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PLANT-ANIMAL INTERACTIONS - ORIGINAL PAPER

Spatial heterogeneity in the relative impacts of foliar quality and predation pressure on red oak, *Quercus rubra*, arthropod communities

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Abstract Predation pressure and resource availability often interact in structuring herbivore communities, with their relative influence varying in space and time. The operation of multiple ecological pressures and guild-specific herbivore responses may combine to override simple predictions of how the roles of plant quality and predation pressure vary in space. For 2 years at the Coweeta LTER in the Southern Appalachian Mountains, we conducted a bird exclosure experiment on red oak (*Quercus rubra*) saplings to investigate the effects of bird predation on red oak arthropod communities. We established bird exclosures at six sites along an elevational gradient and estimated variation in foliar nitrogen and bird predation pressure along this gradient. Foliar nitrogen concentrations increased with elevation while our index of bird predation pressure was variable across sites. Greater arthropod densities were detected inside exclosures; however, this result was mainly driven by the response of phloem feeders which were much more prevalent inside exclosures than on control trees. There was little evidence for an effect of bird predation on the other arthropod guilds. Consequently, there was no evidence of a trophic cascade either in terms of leaf damage or tree growth. Finally, we found more variation in arthropod density among trees within sites than variation in arthropod density among sites, indicating the importance of micro-site variation in structuring arthropod communities.

Keywords Bird predation · Exclosure experiment · Spatial variability · Trophic cascade

Introduction

Predation pressure (top-down), resource availability (bottom-up), and their interactions are important determinants of the distribution and composition of arthropod communities (Denno et al. 2002; Gruner 2004; Hunter and Price 1992; Preszler and Boecklen 1996). By exploring spatial variation in the relative influence that top-down and bottom-up forces have on arthropod communities, we can begin to understand the mechanisms that shape mid-trophic level communities and how changes in the abiotic environment influence these mechanisms (Chase 2003; Chase et al. 2000; Gripenberg and Roslin 2007; Hunter 2001). Spatial variation in the relative effects of top-down and bottom-up forces can be driven by gradients in precipitation (Chase et al. 2000; Van Bael and Brawn 2005), elevation (Preszler and Boecklen 1996), light availability (Richards and Coley 2007), habitat structure (Finke and Denno 2002; Moreau et al. 2006), plant quality (Forkner and Hunter 2000), and nutrient availability (Denno et al. 2002). Consequently, interest now lies in examining spatial variation in the biotic and abiotic forces that act upon

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arthropod communities, and the interactions among them (Denno et al. 2002; Forkner and Hunter 2000; Hunter 2001; Hunter and Price 1992; Preszler and Boecklen 1996; Stiling and Moon 2005).

Species composition of mid-trophic level arthropod communities is often diverse and not all herbivores respond the same way to the same ecological pressures (Denno et al. 2000; Forkner and Hunter 2000). Variation in susceptibility of herbivores to predation can depend on herbivore ontogeny (Chase 2003; Hawkins et al. 1997; Murdoch et al. 2006), feeding strategy (Cornell and Hawkins 1995), and defense mechanisms (Muller and Brakefield 2003). Moreover, herbivore feeding strategy (Ritchie 2000) and life-history (Huberty and Denno 2006) can influence how herbivores respond to variation in plant quality. This diversity of responses may override simple generalizations about the relative strengths of top-down and bottom-up forces on arthropod communities (Hunter 2001).

Theoretical models of trophic interactions predict that the strength of top-down forces depends partially on plant productivity (Oksanen et al. 1981), with high resource availability and quality promoting strong top-down effects on herbivores. While some empirical work indicates that top-down forces are strongest when nutrient availability is highest (Forkner and Hunter 2000), a recent meta-analysis by Borer et al. (2005) found that plant productivity per se does not necessarily generate substantially larger cascading effects. Variation in plant secondary compounds, turnover rates and stoichiometry as well as herbivore and predator biological characteristics can all impact the strength of trophic cascades (Borer et al. 2005).

In terrestrial systems, the impact of avian predators on arthropod abundance and subsequent cascading effects on plants has received considerable attention. Results from these investigations have ranged from strong effects of bird predation that cascade down to primary producers with impacts on plant growth or, as more commonly measured, plant damage (Marquis and Whelan 1994; Mols and Visser 2002; Strong et al. 2000; Van Bael et al. 2003), effects of bird predation on herbivores but no evidence of trophic cascades (Bock et al. 1992; Lichtenberg and Lichtenberg 2002), no effects of bird predation on herbivores (Barber and Marquis 2009; Gruner 2004; Ritchie 2000; Wiens et al. 1991), and effects of bird predation on herbivores contingent upon plant quality (Forkner and Hunter 2000; Sipura 1999) or plant productivity (Van Bael and Brawn 2005). Taken together, these studies suggest that the interaction between insectivorous birds and their arthropod prey depend on plant productivity, plant quality, habitat complexity, and/or species diversity and composition of predator and prey assemblages (Van Bael et al. 2008).

