	PC2	PC1	PC2
Toughness	-0.404	-0.391	0.037	0.218	-0.188	0.612
Water	0.397	0.156	-0.523	0.061	0.484	0.160
Specific leaf area	-0.538	0.192	0.531	0.039	-0.518	0.090
Condensed tannins	-0.316	-0.291	0.193	0.002	-0.245	-0.675
Hydrolyzable tannins	-0.186	0.624	0.524	0.222	-0.453	0.138
Carbon	-0.324	-0.286	0.100	0.772	0.046	-0.343
Nitrogen	0.387	-0.479	-0.348	0.549	0.442	-0.006
% of total variance	33.1	26.0	36.7	18.0	42.9	17.9

Figure captions.

Fig. 1. Mean density of herbivores on bird-excluded and control trees in the six censuses across 2007 and 2008 growing seasons. In no census did bird exclusion affect total herbivore densities. Error bars are 1 s.e.

Fig. 2. NMS ordinations of trees in species space in (A) 2007 and (B) 2008. The ordinations were both three-dimensional but here are projected in the two dimensions that most clearly illustrate the three distinct communities. Note that the May community composition is more distinct from July and August communities in 2008 than in 2007 when many early spring herbivores were killed by a late frost and mid-season herbivores were more numerous in May.

Fig. 3. Relationship between herbivore species richness and leaf quality in (A) May and (B) September 2008. In both censuses, species richness was greater on trees with low hydrolysable tannin content and high nitrogen, which was described by PC2 in May and PC1 in September. The x-axis in (A) is reversed to correspond with (B) so that trees with higher-quality foliage are on the right side of the axis.

Fig. 1

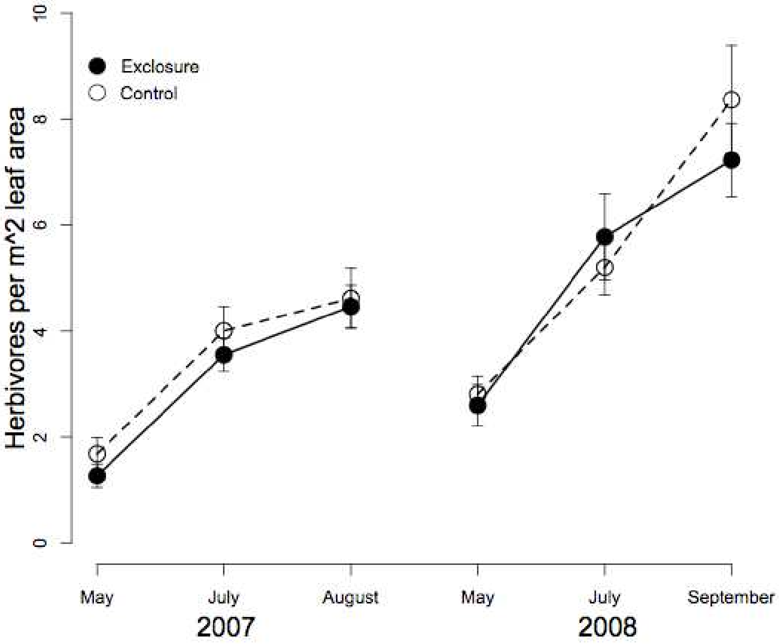

Herbivores per m^2 leaf area
10
8
6
4
2
0
● Exclosure
○ Control
May
July
August
May
July
September
2007
2008

Fig. 2A

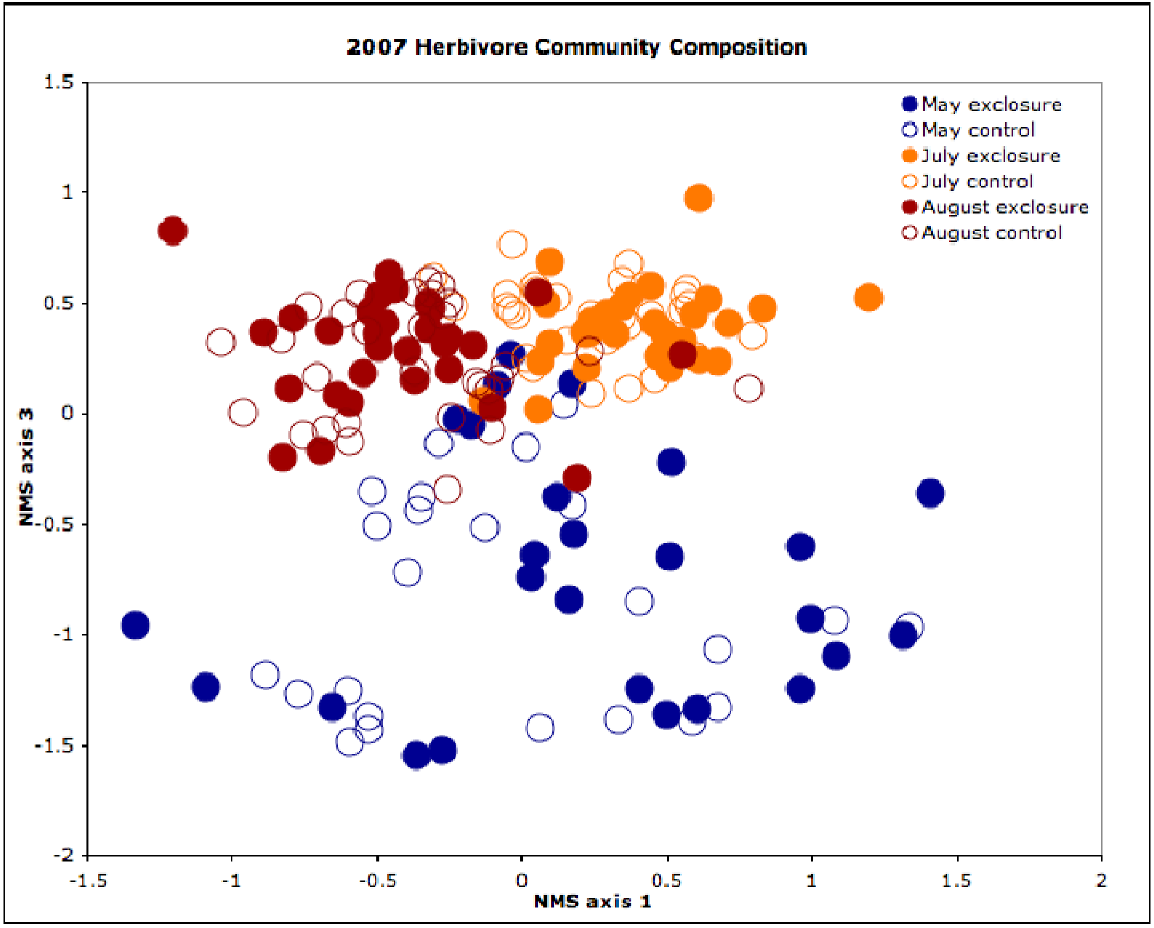

2007 Herbivore Community Composition
May exclosure
May control
July exclosure
July control
August exclosure
August control
NMS axis 3
NMS axis 1
1.5
1
0.5
0
-0.5
-1
-1.5
-2
-1.5
-1
-0.5
0
0.5
1
1.5
2

