

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 350–1000 m. 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

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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 350–1000 m 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 Mar. and Apr. 2006 we constructed bird exclosures on exclusion branches. Exclosures consisted of a 2 cm diam 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 Le Corff, 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 prep.*). Unidentified

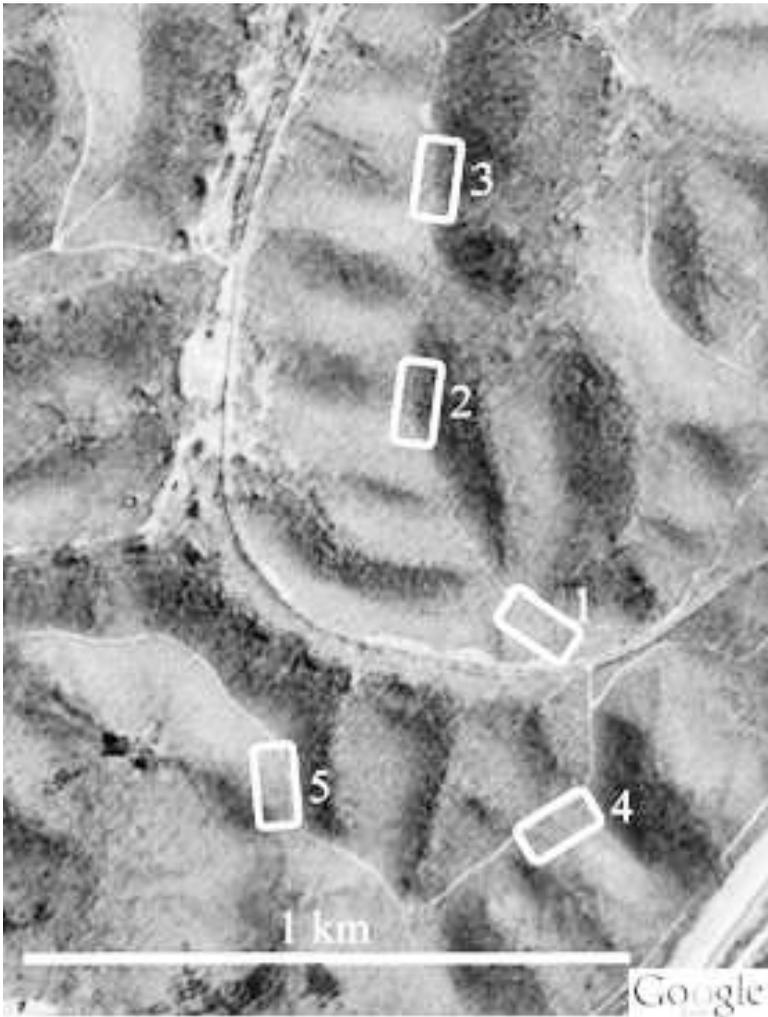


FIG. 1.—Sites 1 through 5 at Tyson Research Center, St. Louis County, Missouri

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 , Le Corff 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 h on three separate days in Jun. 2006. A 100 m transect was measured along the road passing through each site. The observer (N. A. B.) slowly walked the transect for 10 min 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 twig) 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 Sep. 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 (von Ende, 2001) with enclosure 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 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 enclosure treatment and site as fixed factors. In all analyses, a significant site effect indicates spatial variation in the insect community. A significant site \times 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 enclosure 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 \times census interaction $F_{2,40} = 4.853$, $P = 0.013$; Tukey HSD = 2.19, $P = 0.011$), the overall MANOVA treatment \times 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 individuals detected $\text{ha}^{-1} \pm 1 \text{ SE}$, 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 Oct. 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 \times 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