Here, we describe a 2-year manipulation of bird predation along an elevational gradient in the southern Appalachian Mountains. At our site, nitrogen mineralization rates, and subsequently foliar nitrogen levels, increase with elevation (Knoepp and Swank 1998). We utilized this natural gradient to (1) document variation in bird predation pressure, foliar nitrogen, and herbivore densities, (2) investigate spatial variation in the levels of bird predation and foliar nitrogen and how they interact in structuring the insect herbivore community, and (3) determine if birds influence defoliation on, and growth rates of, oak saplings. We hypothesized that (1) the top-down effects of bird predation pressure on herbivores would be strongest at sites where foliar nitrogen is highest and bird predation pressure greatest, (2) the effect of bird predation would differ among herbivore guilds, and finally (3) cascading effects of bird predation on plant productivity would be more prevalent at sites with high levels of foliar nitrogen and bird predation pressure.

Materials and methods

Study site

The Coweeta Hydrologic Laboratory (Coweeta), operated by the US Forest Service, is located in the Nantahala National Forest of western North Carolina (35°03’N, 83°25’W). Mean annual precipitation at Coweeta increases with elevation from 193 cm at low elevation (677 m) to 245 cm at high elevation (1,570 m), and average air temperature is 3°C lower at high elevation than at low elevation (Swank and Crossley 1988). Deciduous oak species (*Quercus* spp.) are the dominant canopy species at Coweeta with an abundant understory of *Rhododendron maximum* and mountain laurel (*Kalmia latifolia)*. Canopy trees are tallest at the lowest elevation site and decrease in size as elevation increases. We are unaware of any foliage-gleaning bats at Coweeta and we did not observe any evidence of deer herbivory at our sites.

Bird exclosure experiment

In February 2005, we established 6 sites spanning the breadth of the elevation gradient at Coweeta: Site 1 (780 m above sea level), Site 2 (980 m), Site 3 (1,180 m), Site 4 (1,300 m), Site 5 (1,400 m), Site 6 (1,570 m). Each site was approximately 3,000 m^2. Within each site we chose 20 red oak, *Quercus rubra*, saplings, with an average height of 162.5 (±4.4) cm, which is similar in height to the understory saplings studied by Van Bael et al. (2003), Van Bael and Brown (2005) and Marquis and Whelan (1994). Saplings had an average of 128 (±7.69) leaves per tree. We randomly assigned 10 saplings per site to the bird exclosure treatment and 10 to the control (non-exclosure). Bird exclosures consisted of polyvinyl chloride (PVC) pipes and rebar, covered with agricultural netting (Bird-X, mesh size 2 × 2 cm; http://www.bird-x.com). These exclosures do not appear to attract arthropods, damage leaves or branches, or significantly reduce light transmittance (Van Bael and Brawn 2005; Van Bael et al. 2003). While the mesh size most likely prevented large adult lepidopterans from accessing the trees, >90% of lepidopterans found on surrounding red oak trees have adult wingspans less than 2 cm (C.B. Zehnder, unpublished data). At the end of the first growing season (fall 2005), we raked leaves into all exclosures to match the surrounding leaf litter accumulation. Exclosures were maintained during the entire course of the experiment (2 growing seasons: spring 2005 to fall 2006).

Arthropod sampling

Budburst phenology varies with elevation and is a fundamental driver of arthropod abundance on oak trees (Hunter 1990). To control for this variation, we standardized sampling by budburst date at each site. Specifically, arthropod sampling and foliar nitrogen measurements were made at each site on days 20, 50, 80, and 110 post-budburst. We calculated date of budburst for each site by monitoring each tree twice weekly in the beginning of April. When 50% of buds on a tree had opened, we noted that date as the date of budburst for that tree, and then averaged the date of budburst across all trees at each site. There was approximately a 2-week difference between budburst at site 1 (low elevation) and site 6 (high elevation).

On each sampling date, the entire sapling was visually surveyed (non-destructive sampling) and arthropods were counted and categorized into feeding guild: galls, leaf chewers, phloem feeders, and arthropod predators. Galls included any type of insect-induced leaf gall, primarily Cecidomyiidae and Cynipidae. Leaf chewers refers to surface-feeding lepidopteran or hymenopteran (sawfly) larvae, because leaf rollers, leaf tiers, leaf miners, weevils, and snails occurred at very low densities during both years of the study and, although some of these groups are known to respond to variation in elevation (Preszler and Boecklen 1996) and tree architecture (Marquis et al. 2002), they were not abundant enough in our study for statistical analysis. Phloem feeders were predominantly aphids, which were not tended by ants. Arthropod predators were predominately spiders, but also included Reduviidae, Syrphidae, and Coccinellidae. We standardized all arthropod densities (per 100 leaves to standardize among different sized trees) by log transformation [ln(x + 1)].