Fig. 2B

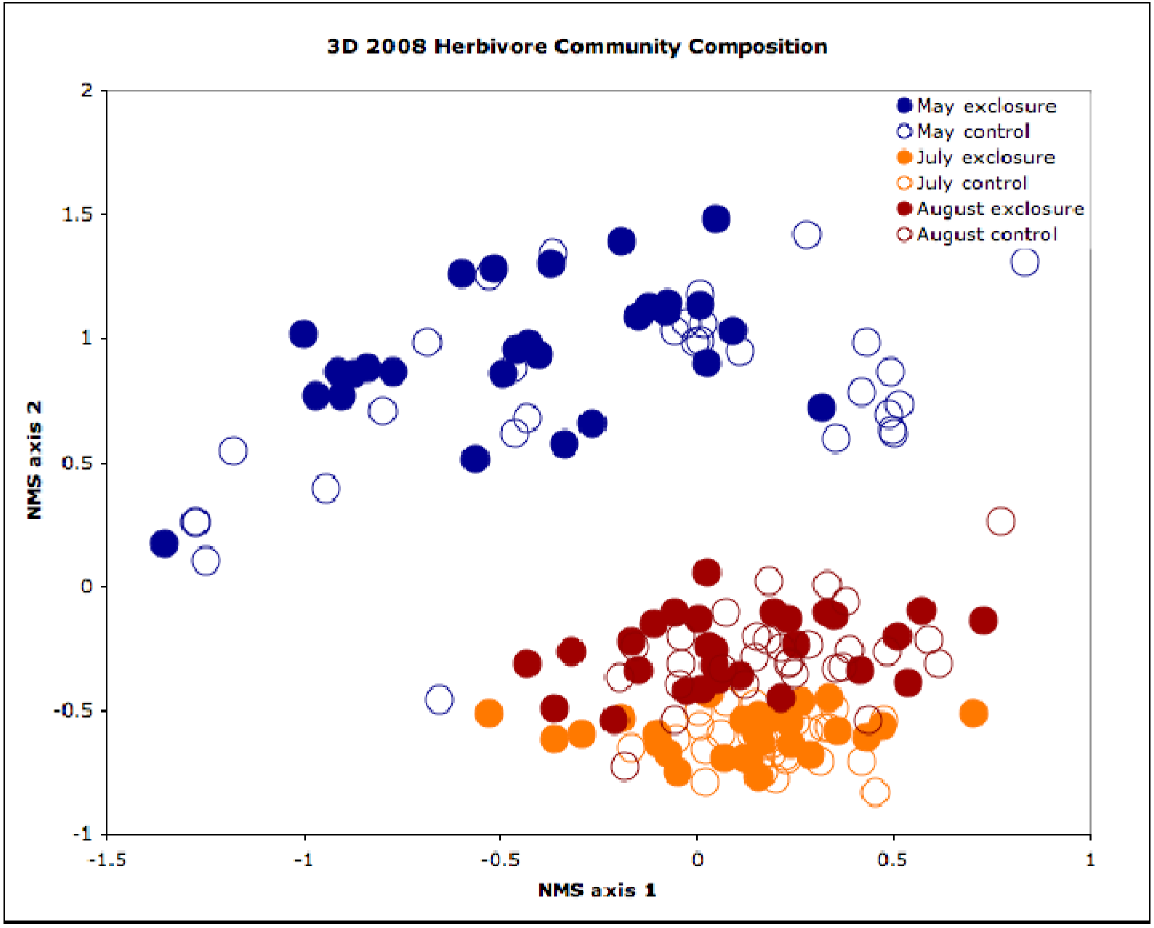
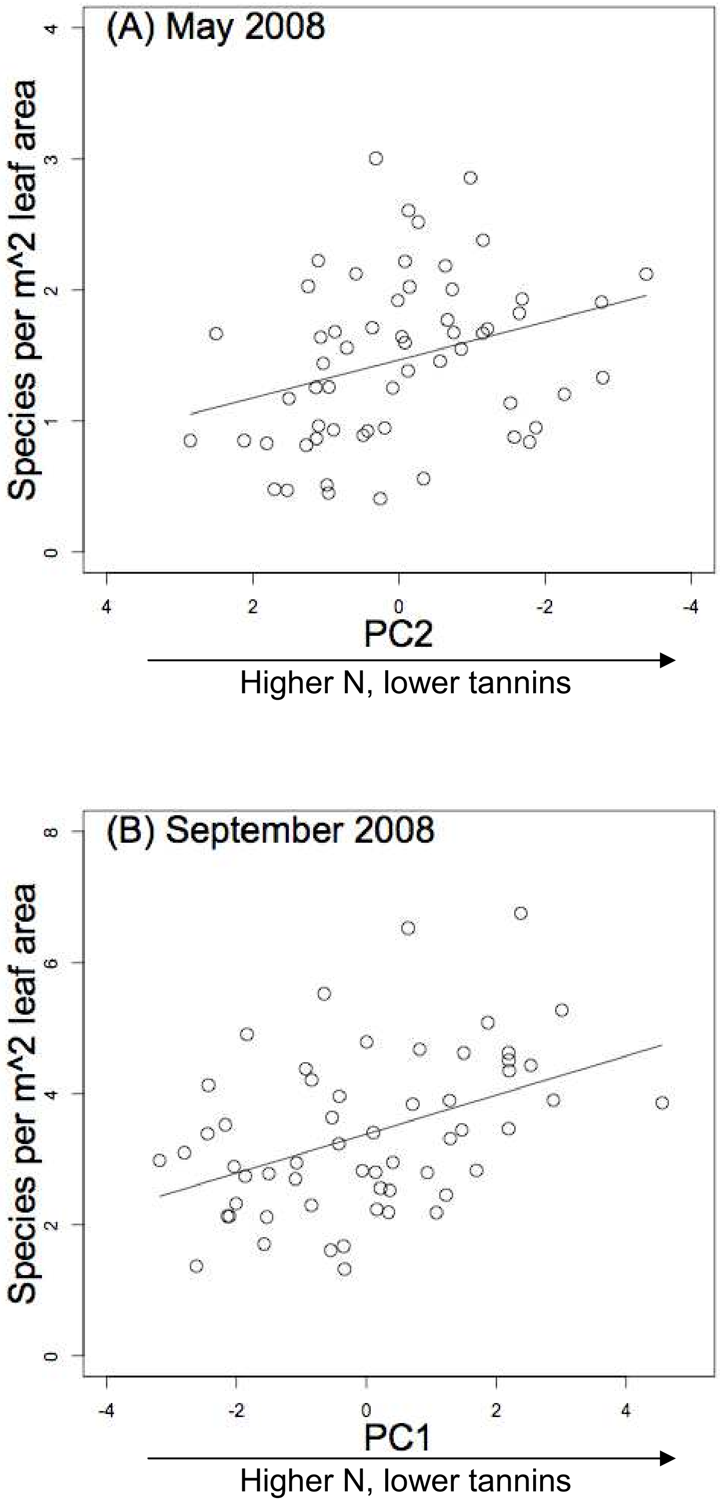

3D 2008 Herbivore Community Composition
● May exclosure
○ May control
● July exclosure
○ July control
● August exclosure
○ August control
NMS axis 2
2
1.5
1
0.5
0
-0.5
-1
NMS axis 1
-1.5
-1
-0.5
0
0.5
1

Fig. 3


(A) May 2008
Species per m^2 leaf area
0
1
2
3
4
4
2
0
-2
-4
PC2
Higher N, lower tannins
(B) September 2008
Species per m^2 leaf area
0
2
4
6
8
-4
-2
0
2
4
PC1
Higher N, lower tannins

Appendix 1.

Table 1. Results of multi-response permutation procedures analyzing the effects of census on herbivore community composition for year and all pairwise census comparisons.

Censuses	*A*	*P*
2007	0.156	<0.0001
2008	0.226	<0.0001
May 2007, Jul 2007	0.118	<0.0001
May 2007, Aug 2007	0.092	<0.0001
May 2007, May 2008	0.072	<0.0001
May 2007, Jul 2008	0.146	<0.0001
May 2007, Sep 2008	0.124	<0.0001
Jul 2007, Aug 2007	0.127	<0.0001
Jul 2007, May 2008	0.217	<0.0001
Jul 2007, Jul 2008	0.075	<0.0001
Jul 2007, Sep 2008	0.180	<0.0001
Aug 2007, May 2008	0.166	<0.0001
Aug 2007, Jul 2008	0.097	<0.0001
Aug 2007, Sep 2008	0.040	<0.0001
May 2008, Jul 2008	0.224	<0.0001
May 2008, Sep 2008	0.189	<0.0001
Jul 2008, Sep 2008	0.112	<0.0001

Table 2. Results of multi-response permutation procedures analyzing the effects of bird exclusion on herbivore community composition for each census.

Censuses	*A*	*P*
May 2007	-0.005	0.814
Jul 2007	0.008	*0.085*
Aug 2007	-0.001	0.496
May 2008	0.010	*0.063*
Jul 2008	0.014	**0.012**
Sep 2008	0.002	0.312

Fig. 1. NMS ordination of July 2007 trees in species space. Although MRPP analysis suggested a marginally significant difference in composition between exclosure and control trees, none is visible in the ordination.

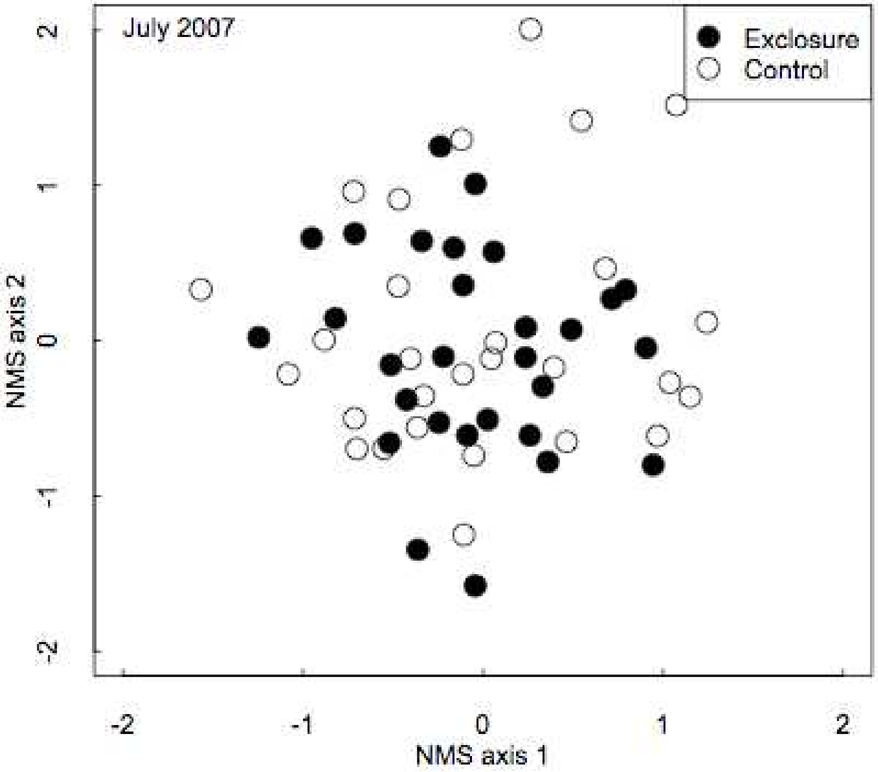


Fig. 2. NMS ordination of May 2008 trees in species space. Although MRPP analysis suggested a marginally significant difference in composition between exclosure and control trees, none is visible in the ordination.