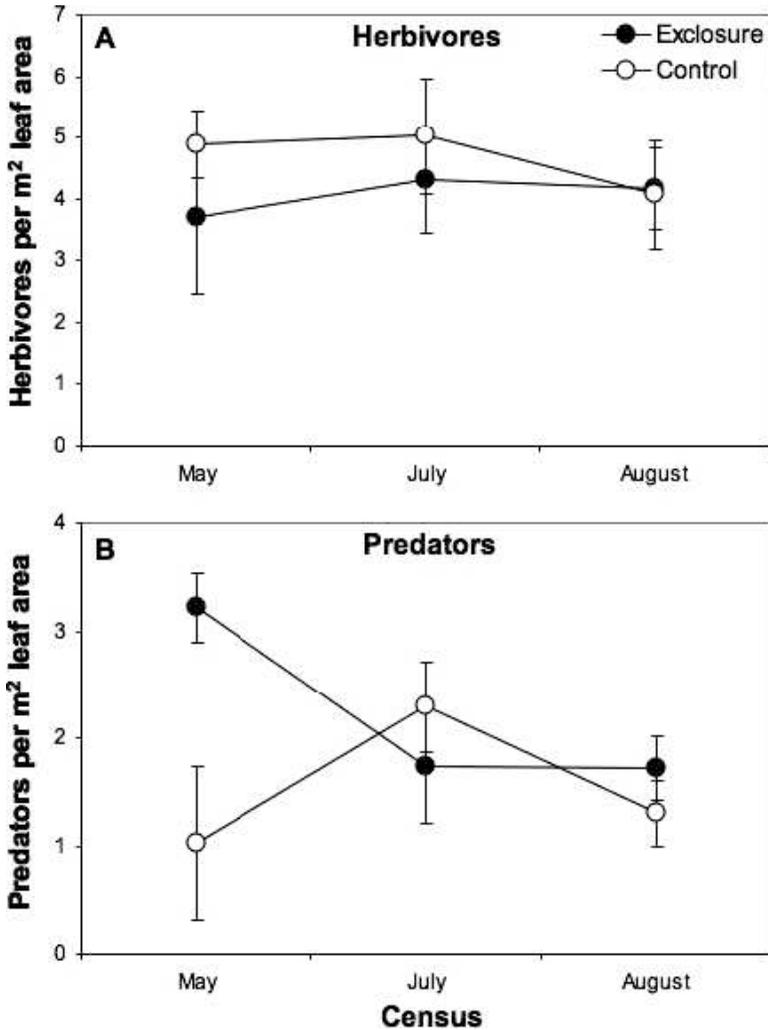


FIG. 2.—Mean abundances (± 1 SE) on exclusion and control trees during May, July and August censuses, pooled across all sites. (A) insect herbivores and (B) arthropod predators. Exclusion of avian predators did not affect abundance of any groups. Although predators were more abundant on exclusion trees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

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).