Foliar nitrogen measurements

In this experiment, we focused on foliar nitrogen because of the previously measured gradient in nitrogen mineralization rates (Knoepp and Swank 1998); however, there are other aspects of plant quality that can influence insect herbivores. A single randomly chosen leaf was collected from each tree on each sampling date to estimate percent foliar nitrogen. These leaves were predominately shade leaves because saplings were in the understory. Oaks have a single flush of leaves in the spring, so leaf age within an individual tree is relatively homogenous. Although sampling a single leaf per tree means that we are unable to estimate within-tree variance, and therefore unable to compare foliar nitrogen among trees within sites, we were concerned that removing multiple leaves per tree on each sampling date over a 2-year period would have uncontrolled consequences for nitrogen allocation in plants (Tao and Hunter 2010). Consequently, we consider our leaf samples to provide estimates of foliar nitrogen for each elevation on each sampling date, but not for individual trees. Leaves were oven dried at 64°C and ground into a fine powder using a ball mill grinder (Spex Certiprep, NJ, USA). Ground samples were weighed into tin capsules with a Mettler UMT2 microbalance (Mettler Toledo, Greifensee, Switzerland) and analyzed with a Carlo Erba NA 1500 CHN analyzer (Carlo Erba, Milan, Italy). We then averaged foliar nitrogen levels at each site for each sampling date.

Index of bird predation pressure

We estimated bird community abundance and composition at each site using 150-m transect counts centered on the experimental trees. All birds detected within 50 m of each transect were recorded. We sampled each transect approximately every 4 days and all sites were monitored on the same day. We conducted 21 counts in 2005 and 24 in 2006. Additionally, we observed foraging behavior at each site following completion of transect counts. We separated the height of foraging observations into four categories, ground (0 m), shrub (>0–3 m), sapling (>3–6 m), and canopy (>6 m), and calculated the proportion of time that each bird species spent foraging at these heights. Due to low sample sizes for some species, we could not estimate site-specific foraging strategies, therefore we pooled all observations of a species to attain an index of where it was most likely to forage. We had no a priori biological reason to assume preferred foraging strata would differ between years; therefore we pooled 2005 and 2006 observations.

To estimate an index of potential predation pressure that the bird community may impose on oak herbivores at the height level of the experimental trees, we multiplied the percent of time that each bird species foraged at the level of the experimental trees (shrub and sapling level) by the mean number of individuals of that species detected at a site. This was repeated for all bird species and the results were summed to obtain a relative index of predation pressure for each site (bird predation index used in the model below). Species for which we had fewer than two foraging observations were assigned a foraging preference equal to the mean foraging preference for all species. Finally, we assumed that Ruffed Grouse (*Bonasa umbellus*), Wild Turkey (*Meleagris gallopavo*), Ruby-throated Hummingbird (*Archilochus colubris*), and woodpecker species imposed no predation pressure on experimental trees because they do not forage on leaf-residing arthropods. We caution the reader that this method does not directly assess foraging pressure and that our results may be influenced by factors such as detection biases and bird foraging preferences that could vary by location.

Defoliation and tree growth estimates

We quantified the impact of herbivores on trees in two ways. First, we measured sapling height at the beginning (spring 2005 before shoot elongation) and conclusion (fall 2006) of the study and then calculated the percentage increase in height for each sapling. Sapling height was measured by holding a tape measure to the base of the sapling and then measuring up to the top of the tallest branch. Second, prior to leaf senescence in September of both years, we measured accumulated defoliation on each sapling using established methods (Hunter 1987; Hunter and Schultz 1995). Briefly, we visually inspected up to 100 leaves on each tree and classified them into one of seven damage classes based on the estimated percentage of leaf area removed (0, 1–5%, 5–30%, 30–50%, 50–70%, 70–90% or >90%). Leaf scars (where a leaf petiole had been attached to a twig) were classified as >90% herbivory. Prior leaf samples for foliar nitrogen analysis left the petiole remaining on the tree with an obvious scissor cut, and we did not include these in our damage estimates. We then averaged these values to generate a single estimate of leaf damage for each sapling. For consistency, C.B.Z. conducted all visual estimates.

Sham exclosures

Based on 2005 (year 1) data, we suspected that the exclosures might protect foliage from falling debris, thus biasing estimates of leaf damage between experimental and control trees. Consequently, in 2006 (year 2), we constructed five 'sham' exclosures at each of three sites (1, 4, and 6) in order to investigate exclosure effects. The sham exclosures were similar to the experimental exclosures except that bird netting was only on the top of the cage and the sides were open to allow bird foraging. Sham exclosure saplings were sampled on the same dates as the other experimental saplings with the same data collected, including arthropod guild abundance and defoliation estimates. We assumed that sham exclosures did not influence bird behavior.

Statistical analyses

Arthropods

We used a general linear mixed model in order to explore effects of site-level and tree-level variables on arthropod densities. We created a two-level hierarchical model where the bird predation index (*Birds*) and average leaf nitrogen concentration (*Nitrogen*) were the site-level effects. The tree-level effect was the presence or absence of an exclosure (*Exclosure*) as this was specific to a particular tree. Our modeling procedure is described below and follows Singer (1998).