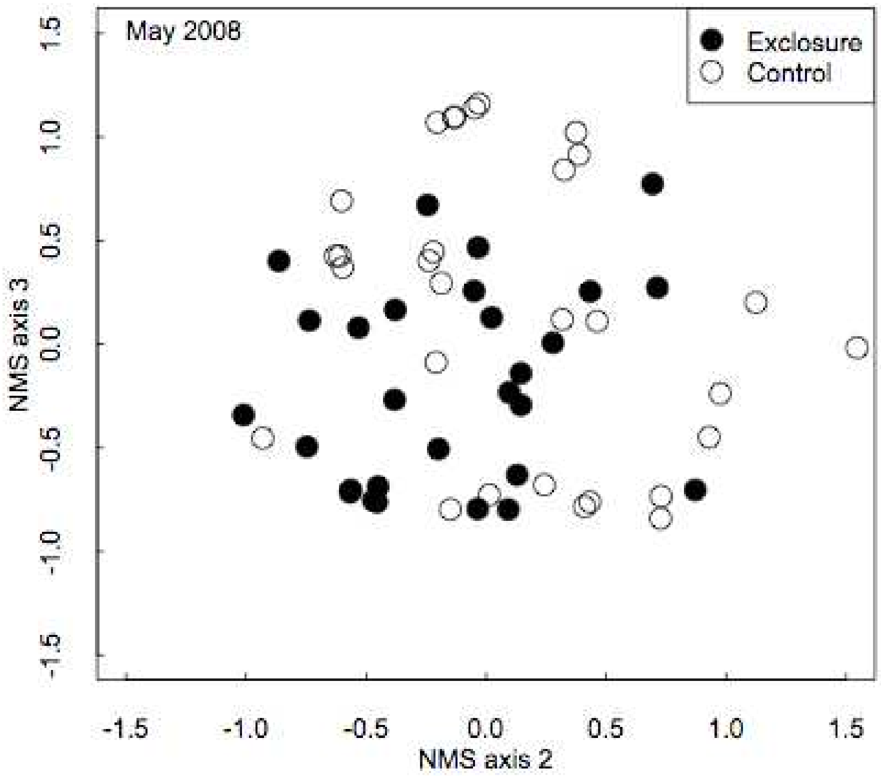
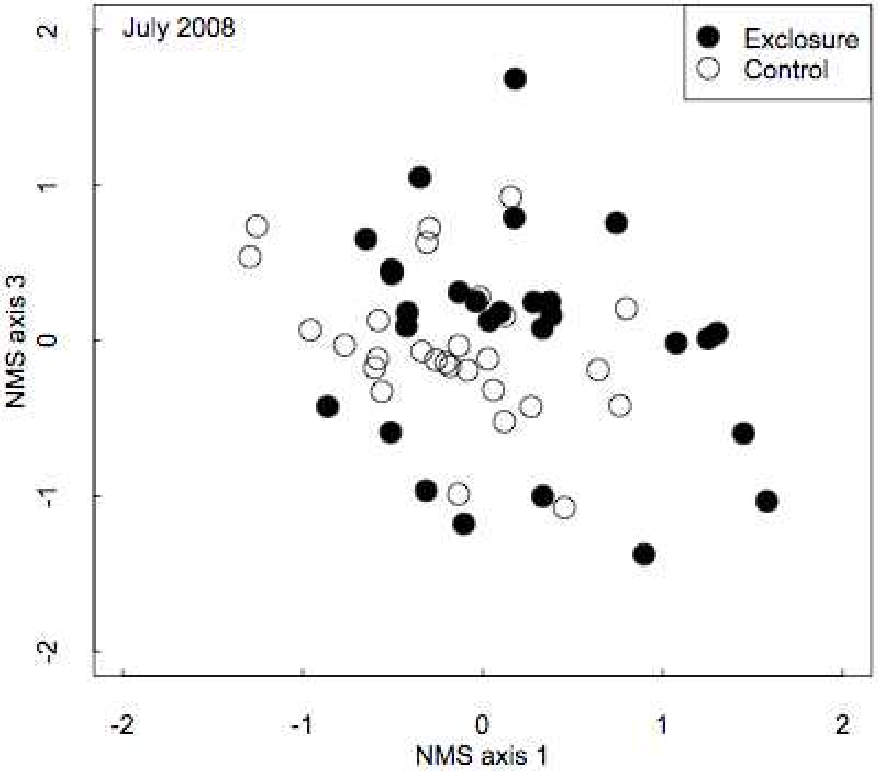


Fig. 3. NMS ordination of July 2008 trees in species space. Although MRPP analysis suggested a significant difference in composition between exclosure and control trees, no clear difference is visible in the ordination.



Appendix 2.

Table 1. Results of MANCOVAs assessing the impact of bird exclusion, leaf quality, and interactions on herbivores. The first column of tables represents analyses of density of all herbivores (total abundance per leaf area) and richness (total number of species per leaf area). The second column, "Feeding guilds," analyzes responses of free-feeders, structure-builders, leaf-miners, and arthropod predators. "Host breadth" models analyze *Quercus* specialists and generalists. In both years, July density, guild, and host data excludes the numerically dominant Asiatic oak weevil (*Cyrtepistomus castaneus*), which was analyzed independently.

	Total density & Richness			Feeding guilds			Host breadth		
	Wilks' Λ	$F_{2,53}$	*P*	Wilks' Λ	$F_{4,51}$	*P*	Wilks' Λ	$F_{2,53}$	*P*
May 2007									
Bird exclusion	0.967	0.912	0.408	0.954	0.618	0.652	0.949	1.425	0.250
PC1	0.989	0.284	0.754	0.941	0.802	0.530	0.954	1.276	0.288
PC2	0.922	2.243	0.116	0.921	1.089	0.372	0.895	3.094	*0.054*
Bird exclusion x PC1	0.981	0.518	0.599	0.958	0.555	0.696	0.990	0.276	0.759
Bird exclusion x PC2	0.969	0.850	0.433	0.977	0.297	0.879	0.970	0.806	0.452

	Total density & Richness			Feeding guilds			Host breadth		
	Wilks' Λ	$F_{2,51}$	*P*	Wilks' Λ	$F_{4,49}$	*P*	Wilks' Λ	$F_{2,51}$	*P*
Jul 2007									
Bird exclusion	0.996	0.099	0.906	0.898	1.392	0.250	0.872	3.729	**0.031**
PC1	0.993	0.191	0.827	0.890	1.519	0.211	0.858	4.208	**0.020**
PC2	0.988	0.314	0.732	0.937	0.824	0.516	0.976	0.630	0.537
Bird exclusion x PC1	0.994	0.150	0.862	0.985	0.181	0.947	0.965	0.914	0.408

Bird exclusion x PC2	0.887	3.240	**0.047**	0.943	0.733	0.574	0.972	0.742	0.481

	Total density & Richness			Feeding guilds			Host breadth		
	Wilks' Λ	*F*	*P*	Wilks' Λ	*F*	*P*	Wilks' Λ	*F*	*P*
Aug 2007									
Bird exclusion	0.996	0.105	0.900	0.865	1.998	0.109	0.988	0.336	0.716
PC1	0.839	5.075	**0.010**	0.832	2.577	**0.048**	0.828	5.494	**0.007**
PC2	0.926	2.129	0.129	0.903	1.373	0.256	0.935	1.849	0.167
Bird exclusion x PC1	0.960	1.101	0.340	0.934	0.897	0.473	0.916	2.432	*0.098*
Bird exclusion x PC2	0.975	0.669	0.517	0.927	1.011	0.411	0.968	0.866	0.418

	Total density & Richness			Feeding guilds			Host breadth		
	Wilks' Λ	*F*	*P*	Wilks' Λ	*F*	*P*	Wilks' Λ	*F*	*P*
May 2008									
Bird exclusion	0.917	2.320	0.109	0.936	1.136	0.344	0.983	0.449	0.641
PC1	0.983	0.437	0.648	0.974	0.437	0.727	0.968	0.847	0.435
PC2	0.839	4.908	**0.011**	0.953	0.831	0.483	0.955	1.193	0.312
Bird exclusion x PC1	0.989	0.277	0.759	0.944	0.987	0.407	0.943	1.528	0.227
Bird exclusion x PC2	0.975	0.662	0.520	0.925	1.346	0.270	0.956	1.164	0.320

	Total density & Richness			Feeding guilds			Host breadth		
	Wilks' Λ	*F*	*P*	Wilks' Λ	*F*	*P*	Wilks' Λ	*F*	*P*
Jul 2008									
Bird exclusion	0.968	0.818	0.447	0.926	0.960	0.438	0.954	1.207	0.308
PC1	0.980	0.500	0.610	0.988	0.144	0.965	0.986	0.351	0.706
PC2	0.965	0.902	0.412	0.905	1.257	0.300	0.955	1.177	0.317
Bird exclusion x PC1	0.982	0.454	0.638	0.980	0.243	0.912	0.974	0.661	0.521
Bird exclusion x PC2	0.991	0.229	0.796	0.937	0.804	0.529	0.962	0.979	0.383

	Total density & Richness			Feeding guilds			Host breadth		
	Wilks' Λ	*F*	*P*	Wilks' Λ	*F*	*P*	Wilks' Λ	*F*	*P*
Sep 2008									
Bird exclusion	0.980	0.501	0.609	0.974	0.317	0.865	0.990	0.252	0.778
PC1	0.809	5.893	**0.005**	0.816	2.713	**0.041**	0.937	1.678	0.197
PC2	0.952	1.276	0.288	0.892	1.455	0.231	0.954	1.218	0.305
Bird exclusion x PC1	0.982	0.468	0.629	0.953	0.589	0.672	0.980	0.508	0.605
Bird exclusion x PC2	0.926	2.000	0.146	0.832	2.431	*0.060*	0.896	2.989	*0.064*

Chapter 4

Light environment and leaf characteristics affect distribution of *Corythuca arcuata* (Hemiptera: Tingidae)

In review: Barber, N. A. Light environment and leaf characteristics affect distribution of *Corythuca arcuata* (Hemiptera: Tingidae).

Abstract

Insect herbivore abundances on host plants are influenced by both plant traits and the physical environment in which that plant grows. This study examined the role of the physical light environment and foliage characteristics in determining abundance of the lacebug *Corythuca arcuata* Say (Hemiptera: Tingidae) on *Quercus alba* L. I censused adult *C. arcuata* across a growing season, quantified leaf characteristics, and measured canopy cover over understory branches of mature *Q. alba.* Using an information-theoretic approach, I evaluated *a priori* hypotheses of the relationship between light, plant traits, and *C. arcuata* abundance. Abundance was best predicted by light environment and carbon content. Adult *C. arcuata* prefer trees growing under an open canopy and trees with low carbon content; abundance also positively correlated with leaf water content. Although carbon and water did not vary with light in this study, low carbon and high water content are often associated with shadier conditions, suggesting that *C. arcuata* faces a trade-off between preferences for physical habitat conditions and host plant characteristics.

Key words: Tingidae, *Corythuca arcuata*, lacebug, oak, light

Introduction

The choice of a host plant by an herbivorous insect is based on both the physical environment in which that plant grows and traits of the host plant itself. For example, some caterpillars bask in the sun or choose sun-exposed host plants to maintain a higher body temperature and increase growth rate (Weiss et al. 1988, Joos et al. 1988), and eggs of tent caterpillars tend to be placed to maximize light exposure (Moore et al. 1988). Some chrysomelid beetles prefer sun-exposed willows (Sipura and Tahvanainen 2000). Plant traits, however, are often influenced by environmental conditions. Examples are increased woodiness of stems in high-salinity environments (Moon and Stiling 2000) and increased tannin content with sun exposure (Dudt and Shure 1994). Simultaneous effects on both the herbivore itself and the plant can lead to potential tradeoffs in contrasting environments. Thus, for the willow example above, chrysomelid beetles feed on sun-exposed leaves even though shaded leaves are higher quality food (Sipura and Tahvanainen 2000).