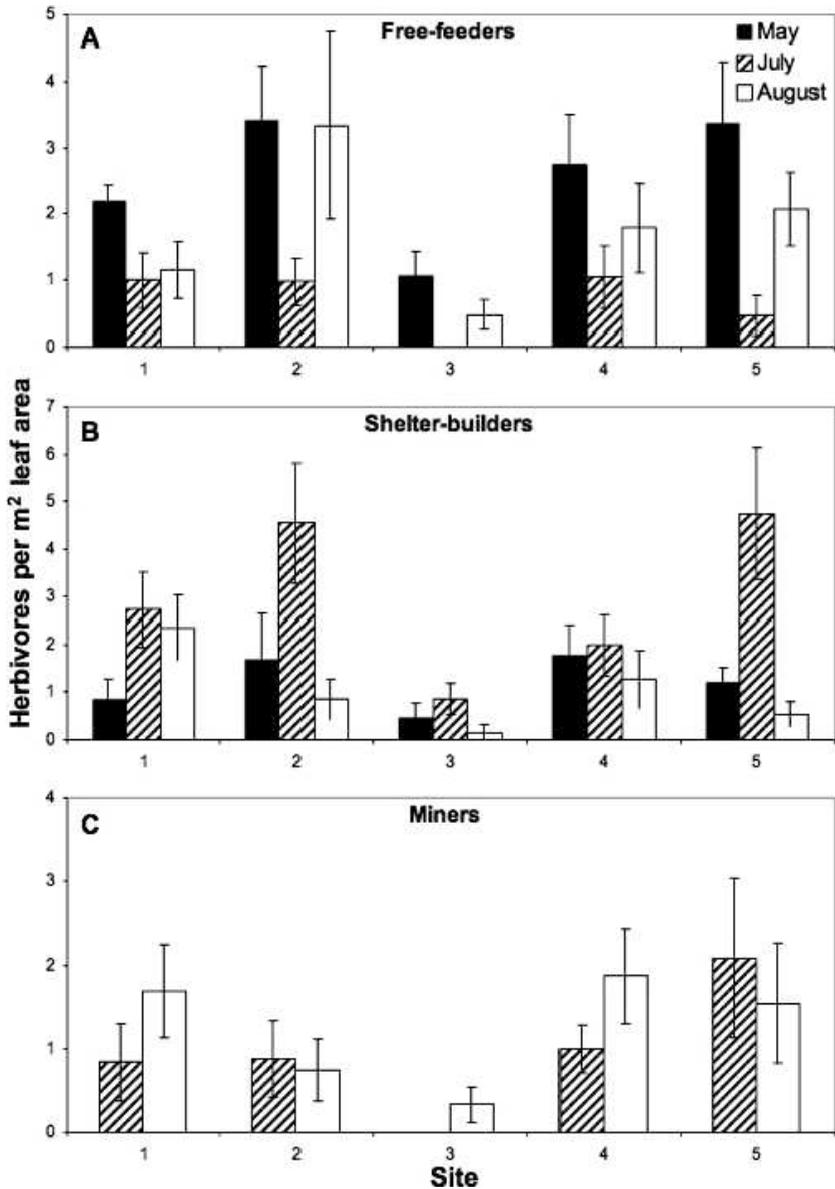


FIG. 3.—Spatial and temporal variation in mean abundances (± 1 SE) of herbivore feeding guilds by census. (A) free feeders, (B) shelter-builders and (C) leaf miners

Abundances of spring arthropod predators were greater within enclosures 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 enclosures given the marginally greater spring leaf damage on enclosure trees.

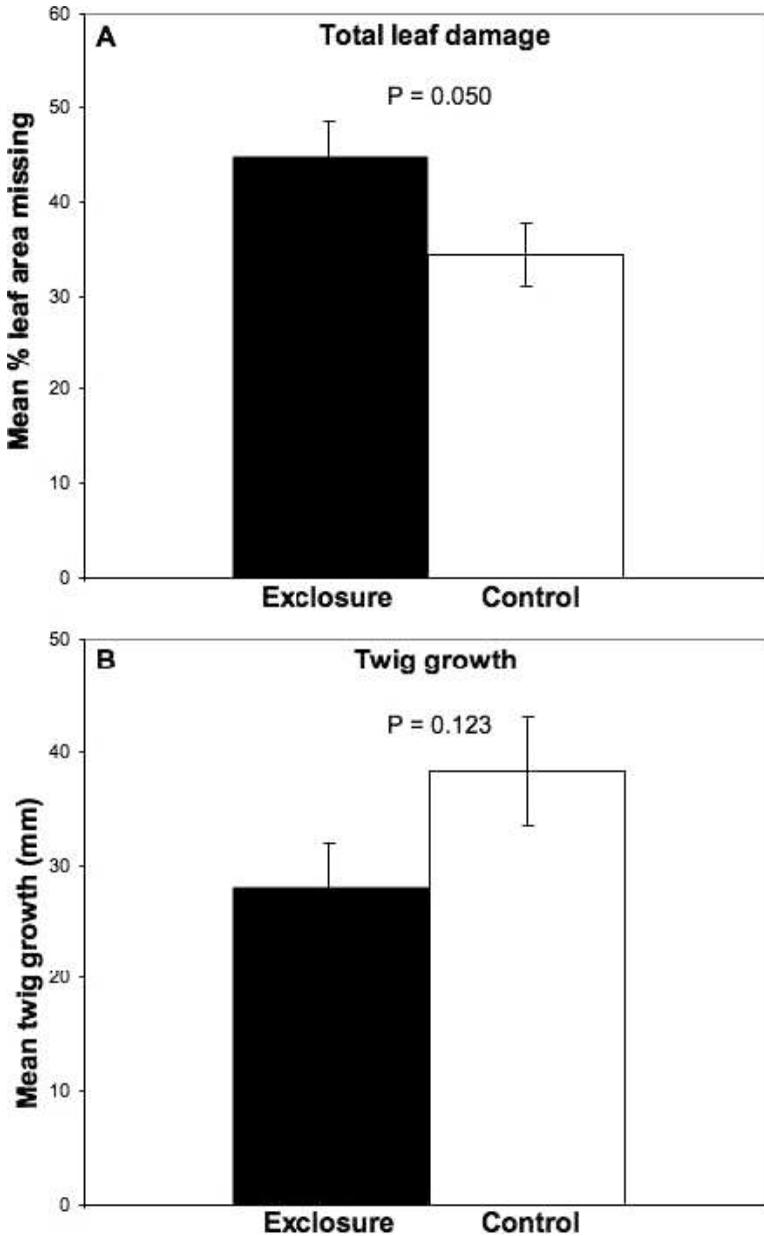


FIG. 4.—(A) Mean leaf damage (± 1 SE) on exclosure and control trees at the end of the growing season. Bird exclusion resulted in significantly higher leaf damage on exclosure trees. (B) Mean twig growth (± 1 SE) on exclosure and control trees in summer 2007. Although twig growth was lower numerically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

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 \times treatment interactions, indicating that the indirect effects 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 Jun., 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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