Model specifics

We first calculated the amount of variation in arthropod densities between site–year groups and within site–year groups by fitting a hierarchical model that grouped trees by site–year combinations (12 site × year combinations). While there was a lack of independence amongst combinations due to individual trees being sampled in multiple years, we measured nitrogen content and bird predation at this level and used these groupings to help increase sample size. This model included date as a nuisance variable fixed effect to control for variation among sampling dates within a year which we were not specifically interested in but assumed would influence arthropod density. We used the covariance estimate from this model to estimate the percent of variation in arthropod densities explained by differences among the site–year groups and within site–year groups (Singer 1998). This estimate of among site–year groups was also used as a baseline for evaluating the explanatory strength of *Birds* and *Nitrogen*, which was specific to each site–year group. We then fit a linear model relating *Birds* and *Nitrogen* to arthropod densities. We allowed the intercept to vary randomly in order to evaluate the effects of *Birds* and *Nitrogen* among site–year groups. Finally, we used the covariance estimate of this model to evaluate how much variation in arthropod densities was explained by *Birds* and *Nitrogen*.

To assess the importance of the tree-level predictor, *Exclosure*, we fit a linear model relating it to arthropod densities. When evaluating *Exclosure*, we allowed it to vary randomly because we believed its effect on arthropod densities might differ among site–year groups. We then used the residual variance for this model to assess the amount of variation in arthropod densities within a site–year groups that was explained by *Exclosure*. Finally, we modeled the effect of *Birds* and *Nitrogen* on the effect *Exclosure* had on

Table 1 Description of models tested

Model	Explanation
Null	Arthropod densities fluctuate among sampling dates. None of the other variables measured strongly influences arthropod density
Birds	Bird density, as estimated from transects, best explains arthropod density (site-level variable)
Nitrogen	Foliar nitrogen concentrations, averaged across all trees at each site, best explain arthropod densities (site-level variable)
Exclosure	The presence of an exclosure best explains arthropod density (tree-level variable)
Birds + exclosure	Including both birds and exclosures in the model provides the best fit to the arthropod density data
Nitrogen + exclosure	Including both nitrogen and exclosures in the model provides the best fit to the arthropod density data
Nitrogen × exclosure	The effect of the exclosure on arthropod densities varies with foliar nitrogen concentrations
Birds × exclosure	The effect of the exclosure on arthropod densities varies with bird predation level

All models include date as a random effect. Nitrogen and birds were never included in the same model because of the strong positive correlation between the two variables

arthropod densities because we believed that the influence of *Exclosure* might be tempered by *Birds* and *Nitrogen*. There was some correlation between *Birds* and *Nitrogen* (correlation coefficient = 0.57), therefore we never included both of these predictors in the same model. In total, we fit eight different models for each arthropod guild relating arthropod densities to *Birds*, *Nitrogen*, *Exclosure*, and their combinations and interactions (Table 1). We evaluated the relative fit of each of the preceeding models using an information theoretic approach and provide estimates of effect sizes from the best fitting model based on AICc (Burnham and Anderson 2002).

Model analyses

All models were fit using PROC MIXED (SAS Institute 2006) with the unstructured components type error structure. Analysis of model residuals from the global model for each arthropod guild indicated that the data were not normally distributed. Standard transformations failed to remedy the problem due to the large number of zeros associated with the data. However, for ease in interpretation we chose to model arthropod densities using random effects linear regression and caution the reader that our results may be subject to the problems associated with non-normality of data and linear regression.

Defoliation estimates and sapling growth

Defoliation estimates were analyzed separately for each year by two-way ANOVA. Exclosure and site were main effects, and defoliation estimates were arcsine square-root transformed prior to analysis. Percent change in sapling height over the entire 2-year period was analyzed by two-way ANOVA with exclosure and site as main effects.

Sham exclosure

Sham exclosure (2006 only) measurements were analyzed separately for each site because we were not interested in comparing the effects of sham exclosures among sites. Total arthropod abundances for each guild (summed over 4 sampling dates), as well as end-of-season defoliation estimates were the response variables and exclosure (3 levels: control, sham, exclosure) was the main effect.

Results

In both years, more birds were detected along transects at mid-elevation sites than at high or low elevation sites (Fig. 1). Time spent foraging in the shrub/sapling layer was estimated for over 20 bird species (Appendix Table 1). Estimated bird predation pressure at the shrub/sapling layer was highest at sites 4 and 5, and lowest at site 1 (Fig. 1). Foliar nitrogen concentrations did not differ between years but did increase with elevation (Fig. 2) and decreased throughout the growing season (data not shown). Overall, the bird exclosures had the strongest influence on phloem feeder densities and a negligible effect on other arthropod guilds (Fig. 3).