Very little is known about host plant selection by natural populations of Tingidae (Hemiptera) or lacebugs. Most of the literature on this family addresses the potential for biocontrol of invasive plants (Williams et al. 2008) or impacts and control of pest lacebugs on ornamental plants, especially *Stephanitis pyrioides* (azalea lacebug) (Casey and Raupp 1999). This work has shown that occurrence of and damage by *S. pyrioides* is influenced by light environment and leaf quality (Shrewsbury and Raupp 2000, Bentz 2003) and potentially by predators (Trumbule and Denno 1995).

A few studies have focused on host choice by *Corythuca arcuata,* the oak lacebug, a widespread species that ranges across southern Canada and much of the eastern United States and usually specializes on *Quercus* spp., although it can occur and complete its life cycle on members of Rosaceae such as *Rubus* and *Malus* (Bernardinelli 2006). Connor (1988) investigated *C. arcuata* preferences on *Q. alba* saplings grown under varying water conditions, finding that lacebugs preferred plants with higher water levels. He suggested that leaf toughness might act as a cue for host choice, as toughness is often negatively correlated with water content and may interfere with feeding of *C. arcuata*, which pierce leaves with the stylus to suck leaf sap from the mesophyll.

Kay et al. (2007) studied *C. arcuata* distribution in relation to fire frequency and how fire conditions affected leaf quality. Abundance was greater in frequently burned areas where light levels were higher on saplings of *Q. macrocarpa*, the local host plant. Overall, adult abundances were positively associated with C content and negatively with N and cellulose. Oviposition occurred more frequently on trees with low lignin and cellulose but higher total phenolics. However, these correlations mirrored leaf quality differences between the burn treatments and may have simply represented habitat choice based on the physical environment (i.e., light conditions). When examining adult abundances within common burn treatments or light environments, the only correlation with leaf quality was a preference for low-N plants in sunny gaps, although eggs occurred more frequently on plants with higher lignin and starch.

Thus Connor (1988) and Kay et al. (2007) present different, although not necessarily conflicting, host plant preferences of *C. arcuata*. The former predicted that high-water, low-toughness plants should be preferred, while the more recent work suggested lacebugs may seek plants with high content of C and some C-based compounds (phenolics) but low N and other C-based constituents that contribute to toughness such as lignin and cellulose (Coley 1983). Here I present an analysis of host plant preferences of *C. arcuata* on *Q. alba*. My purpose was to determine which leaf traits determine these preferences and what role light plays in this choice.

Methods

I studied *C. arcuata* at Tyson Research Center, an 809-ha field station owned by Washington University near Eureka, Missouri, USA. The study area was a southwest-facing slope with shallow rocky soils. *Quercus alba* is a canopy co-dominant tree (with other *Quercus* and *Carya* spp.) and is particularly common on drier southwest slopes such as this.

I performed this study in conjunction with a larger study on the effects of insectivorous birds on the leaf-chewing herbivore community of *Q. alba*. In early 2007, I chose 60 mid-story to canopy-height *Q. alba* with accessible understory branches and built bird exclosures around these branches on 30 of the trees. I censused herbivores on these trees three times in 2007 and 2008, at known peaks in oak-feeding herbivore abundance in Missouri (Marquis and Whelan 1994, Marquis and LeCorff 1997, Forkner et al. 2004). The data for the current study were collected during the herbivore surveys in mid-May, early July, and early September 2008. I did not expect bird exclusion to affect *C. arcuata* abundance because their small size makes them unlikely prey items for insectivorous birds (Strong et al. 2000, Van Bael et al. 2008).

To census trees, I inspected the tops and bottoms of all leaves on experimental branches and recorded the number of adult *C. arcuata* present. Adults rest on the underside of *Q. alba* leaves and are highly visible given their distinct patterning. *C. arcuata* do not seem to be affected by census activities and are reluctant to move, even when prodded; this observation is consistent with those of Kay et al. (2007). I recorded the number of leaves inspected, with a goal of at least 400 leaves per branch, but some branches had fewer leaves. At the end of the season, I collected 30 leaves from each tree to measure damage from leaf-chewing herbivores through digitizing and pixel-counting; this provided an estimate of average leaf size for each branch. Average leaf size was multiplied by the number of leaves inspected in each census to estimate the total leaf area surveyed on each branch. Abundances of *C. arcuata* were expressed as number/m^2 leaf area based on this value. To characterize the light environment of each tree, I measured canopy cover in late June using four readings from a concave spherical densiometer positioned directly above experimental branches (Lemmon 1956).

Immediately following each census period, I collected three leaves from each tree. These leaves were stored in plastic ziplock bags. Within two hours, I weighed leaves to obtain wet mass and measured leaf toughness using a penetrometer (Force Dial FDK 32, Wagner Instruments, Greenwich, CT). I transported leaves to the laboratory on ice and stored them at –80˚C before freeze-drying for 96 hours. I obtained leaf water content from the dry mass (% water = 1-(dry mass/wet mass)). I ground dried leaves for use in chemical analyses. Following extraction in acetone, I colorimetrically assayed condensed tannins using the acid-butanol technique (Rossiter et al. 1988, Waterman and Mole 1994) and hydrolysable tannins using the potassium iodate technique (Bate-Smith 1977, Schultz and Baldwin 1982). Absorbances of each tree were compared to a curve constructed from pooled bulk standard samples of known concentration and expressed as percentages of starting leaf tissue mass. Kay et al. (2007) found a marginally significant effect of total phenolics on *C. arcuata*; I took a more detailed look at this effect by breaking down phenolic content into condensed and hydrolysable tannins, two common classes of phenolics that are considered important to insect herbivores (Forkner et al. 2004, Barbehenn et al. 2006, Roslin and Salminen 2008). I determined carbon and nitrogen content by microcombustion (Perkin-Elmer Series II CHNS/O Analyzer 2400).

To characterize *C. arcuata* abundance on each tree across the growing season, I summed abundance across the three surveys. Because leaf traits change during the season as leaves expand, harden, and accumulate more carbon from photosynthesis, I created indices of each leaf trait using z-scores. Within each census, I transformed each leaf-trait to z-scores and summed scores for this trait across the three censuses. In this way trees with consistently high values of a trait will be more positive, consistently low trees will be negative, and average trees should have values near zero. This technique has been similarly used to create indices of leaf defense by other researchers (Fine et al. 2006, Agrawal and Fishbein 2008). Experimental branches on three trees that died prior to or during the study period were excluded from analyses. Leaves collected to estimate total leaf area were lost in the field for one tree, so I also excluded this tree. Analyses are based on the remaining 56 trees.

I used multimodel inference, an information-theoretic approach (Burnham and Anderson 2002, Anderson 2008), to evaluate support for models based on *a priori* hypotheses regarding the factors potentially determining abundance of *C. arcuata*. This method allows for simultaneous evaluation of multiple models (hypotheses) and quantifies the relative support for each model given the data while avoiding the potential pitfalls of spurious correlations common to stepwise regression methods (Whittingham et al. 2006). I evaluated models using Akaike's information criterion corrected for small sample size (AICc) and ranked models using ΔAICc, the difference between a model and the highest-ranked (lowest AICc value) model. These values are used to calculate Akaike weights (w_i, "model probabilities"), which provide a relative measure of support for the model and are interpreted as the probability that model *i* is the best model in the set of candidate models. Because these weights are relative, they allow for direct comparisons of the support for models: e.g., a model with $w = 0.1$ has twice the support as a model with $w = 0.05$.

I constructed a set of additive models to compare the effect of light environment and foliage characteristics on *C. arcuata* abundance. To evaluate the role of basic leaf constituents, two models included carbon and nitrogen individually as independent variables, and a third model included carbon:nitrogen ratio, as this is often a measurement of the accessibility of leaf nutrients. I included models based on Connor's (1988) predictions that included water content and leaf toughness together and independently, a model to determine the impact of leaf defensive chemistry using concentrations of both condensed and hydrolysable tannins, and all variables combined in a global model. Because I expected light to have a strong impact on *C. arcuata* abundance based on the results of Kay et al. (2007), I constructed additional models identical to those above but with canopy cover measurements included as an independent variable. These models determine how lacebug abundance varied with leaf characteristics while controlling for the effects of light. Lastly I included a model with only light (canopy cover) as an independent variable.

I used general linear models and log-transformed all *C. arcuata* abundances (using $\ln(x + 1)$) to normalize model residuals. One was added to abundances to account for zeros in the dataset (20.6% of observations, mostly in September census). One outlier tree with exceptionally high lacebug abundance (nearly 5 standard deviations from the mean) was excluded from the dataset, which improved model fit. All analyses were performed in R (R Development Core Team 2008).

Results

Lacebugs were common throughout the study period, although abundance declined by more than half from the mid-summer census to the fall census, during which they were absent from 40% of trees (Fig. 1). Abundances on trees were positively correlated among consecutive censuses, although not between May and September censuses (r = 0.017, *P* = 0.902; May-July, r = 0.381, *P* = 0.004; July-September, r = 0.297, *P* = 0.028). As expected, bird exclusion had no effect on *C. arcuata* abundance (mean abundance ± 1 s.e. lacebugs per m^2 leaf area, exclosures: 1.78 ± 0.27, controls: 1.74 ± 0.22, *t* = 0.124, *P* = 0.902). Light was not significantly correlated with any measured leaf characteristics except hydrolysable tannin content (r = 0.306, *P* = 0.023).

Model results are presented in Table 1. The model including light and C was the highest-ranked model; *C. arcuata* abundance increased on high-light trees under a more open canopy (β ± 1 s.e. = 0.033 ± 0.012) and decreased with C content (β = -0.083 ± 0.029). Generalized R^2 for this model (Nagelkerke 1991) based on the maximum likelihood estimate was 0.254. This model has more than three times the support of the second-ranked model, which included light and water and revealed increasing *C. arcuata* abundance with both variables. The global model with light was ranked third, but it and all other models were poorly supported. All models containing light were more highly-ranked than the equivalent model in which light was excluded.