Galls

We detected an average (SE) of 11.7 (1.4) galls per 100 leaves on control trees and 9.0 (1.0) per 100 on exclosure trees, irrespective of site, year, or date. The majority of variation (82%) in gall densities was amongst trees within a site–year group (Fig. 3). Foliar nitrogen levels failed to explain any of the variation among site–year combinations in gall densities, and the presence of an exclosure failed to explain any of the within site–year combination variation. Variation in bird density explained ~2% of the among site–year variation. Consequently, the model that included *birds* as a level-2 predictor provided a marginally better fit to the data in comparison to the other models (Table 2) and there was some evidence that gall densities increased with increasing bird density (Table 3).

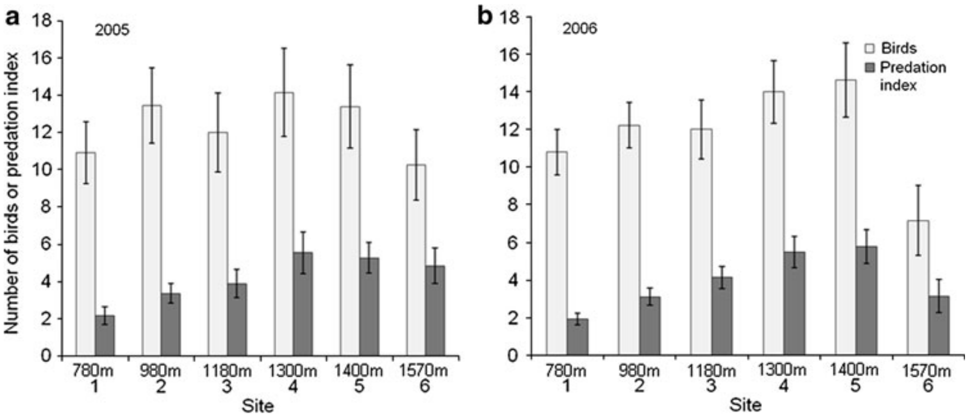

Fig. 1 Bird predation pressure along the elevation gradient in 2005 (**a**) and 2006 (**b**). *Light gray bars* show the mean numbers of birds (±95% CI) detected during 30-min transect counts across all sites and *dark gray bars* show bird counts weighted by foraging strata preference (±95% CI). Site elevation (m above sea level) is indicated below each set of *bars*

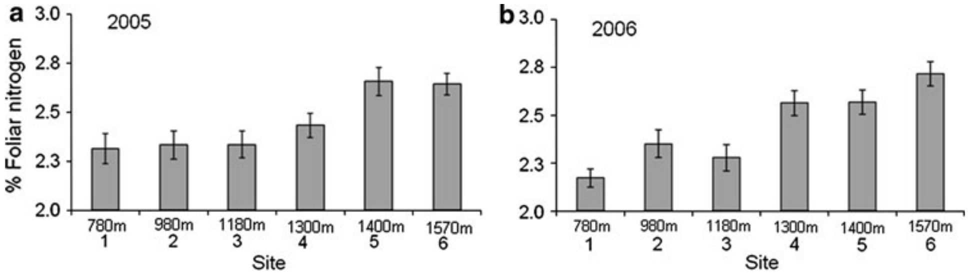

Fig. 2 Effects of elevation on percent foliar nitrogen of *Q. rubra* leaves ($n = 20$ trees per site ± 1 SE) averaged over 4 sampling dates in **a** 2005 and **b** 2006

Leaf chewers

We detected an average (SE) of 1.5 (0.3) leaf chewers per 100 leaves on the control trees and 1.5 (0.3) per 100 on the exclosure trees, irrespective of site, year, or date. The majority (95%) of variation in leaf chewer density occurred among trees within site–year combinations. None of the explanatory models explained variation in leaf chewer densities better than the null model (Table 2).

Phloem feeders

We detected an average (SE) of 21.5 (2.0) phloem feeders per 100 leaves on the control trees and 61.8 (15.8) per 100 on the exclosure trees, irrespective of site, year, or date. Phloem feeder densities were higher inside the exclosures than on control trees (Fig. 3, Table 3) and the model with an exclosure effect provided the best fit to the data (Table 2), while 64% of the variation in phloem feeder density was within site–year combinations. Differences in bird predation levels explained ~2% of the remaining (36%) variation, while foliar nitrogen levels explained ~6% of the variation between site–year combinations.

Arthropod predators

We detected an average (SE) of 2.0 (0.1) arthropod predators per 100 leaves on the control trees and 2.3 (0.1) per 100 on the exclosure trees, irrespective of site, year, or date. The index of bird predation pressure, foliar nitrogen concentration, the presence of an exclosure, and their interactions failed to explain variation in arthropod predator densities better than the null model (Table 2). The majority (92%) of variation in arthropod predator densities was among trees within site–year combinations.

Total arthropods

We detected an average (SE) of 36.6 (2.3) arthropods per 100 leaves on the control trees and 74.5 (15.8) per 100 on the exclosure trees, irrespective of site, year, or date. The model that included the effect of the exclosure and bird density provided the best fit for total arthropod densities. Total arthropod densities were higher on exclosure trees than on control trees and total arthropod densities were greater at sites with a greater index of bird predation (Figure 3, Table 3). Most of the variation (85%) in total arthropod density was within site–year combinations.

Defoliation

In both years, percent defoliation was higher on control trees than on exclosure trees and 2005 defoliation levels were higher at lower elevations (Fig. 4: 2005 site: $F_{5,102} = 5.99$, $P < 0.001$; exclosure: $F_{1,102} = 18.79$, $P < 0.001$; site × exclosure: $F_{5,102} = 1.25$, $P = 0.165$; 2006 site: $F_{5,101} = 1.85$, $P = 0.111$; exclosure: $F_{1,101} = 11.85$, $P = 0.001$; site × exclosure: $F_{5,101} = 0.74$, $P = 0.597$).

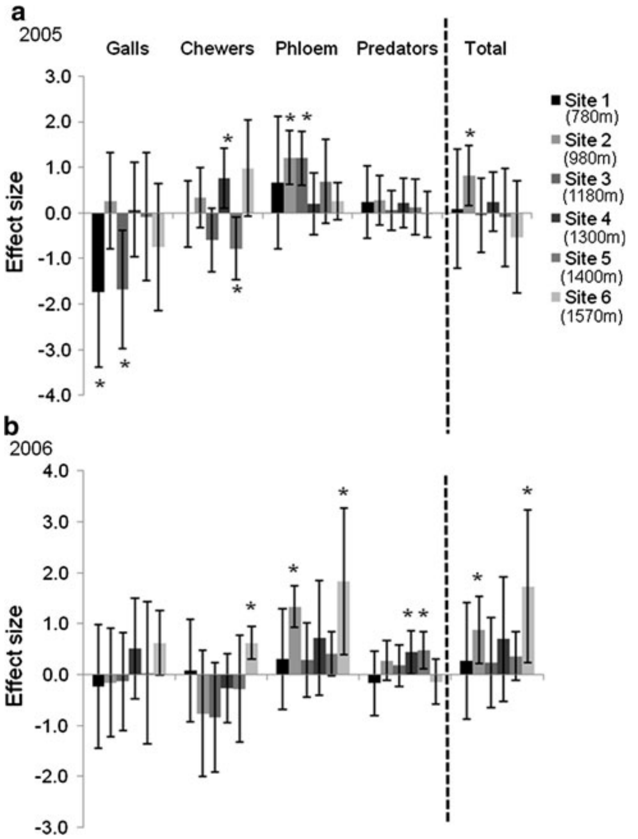

Fig. 3 Effect sizes ($\log_e$ ratio) of bird exclusion on red oak arthropods; arthropod values were averaged over four sampling dates in **a** 2005 and **b** 2006. Values of 0 indicate that arthropod density was equal on exclosure and control trees, positive values suggest that the exclosure had a positive effect on arthropod density, whereas a negative effect size indicates that the exclosure had an adverse impact on density. *Errors* represent 95% confidence intervals; an *asterisk* above or below *bars* indicates confidence intervals not overlapping zero

Tree growth

Sapling growth over 2 years varied among sites, with the largest increase in height at sites 1 and 4 [average sapling height increase (SE), site 1: 14.13 cm (2.96); site 2: 6.94 cm (4.34); site 3: 3.15 cm (2.22); site 4: 12.25 cm (2.91); site 5: 7.63 cm (2.92), 5.05 cm (2.88)]. The bird exclosures had no effect on tree growth (data not shown, site: $F_{5,101} = 2.78$, $P = 0.021$; exclosure: $F_{1,101} = 0.70$, $P = 0.404$; site × exclosure: $F_{5,101} = 1.31$, $P = 0.265$).

Sham exclosures

Sham exclosures exhibited the same defoliation levels as regular exclosures (i.e. lower levels than those on unprotected trees) which indicates that the exclosures likely protected trees from falling debris (Appendix Fig. 1; Site 1: exclosure: $F_{2,18} = 2.31$, $P = 0.128$; Site 4: $F_{2,22} = 4.45$, $P = 0.024$; Site 6: $F_{2,22} = 0.89$, $P = 0.427$). There was no difference among control, sham, or exclosure trees in the total number of leaf chewers, phloem feeders, gall formers or arthropod predators at any of the three sites (data not shown, $P > 0.05$ for all comparisons at all sites).

Discussion

Foliar nitrogen, bird predation pressure, and arthropod densities all varied along the elevation gradient in ways that did not necessarily conform to our original predictions. Foliar nitrogen content increased with increasing elevation and, while we predicted that bird predation pressure would increase in a similar fashion, our estimate of bird predation pressure was highly variable among sites with no clear influence of elevation on bird activity patterns. The responses of the arthropod community to these top-down and bottom-up effects were also highly variable among guilds and sites along the elevation gradient. However, while we predicted that arthropod guilds would be influenced by top-down and bottom-up factors acting at the site-level, our results suggest that arthropod densities were more highly variable within sites than among sites. This high level of within-site variation could confound detection of site-level top-down and bottom-up forces.