Discussion

The results support the prediction that both light environment and host plant leaf characteristics influence the distribution of *C. arcuata*. As expected from the findings of Kay et al. (2007) and other work on Tingidae, light conditions on host plants had a strong positive effect on adult lacebug abundance (Fig. 2). Support for this model was greater than that for any leaf characteristic except C. Not surprisingly, these two factors combined represented the best model for predicting lacebug abundance ($w = 0.563$), which explained more than a quarter of the variance in abundance ($R^2 = 0.254$). Preference for plants in higher-light environments agrees with Kay et al. (2007), but the relationship between lacebug abundance and C content does not: in this study, both the correlation with C alone and the partial correlation with C when controlling for the effects of light environment were negative (Fig. 3).

This analysis corroborated Connor's (1988) experiment demonstrating preference for increased leaf water content but not his suggestion that toughness is an important cue. The model containing light and water ranked second with moderate support ($w = 0.166$). Higher water content could facilitate feeding by sucking insects by making it easier to obtain soluble carbohydrates and other nutrients. However, the prediction that leaf toughness was an important cue for lacebugs in choosing hosts was not supported. Although the model containing light, water content, and toughness was ranked fourth highest, the model received poor support ($w = 0.066$). Further, the AICc for this model was approximately the AICc value of the light and water only model +2. When calculating AICc, the addition of a predictor variable increases the value of the criterion by about 2 as a penalization for reducing parsimony. In this case, the addition of toughness incurs the penalization but does not then decrease AICc by adding information. Anderson (2008) refers to this as a "pretending variable." Models including toughness alone or toughness with light were very poor ($w < 0.01$).

Defensive chemistry models, which included condensed and hydrolysable tannin concentrations, received very low support ($w < 0.006$). This result suggests that carbon-based phenolic defenses have little influence on *C. arcuata,* despite the important role they are thought to have in resistance against leaf-chewing herbivores (Feeny 1970, Forkner et al. 2004, Roslin and Salminen 2008). Similarly, the nitrogen models and the carbon:nitrogen models were not supported by the data either with ($w = 0.012$ and $w = 0.010$, respectively) or without (both $w = 0.001$) light as a variable. Kay et al. (2007) found a negative correlation between adult abundance and nitrogen when examining sun-exposed leaves in forest gaps, but this pattern was not apparent in this study. It is possible that nitrogen is not the most important nutrient for *C. arcuata*: phosphorus, which was not measured here, can correlate with increased adult mass in lacebugs (Kay et al. 2007), and is thought to be a limiting factor for many insect herbivores (Elser et al. 2000).

Taken together, these results suggest that *C. arcuata* may prefer particular abiotic conditions (high light environment) as well as particular host plant foliage characteristics (lower total carbon and higher water content). This combination of preferences, however, seems contradictory. Although these traits were uncorrelated with light in this study, leaves of sun-grown *Q. alba* frequently have higher carbon and lower water content (unpublished data). I propose two possible explanations for this apparent contradiction in preferences. Lacebug egg hatching rate increases and development time decreases with higher temperatures in a number of species of Tingidae (Eguagie 1972, Braman and Pendley 1993). Adult *C. arcuata* may select habitats with abiotic conditions that optimize these aspects of fecundity and then search for individual hosts with preferred leaf quality. Another potential explanation is that the third trophic level has a strong impact on *C. arcuata* distribution. Predation on azalea lacebugs is thought to be higher in shaded habitats, resulting in higher abundances in sunny areas, despite the lower food quality of sun-exposed plants (Trumbule and Denno 1995). Bird exclusion had no effect on oak lacebug abundance in my experiment, but arthropod predators could drive a pattern similar to that in azalea lacebugs. Plants under a more closed canopy may be preferred by *C. arcuata*, but higher predator abundance on these trees could reduce lacebugs so they are more numerous on sunny trees, as observed here.

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Table 1. Model selection results for abundance of adult *C. arcuata* on *Q. alba.*

Model	*K*	*AICc*	Δ_i	w_i
Light + C	4	56.154	0.000	0.563
light + water	4	58.599	2.445	0.166
light + C + N + C:N + water + tough + hydro + cond	10	60.408	4.254	0.067
light + water + tough	5	60.445	4.291	0.066
C	3	61.470	5.316	0.039
light	3	62.030	5.876	0.030
C + N + C:N + water + tough + hydro + cond	9	62.459	6.305	0.024
light + C:N	4	63.889	7.735	0.012
light + tough	4	64.258	8.104	0.010
light + N	4	64.300	8.146	0.010
light + hydro + cond	5	65.243	9.089	0.006
water	3	65.883	9.729	0.004
water + tough	4	67.787	11.633	0.002
C:N	3	69.128	12.974	0.001
N	3	69.713	13.559	0.001
tough	3	69.858	13.704	0.001
hydro + cond	4	71.206	15.052	0.000

K, number of estimated parameters in model (including intercept and residual variance); w_i, Akaike model weight; C, carbon; N, nitrogen; hydro, hydrolysable tannins; cond, condensed tannins; water, % water content; tough, leaf toughness.

Figure legends

Fig. 1. Mean (± 1 s.e.) abundance of oak lacebug (*C. arcuata*) in each census. Abundance is expressed as the number of lacebugs counted per m^2 leaf area inspected.

Fig. 2. Residual abundance (controlling for correlation with C content) plotted against light index (a measure of canopy openness, see text). Lacebugs are more abundant on oaks in higher-light conditions.

Fig. 3. Residual abundance (controlling for correlation with light) plotted against carbon index (see text). Lacebugs are less abundant on oaks with higher leaf C content.