We found some evidence that top-down forces influenced arthropod density. Bird predation, as measured by the presence or absence of an exclosure, was an influential determinant of total arthropod density, mainly because of its influence on phloem feeders, which were the only guild to exhibit a response. However, we did not detect a bottom-up effect of foliar nitrogen on total arthropod density nor on any individual arthropod guild at the site-level. In addition, the influence of bird predation did not increase along the natural elevational gradient in foliar nitrogen concentrations, as we originally predicted it would based on both theoretical (Oksanen et al. 1981; Power 1992) and empirical research (Cornelissen and Stiling 2006; Denno et al. 2002; Forkner and Hunter 2000; Stiling and Moon 2005). We may have failed to detect a bottom-up effect, as well as any interaction between top-down and bottom-up forces, because of the amount of variation that existed among trees within sites in comparison to differences among sites. Local, small-scale variation in biotic and abiotic factors apparently had a larger influence on arthropod densities than did large-scale changes in elevation, foliar nitrogen levels, or bird densities. Within site variability in bird foraging patterns, plant species composition and plant density could all potentially impact arthropod densities and lead to the high degree of within site variation. It is also possible that that the measured

Table 2 Comparison of general linear mixed models relating predictors of interest to arthropod densities; the number of model parameters is in parentheses following each model

Model	Gall formers			Leaf chewers			Phloem feeders			Arthropod predators			Total arthropods		
	AICc	ΔAICc	AICc wt	AICc	ΔAICc	AICc wt	AICc	ΔAICc	AICc wt	AICc	ΔAICc	AICc wt	AICc	ΔAICc	AICc wt
Null (4)	2,972.1	1.2	0.26	**2,417.6**	**0**	**0.57**	2,924.8	24.7	0	**1,694.9**	**0**	**0.39**	2,746.2	10.6	0
Birds (5)	**2,970.9**	**0**	**0.47**	2,419.6	2	0.21	2,926.7	26.6	0	1,696.8	1.9	0.15	2,748.2	12.6	0
Nitrogen (5)	2,973.8	2.9	0.11	2,419.7	2.1	0.2	2,926.1	26	0	1,695.2	0.3	0.34	2,747.0	11.4	0
Exclosure (5)	2,976.0	5.1	0.04	2,425.5	7.9	0.01	**2,900.1**	**0**	**0.43**	1,699.3	4.4	0.04	2,736.5	0.9	0.22
Birds + Exclosure (6)	2,975.5	4.6	0.05	2,426.9	9.3	0.01	2,902.2	2.1	0.15	1,701.2	6.3	0.02	**2,735.6**	**0**	**0.34**
Nitrogen + Exclosure (6)	2,976.4	5.5	0.03	2,427.5	9.9	0	2,901.7	1.6	0.19	1,699.8	4.9	0.03	2,738.0	2.4	0.1
Nitrogen × Exclosure (7)	2,976.7	5.8	0.03	2,429.4	11.8	0	2,903.4	3.3	0.08	1,701.4	6.5	0.02	2,739.3	3.7	0.05
Birds × Exclosure (7)	2,977.0	6.1	0.02	2,427.1	9.5	0	2,902.2	2.1	0.15	1,701.6	6.7	0.01	2,736.0	0.4	0.28

Best fit models for each guild are highlighted in bold

range of foliar nitrogen may not have been large enough to influence insect herbivore numbers. Additionally, while foliar nitrogen is known to be important to insect herbivores it is not the only determinant of plant quality. Other aspects of plant quality, such as leaf toughness, nitrogen, phosphorus and carbon ratios, phenolic compounds, and other secondary compounds may influence herbivore performance (Lill and Marquis 2001; Rossiter 1988; Zehnder and Hunter 2009).

Bird exclosure experiment

We predicted that the insectivorous bird community at Coweeta would influence arthropod guilds based on their vulnerability to predation. This prediction held for the protected galls and the vulnerable phloem feeders. Phloem-feeding arthropods were extremely numerous on the experimental trees with bird predation reducing their densities on control trees (Fig. 3, Table 3). This result is consistent with previous work on oaks and ponderosa pines (*Pinus ponderosa*) that also reported significant effects of bird predation on aphids (Forkner and Hunter 2000; Mooney and Linhart 2006). Given the rapidity with which aphids reproduce, even a small difference in aphid density early in the season, caused by bird predation, may lead to a large difference in density over time.

Leaf chewers and arthropod predators represent a large proportion of the diet of the bird species that we detected at Coweeta, and lepidoptera larvae are widely considered to be the energetic currency upon which insectivorous songbirds rely for breeding (Greenberg 1995). However, protection from bird predation did not increase densities of these guilds. One possible explanation is that leaf chewer and arthropod predator densities, which were 10 times lower than those of phloem feeders, were too low in our study system for a top-down effect to be measurable.

Another possible explanation is that bird predation imposes both negative direct and positive indirect effects on some arthropod guilds via intraguild predation (Hunter 2009; Polis and Strong 1996). Birds commonly prey upon spiders and feed spiders to fledgling young (Gunnarsson 2007). When predators prey upon both herbivores and other predators, the reticulate food web of direct and indirect interactions may cause net predator effects to weaken before herbivore abundance and plant biomass are affected (Polis and Strong 1996). However, a recent meta-analysis examining interactions among predators found that, contrary to predictions, intraguild predation by birds may not weaken trophic cascades, and in systems where birds act as strong intraguild predators, they also strongly impact herbivorous arthropods (Mooney et al. 2010). In 2006, we did observe some weak positive effects of bird exclosure on arthropod predator densities at two sites

Table 3 Parameter estimates from the best fit model for each arthropod guild

	Galls		Leaf chewers		Phloem feeders		Predators		Total arthropods	
Predictor	Estimate	CI	Estimate	CI	Estimate	CI	Estimate	CI	Estimate	CI
Intercept	0.209	–0.783 to 1.201	0.899	0.736–1.062	2.774	2.288–3.260	1.317	1.192–1.442	3.046	2.466–3.626
Date20	0.369	0.146–0.592	–0.023	–0.190 to 0.144	–1.912	–2.122 to 1.702	–0.864	–0.976 to 0.752	–1.123	–1.317 to 0.929
Date50	0.362	0.139–0.585	0.040	–0.127 to 0.207	–1.296	–1.506 to 1.086	–0.20	–0.632 to 0.408	–0.728	–0.922 to 0.534
Date80	0.007	–0.216 to 0.230	–0.159	–0.326 to 0.008	–0.228	–0.438 to 0.018	–0.307	–0.419 to 0.195	–0.200	–0.394 to 0.006
Birds	0.224	–0.007 to 0.455	–	–	–	–	–	–	0.131	0.002–0.260
Exclosure	–	–	–	–	0.413	0.180–0.646	–	–	0.223	0.024–0.423

CI Confidence interval

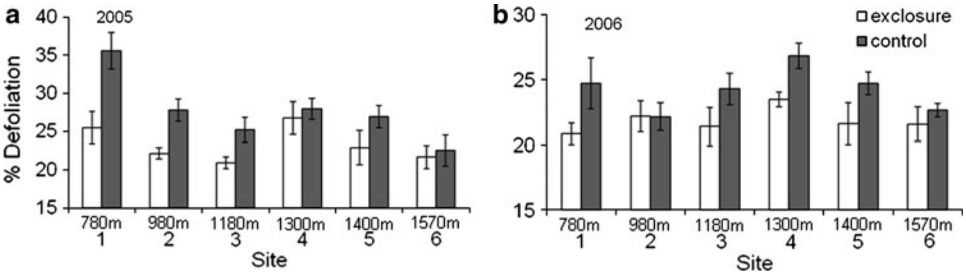

Fig. 4 Effects of bird predation and elevation on percent defoliation of *Q. rubra*. Elevation increases from site 1 to site 6. *Light grey bars* are the bird exclosure treatment and *dark grey bars* are the controls. Values are means of 10 trees ± 1SE

(Fig. 3), illustrating at least the potential for intraguild predation in our system.

Trophic cascades

Given that we did not find any effects of bird predation on leaf chewing insects, it is not surprising that we found no evidence for a trophic cascade measured either in terms of leaf damage or sapling growth. Although we measured relatively high levels of damage, this did not correlate with leaf chewer density. Rather, the sham cages indicated that much of the measured leaf damage was most likely caused by physical abiotic stressors such as branches that would fall and rip or tear off leaf pieces. The amount of damage imparted by falling debris was quite large, as indicated by the difference between sham and control trees. In fact, piles of branches and leaves were frequently found, and removed, from the exclosure tops after summer rainstorms (C.B.Z., personal observation). These observations and results suggest that field estimates of leaf damage in some forest systems may include unrecognized variation introduced by falling debris. We also note that the nearly threefold increase in phloem-feeder density that occurred in bird exclosures was insufficient to influence tree growth over the time period studied here. We tentatively suggest that the occurrence of trophic cascades may demand higher average herbivore production than we observed in our study system.

Conclusions

At our site in the southern Appalachians, foliar nitrogen levels increased with elevation. However, neither insect–herbivore densities nor bird densities followed this pattern. Bird predation reduced phloem feeder densities, but did not consistently affect other arthropod guilds and we found no evidence for an interaction between top-down and bottom-up forces influencing insect herbivore densities. For all arthropod guilds, within-site variation in density was much greater than among site variation. While we made comparisons among sites in space, we did not investigate issues of spatial scale per se. As in previous studies (Forkner and Hunter 2000; Lichtenberg and Lichtenberg 2002; Marquis and Whelan 1994; Van Bael and Brawn 2005), we used individual trees as units of observation and bird exclusion. Future research should consider explicitly how the relative strengths of bird predation and plant quality vary among spatial scales, from individual trees within sites to the stand level and beyond. Scaling up may provide an improvement in explanatory power that is currently lacking in our understanding of arthropod community structure on forest trees.

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