Fig. 1

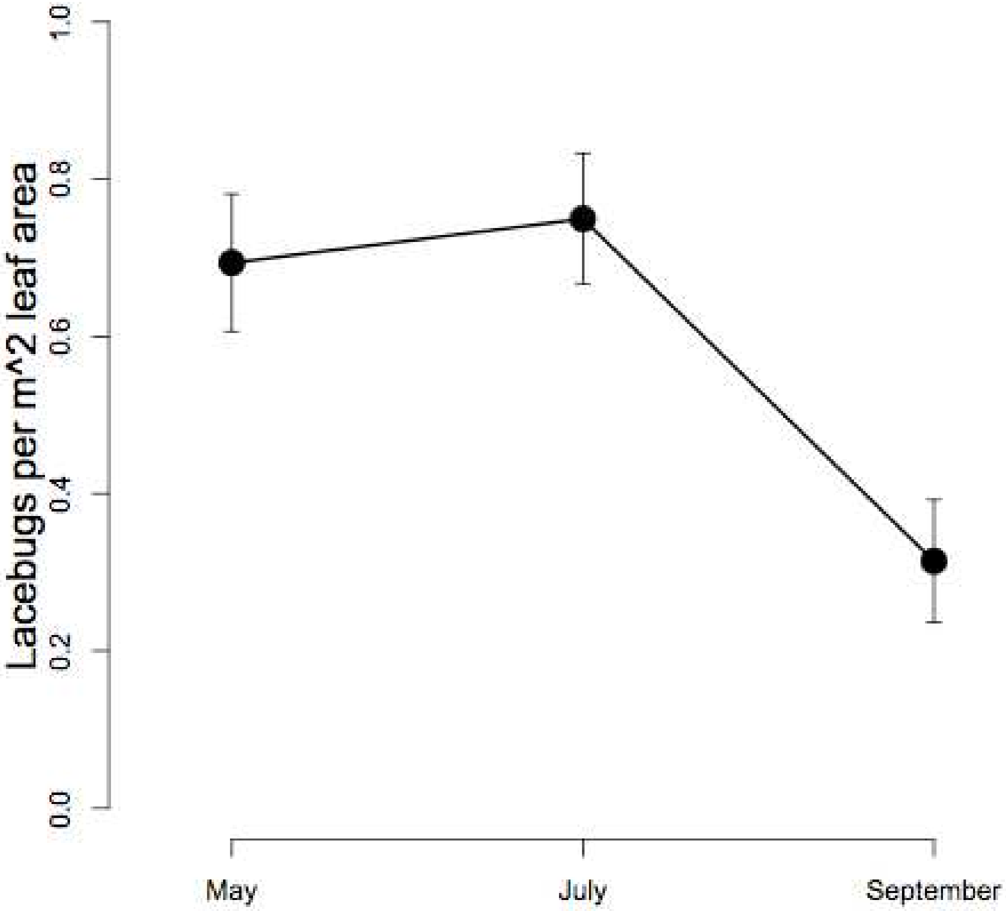


Fig. 2

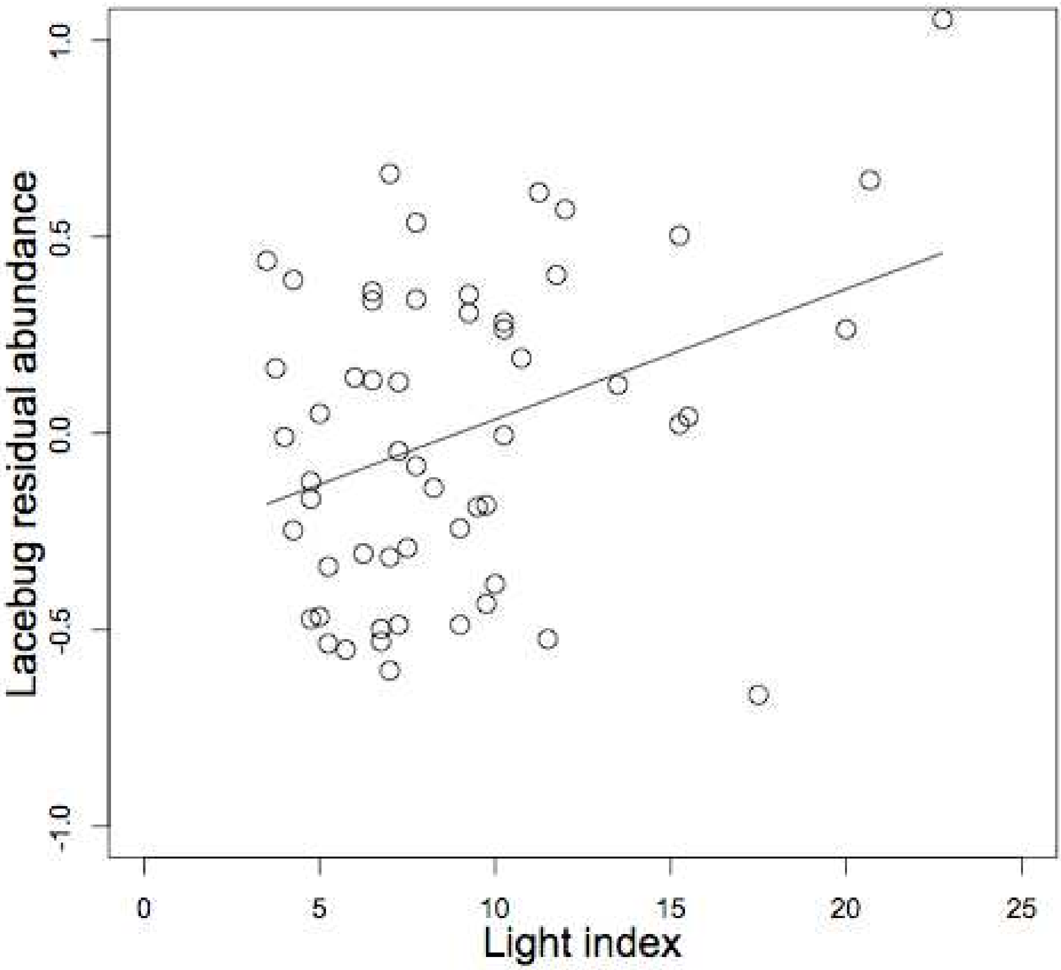
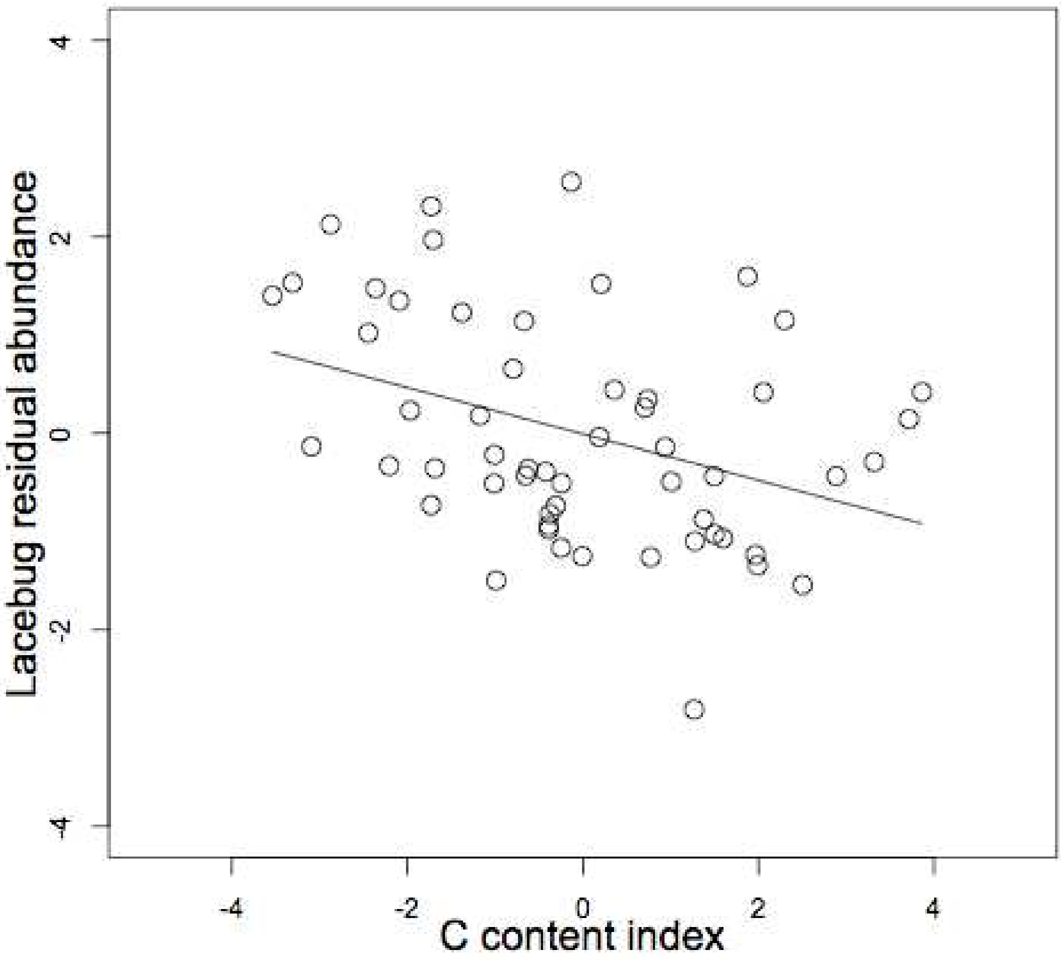

1.0
0.5
0.0
-0.5
-1.0
Lacebug residual abundance
0
5
10
15
20
25
Light index

Fig. 3



Chapter 5

Invasive prey impacts the abundance and distribution of native predators

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Abstract

While an extensive literature exists on the negative effects of invasive species, little is known about their facilitative effects on native species, particularly the role of invasives as trophic subsidies to native predators. The invasive gypsy moth (*Lymantria dispar*) undergoes periodic outbreaks during which it represents a super-abundant food source for predators capable of consuming it, particularly native cuckoos (*Coccyzus erythropthalmus* and *C. americanus*). We examined how gypsy moth outbreaks affect the abundance and distribution of cuckoos using the North American Breeding Bird Survey and 29 years of U. S. Forest Service gypsy moth defoliation records. Abundances of both Black-billed and Yellow-billed Cuckoos were significantly above average during outbreaks, but populations were average or below-average in preceding and subsequent years, suggesting that cuckoos are immigrating to defoliations during outbreak years. Spatial analyses showed that cuckoo abundances ~40-150 km outside of defoliation areas were significantly below-average, and these under-occupied breeding areas extend in all four compass directions around outbreaks. This result supports the idea that cuckoos locate gypsy moth outbreaks during a post-migratory nomadic phase. By shifting the annual distribution of cuckoos, gypsy moths may be shifting the trophic impact of cuckoos across large distances, which could affect native insect herbivores and plants.

Key words: invasive species, predation, gypsy moth, *Lymantria dispar*, cuckoo, *Coccyzus,* spatial distribution, outbreak

Introduction

The negative impacts of invasive species are well-documented (Vitousek et al. 1996, Mack et al. 2000). They frequently reduce population sizes of native species through competitive interactions (Vilá et al. 2004) or direct predation (Salo et al. 2007). Less attention has been paid to facilitative effects of invasives on native members of their new community. A recent review by Rodriguez (2006) found that facilitation by invasives occurs in a variety of habitats and through a number of mechanisms including habitat alteration, pollination, competitive and predator release, and trophic subsidies, although few examples exist for any one of these areas.

The role of invasives as trophic subsidies is of particular interest because there has been little investigation into the impacts of invasive species on native predators. Because invasives often attain high abundances, they may represent an important food source to native predators capable of exploiting them. Although the phenomenon of natives consuming introduced species is widespread and includes herbivores feeding on non-native plants (Memmott et al. 2000, Trowbridge 2004), frugivores consuming fruit of alien plants (Witmer 1996, Gosper et al. 2006), and consumers eating non-native animals (Spencer et al. 1991, Harding 2003, deRivera et al. 2005), rarely have ecologists documented an increase in abundance of the native consumer. Examples include mice feeding on an insect introduced for biocontrol (Ortega et al. 2004) and the well-known case of golden eagles (*Aquila chrysaetos* L.) depredating feral pigs (*Sus scrofa* L.) on the California Channel Islands (Roemer et al. 2002).

Two lines of evidence suggest that outbreaks of non-indigenous gypsy moths (*Lymantria dispar* L.) may represent a trophic subsidy for North American cuckoos. First, few birds eat gypsy moth caterpillars, presumably due to their hair-like setae (Forbush and Fernald 1896, Whelan et al. 1989), but cuckoos are often considered "hairy" caterpillar specialists (Hughes 1999, 2001) and may even prefer gypsy moths to native caterpillar prey (Cooper et al. 1990). Historical anecdotes suggest that cuckoo abundances have increased locally during gypsy moth outbreaks (Brewer et al. 1991). One previous study examined cuckoo abundance in relation to gypsy moth outbreaks: Gale et al. (2001) used Breeding Bird Census data from six sites that had experienced defoliations. They found that cuckoo abundances at these sites actually tended to increase one or two years before the year of highest gypsy moth caterpillar abundance, considered to be the outbreak. Secondly, cuckoos are well-known to specialize in exploiting insect outbreaks. They have been reported feeding on outbreaks of tent caterpillars (*Malacosoma* spp.) and fall webworms (*Hyphantria cunea* Drury) (Hughes 1999, 2001) and to occur at high population densities during periodical cicada emergences (Koenig and Liebhold 2005).

Here we test the hypothesis that gypsy moth outbreaks affect the abundance and distribution of native cuckoos using data from the North American Breeding Bird Survey (BBS) and digitized gypsy moth defoliation records. Specifically, we ask: (1) do cuckoos exhibit a positive numerical response to outbreaks, and (2) does this response vary through space in relation to the outbreak? Our results demonstrate a local increase in abundance of these bird species and suggest it is due to migration to outbreak sites rather than an impact on reproductive success.

Methods

Study species

The gypsy moth (Lepidoptera: Lymantriidae) is a widespread Eurasian species that was introduced to Massachusetts in the 1860s (Forbush and Fernald 1896) and has spread across the northeast United States and southeast Canada (Johnson et al. 2006). Outbreaks of gypsy moth are cyclic and occur on an approximately 10-year cycle, causing large-scale defoliation of deciduous forests (Johnson et al. 2005). Damage by larvae peaked in the early 1980s, with annual defoliation >50,000 km^2, but more recently defoliations have been less extensive (USDA Forest Service 2008). While the definition of "invasive" is debatable (Richardson et al. 2000, Lockwood et al. 2006), we refer here to the gypsy moth as invasive because it is a non-native species whose range is expanding and has a significant impact on the structure and processes of its invaded ecosystems.

Two native cuckoo species occur in the northeast United States, Black-billed (*Coccyzus erythropthalmus* Wilson) and Yellow-billed Cuckoos (*C. americanus* L.). Both are neotropical migrants that generally breed from May-September in woodlands, often within areas of dense scrub or thickets (Hughes 1999, 2001).

Data collection and analyses

The BBS is a standardized census of North American birds conducted since 1966. The survey consists of individual transects ("routes") 39 km in length spread across the

United States and Canada. Volunteers record the identity and number of birds seen and heard during 3-min stops at 50 evenly spaced points along the route (Sauer et al. 2005).

We used digitized maps of gypsy moth defoliation records from 1975-2003 provided by personnel at the USDA Forest Service Forestry Sciences Laboratory at Morgantown, WV. These maps were compiled from state defoliation monitoring data by Andrew M. Liebhold; paper maps sketched during annual aerial surveys from each state were scanned and georeferenced to create a database of northeast U. S. gypsy moth defoliation records. For details of the database and its creation, see Liebhold et al. (1997).

We matched GIS maps of BBS routes with defoliation maps for the years 1975-2003. For each route, any year that a part of the route intersected a defoliation polygon was designated a defoliation year for that route. Each year per route was assigned a year since defoliation (ysd) value. Thus all defoliation years for a route were given a value of ysd = 0, the year immediately following was given ysd = 1 if not defoliated, the next year ysd = 2 if not defoliated, and so on. Given the results of Gale et al. (2001), it was important to include years preceding defoliation as well. For all defoliations that were preceded by at least five non-defoliation years, we assigned ysd = -1 through ysd = -5 for those years.

We downloaded abundance data for both cuckoo species for all routes in states where gypsy moth had established by 2003. We excluded routes on which cuckoos had never been recorded and routes with < 10 years of data during the study period. We standardized abundances following Koenig and Liebhold (2005). Because both species have experienced long-term population declines since the BBS was established (Sauer et al. 2005), we removed long-term trends from each route with linear regression. Prior to regression, raw abundances were log-transformed to normalize regression residuals. Residuals from each regression were transformed into z-scores with mean = 0 and SD = 1. In this way, a standardized abundance of zero can be considered the long-term average abundance of that species for that route. Standardized abundance > 0 is an above-average abundance for that route, and < 0 is below-average.

To answer our first question, if cuckoos exhibit a positive numerical response to gypsy moth outbreaks, we averaged abundances with the same ysd value within each route, and only routes that included all ysd values from -5 to 10 were retained for analyses (n = 81 for Black-billed, n = 76 for Yellow-billed). Standardized abundances for routes were analyzed with repeated-measures ANOVA with ysd as within-subject factors. Abundance was the response variable and year was the independent variable. The sphericity assumption (an assessment of the circularity of the variance-covariance matrix; von Ende 2001) was violated for Black-billed, so we adjusted the degrees of freedom using the Huynh-Feldt epsilon ($\varepsilon > 0.9$).

To determine if the response of cuckoos varied spatially, we included all routes with cuckoos and ≥ 10 years of data in the invaded states (n = 638 for Black-billed, n = 630 for Yellow-billed). For each year and route, we obtained the distance from the starting point of each route to the nearest defoliation and the bearing in degrees from the defoliation to the route. Routes were divided into those north (315°-45°), east (45°-135°), south (135°-225°), and west (225°-315°) of the outbreak. For all routes combined, and for each cardinal direction individually, we plotted annual standardized abundance against distance to the nearest defoliation in that year. We fit a LOWESS curve and bootstrapped by re-sampling the curve 500 times. From these replicate re-samples we obtained 95% confidence intervals.

Results

Abundances of cuckoos varied significantly among years since defoliation (Black-billed, $F_{13.3,1066.8} = 7.08$, $P < 0.001$; Yellow-billed, $F_{15,1125} = 9.631$, $P < 0.001$). Both cuckoo species showed a strong, positive numerical response during gypsy moth outbreaks. Abundances in years preceding outbreaks did not differ from average or were below-average. The peak in abundance during outbreaks disappeared by the following year in Yellow-billed and by two years in Black-billed (Fig. 1). Abundances of both species were also significantly below-average 3-4 years after an outbreak.

The response of cuckoos to defoliations varied spatially in relation to the gypsy moth outbreak. For both cuckoos, abundance at the defoliation site was high but rapidly declined away from the defoliation and was significantly below average from 44-159 km away for Black-billed and 40-140 km away for Yellow-billed (Fig. 2, top panels).

This spatial response (high abundance at a defoliation but below-average at greater distances) was consistent in all directions for both species (Fig. 2, lower panels). The extent of these low abundances varied, but extended as far as 172 km. These patterns were significant (upper bound of 95% CI falls below 0) for all but Black-billed Cuckoos east of defoliations. For distances between 58-70 km, Black-billed Cuckoos east of defoliations were marginally less abundant than average (90% CI falls below 0).

Discussion

Gypsy moth outbreaks had a strong effect on the abundance of both Black-billed and Yellow-billed Cuckoos. The number of cuckoos recorded on BBS routes during outbreaks was significantly greater than average route abundance. For Yellow-billed Cuckoos, the number recorded both before and after the outbreak did not differ from, or were below, average, while for Black-billed Cuckoos the second year following the outbreak was also higher. That cuckoos are more abundant in the outbreak year suggests that the numerical response is not the result of an earlier positive local reproductive response. That is, if cuckoos had higher reproductive rates due to the abundant food resource that gypsy moth caterpillars represent, the higher abundances would not be apparent until the year after an outbreak. BBS routes are surveyed in the early breeding season to record adults, and recently fledged juveniles are excluded from counts. Cuckoos may indeed exhibit a positive reproductive response to gypsy moth outbreaks, but such a result is not apparent in our data, except perhaps for Black-billed Cuckoos. Both species declined in abundance in the year after a defoliation, but Black-billed abundances remained significantly above-average for that year (Fig. 1). Local banding studies, spanning a pre- and post-outbreak period, would be needed to determine the relative contribution of immigration versus reproduction to changes in abundance.

These results differ from the those of Gale et al. (2001), who found that cuckoos of both species increased at some sites one or two years prior to the major defoliation year of a gypsy moth outbreak. However two of the six sites they examined showed a pattern similar to the current study, in which abundances increased only in the outbreak year. The differences in our results may be due to different methods of designating "outbreak years." Gale et al. (2001) state that gypsy moths were typically present for multiple years at their sites, so they used firsthand accounts by observers to identify the year in which defoliation was most extreme as the outbreak. We designated outbreak years as those in which defoliation was recorded in the defoliation database; defoliation levels of approximately 30% or greater are necessary for detection (Liebhold et al. 1997). Defoliation levels during outbreak years in Gale et al. (2001) are estimated at 50-100%. Thus in a multiple-year outbreak, Gale et al. (2001) may have considered the earlier years of the outbreak as "pre-outbreak" and only the later, most severely defoliated year as the outbreak itself. Our method would consider all these years as "outbreak years," while "pre-outbreak years" would be those with no recorded defoliation.

Our spatial analysis suggests that the source of the increased local cuckoo population during an outbreak is the region surrounding defoliations extending tens to hundreds of kilometers away. As these birds move from the surrounding landscape into defoliation areas, they leave presumably suitable nesting sites unoccupied or underoccupied, creating a trough of low abundances outside gypsy moth outbreaks. But if outbreaks "draw in" cuckoos from great distances, how do these birds locate concentrated food resources? Hughes (1999, 2001) proposed that cuckoos enter a "post-migratory nomadic phase" upon reaching their breeding grounds in late spring or early summer, during which they wander across the landscape in search of suitable breeding conditions.

Our data support the existence of this nomadic phase. If cuckoos were simply migrating north in spring and stopping to nest when they encountered a gypsy moth outbreak, the underoccupied sites would be concentrated to the north of defoliated areas because most birds would stop migrating before reaching these areas. But the trough of low abundances surrounds gypsy moth defoliations, and is actually broader to the south than the north for Yellow-billed Cuckoos and extends further to the south and to the north for Black-billed. This pattern would be expected if cuckoos wandered across large areas in search of abundant food. Additionally, cuckoos have a delayed nesting phenology relative to most other Neotropical migrants (Hughes 1999, 2001), consistent with the idea of a wandering period in late spring and early summer.

To our knowledge, the only other example of a population shift by a native predator in response to invasive prey is golden eagles on the Channel Islands of California. Introduced feral pigs acted as a trophic subsidy, allowing eagles to colonize the islands to the detriment of the eagles' other choice prey, the endangered island fox (*Urocyon littoralis* Baird) (Roemer et al. 2002). The eagles were not present on the islands prior to 1994. This change in eagle distribution led to a restructuring of the islands' food webs and nearly drove the fox to extinction on several islands. In contrast, gypsy moth outbreaks cause a redistribution of cuckoos within their current range, and presumably a redistribution of their predation impact, reducing it in some areas and increasing it in others. The exact strength of the trophic impact of cuckoos on forest food webs is unknown. Insectivorous birds can have important effects, both directly on insect prey (Holmes et al. 1979) and indirectly on plants by consuming herbivorous insects (Marquis and Whelan 1994, Van Bael et al. 2008). Additionally, because cuckoos may specialize on hairy or spiny caterpillars, a gypsy moth outbreak may reduce the predation pressure on native hairy caterpillars in the regions adjacent to the outbreak. At the same time, the outbreak may increase predation on these natives within the outbreak, resulting in apparent competition between the invasive and native insect herbivores. Increased densities of cuckoos could also benefit their own predators and increase transmittance of pathogens and parasites.

This study draws attention to the complexity of interactions between exotic and native species. Non-natives have caused innumerable declines in native species, but by the very fact that they are embedded within ecological networks, they will have both negative and positive interactions with indigenous species. Positive interactions are recognized as important forces in community dynamics (Bertness and Callaway 1994). These interactions can be either direct consumptive (trophic subsidies) or non-consumptive (e.g., mutualisms) interactions or indirect interactions (e.g., habitat amelioration). Further studies are needed to generalize about the role and effects of non-native species as trophic subsidies for native predators, particularly when populations of the alien exhibit large fluctuations in the new environment. For example, invasive populations of species as varied as zebra mussels (*Dreissena polymorpha* Pallas) (Strayer & Malcolm 2006), house mice (*Mus domesticus* L.) (Singleton *et al.* 2007), and garlic mustard (*Alliaria petiolata* (M. Bieb.) Cavara & Grande) (Nuzzo 1999) can vary annually in abundance. During high points in these cycles, they may represent important prey for native consumers and thus affect predator population sizes and community structure in invaded regions.

We do not wish to downplay the threat to biodiversity posed by invasives, yet from the point of view of an organism on the receiving end of these positive interactions, an invasive species could be considered “beneficial.” This would seem to be the case for cuckoos and gypsy moths, although verifying this would require observations of nesting success and fledgling survival and comparison to non-invaded areas. Habitat changes due to gypsy moth defoliation, such as a more open canopy due to overstory tree mortality and increased shrub-layer growth, may also benefit understory-nesting bird species like Eastern Towhees (*Pipilo erythrophthalmus* L.) (Bell and Whitmore 1997, 2000). Nonetheless gypsy moth outbreaks are destructive and can cause severe economic loss through tree mortality and may increase encroachment of red maple (*Acer rubrum* L.) into oak-dominated woodlands (Fajvan and Wood 1996, Jedlicka and Vandermeer 2004). For some birds, gypsy moths may also increase nest parasitism by Brown-headed Cowbirds (*Molothrus ater* Boddaert) (Bell and Whitmore 2000).

A more difficult issue is how to view these positive interactions in conservation decision-making and practice. In situations where the non-native provides a beneficial service to a native species of conservation concern, management decisions should weigh these benefits against potential ecological costs. Thus invasion biology theory needs to incorporate positive interactions and particularly the potential role of invasives as trophic subsidies when considering both the effects and management of invasive species.

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Figure legends

Fig. 1. Mean standardized abundance of cuckoos during and following gypsy moth outbreaks. Error bars show 95% CI, and arrows indicate defoliation years. Here, standardized abundance of 0 is the detrended, long-term average abundance on a BBS route (see Methods).

Fig. 2. Distribution of cuckoos in response to gypsy moth defoliation. Top panels, standardized abundance plotted against distance to nearest defoliation. Lines are upper and lower bounds of 95% CI based on bootstrapped replicates of locally weighted regression. Bottom panels, directional distribution relative to nearest defoliation event. The center of the figure represents the location of a hypothetical defoliation. Black regions of the figure are significnatly greater than average abundance; gray regions are significantly below average abundance; white regions do not significantly differ from average abundance.

Fig. 1

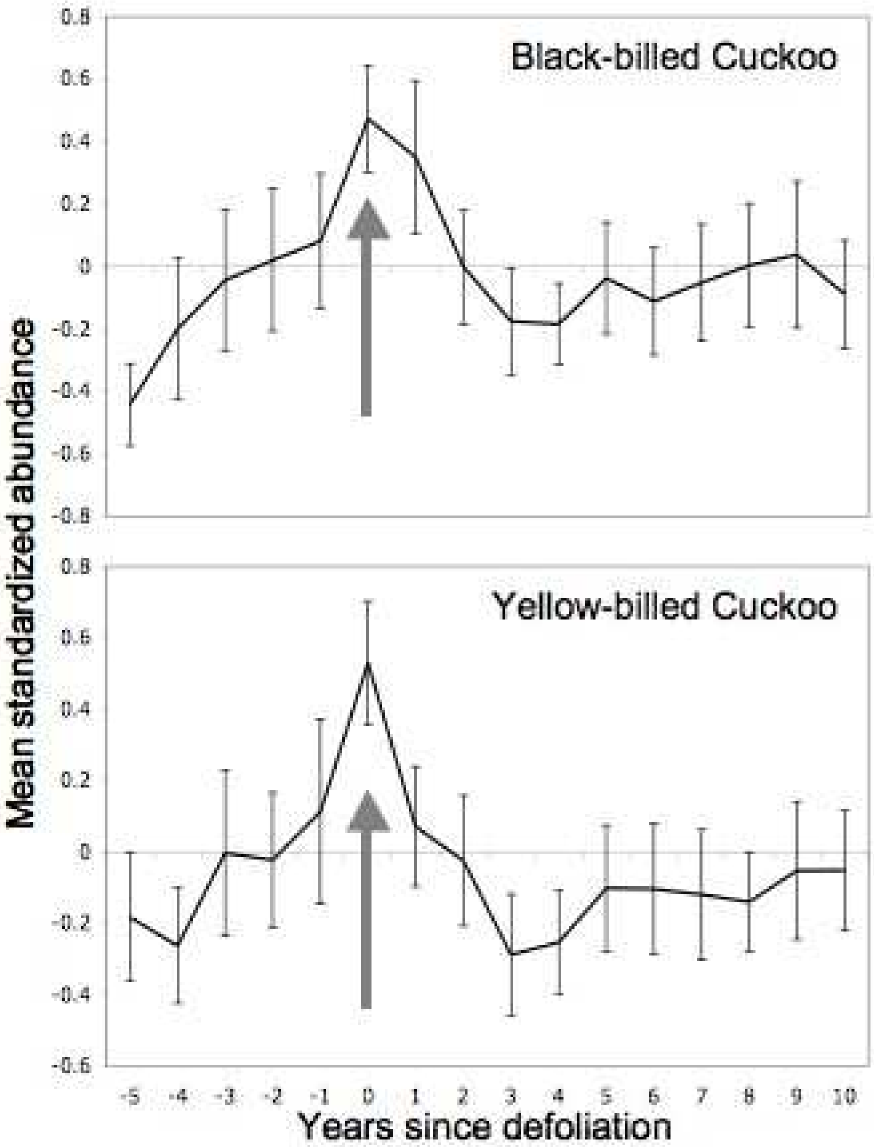
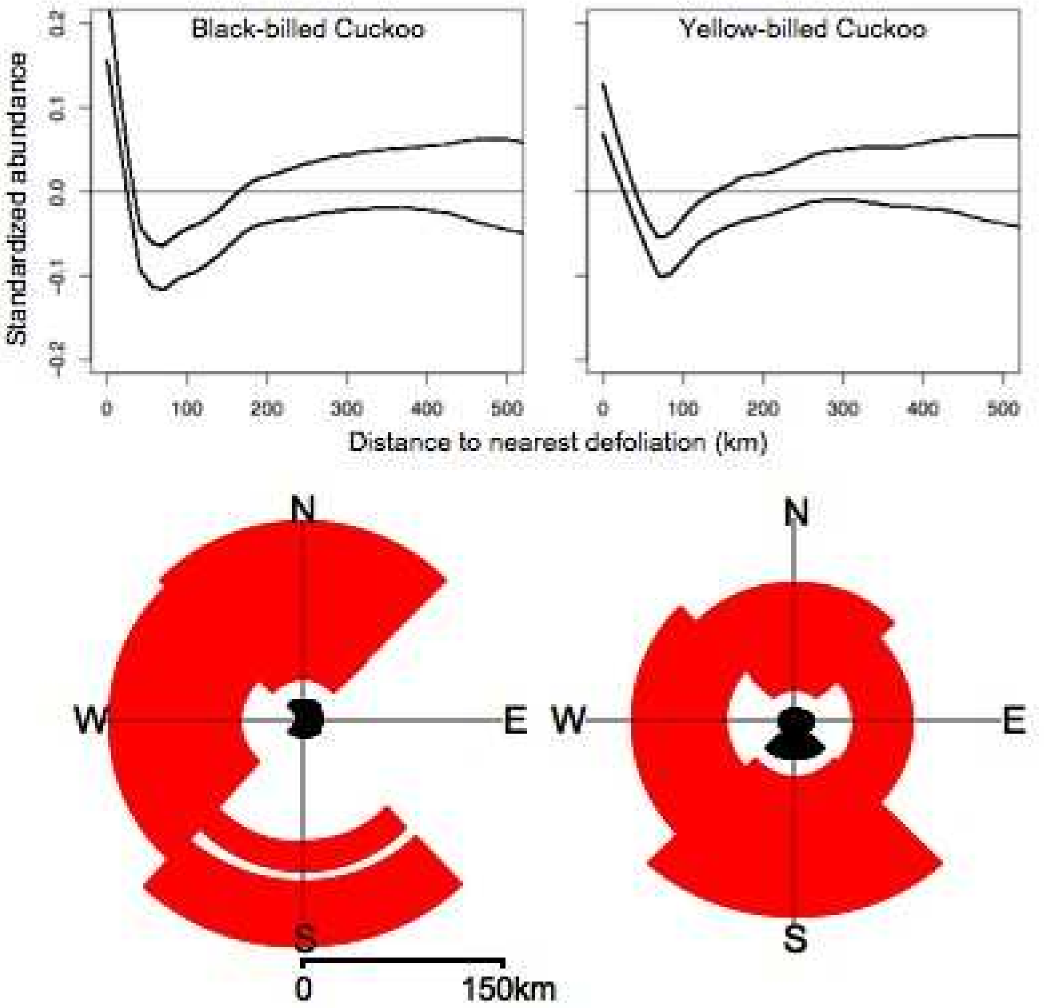

Black-billed Cuckoo
Yellow-billed Cuckoo
Mean standardized abundance
Years since defoliation
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-5
-4
-3
-2
-1
0
1
2
3
4
5
6
7
8
9
10

Fig. 2


Black-billed Cuckoo
Yellow-billed Cuckoo
Standardized abundance
0.2
0.1
0.0
-0.1
-0.2
0
100
200
300
400
500
Distance to nearest defoliation (km)
N
W
E
S
0
150km