Effects of bird predation on arthropod abundance and tree growth across an elevational gradient

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Considerable uncertainty surrounds the conditions under which birds can cause trophic cascades. In a three-year experiment, we studied the direct and indirect effects of insectivorous birds on arthropod abundance, herbivory, and growth of striped maple *Acer pensylvanicum* saplings in a northern hardwood forest of central New Hampshire, USA. We manipulated bird predation by erecting exclosures around saplings and directly manipulated herbivory by removing herbivores. We also examined how climate modifies these interactions by replicating the experiment at three locations along an elevational gradient. Effects of bird predation were variable. Overall, mean arthropod biomass was 20% greater on saplings within bird exclosures than on controls (p<0.05). The mean biomass of leaf-chewing herbivores, primarily Lepidoptera larvae, was 25% greater within exclosures but not statistically different from controls. To a lesser degree, mean herbivore damage to foliage within exclosures exceeded that of controls but differences were not significant. We also did not detect significant treatment effects on sapling shoot growth. The high understory vegetation density relative to bird abundance, and low rate of herbivory during the study (mean 5% leaf area removed, controls), may have limited the ability of birds to affect sapling growth. Climate effects operated at multiple scales, resulting in a complex interplay of interactions within the food web. Regional synchrony of climatic conditions resulted in annual fluctuations in herbivore abundance and tree growth that were shared across elevations. At the same time, local environmental variation resulted in site differences in the plant, herbivore, and bird communities. These patterns resulted in a mosaic of top–down strengths across time and space, suggesting an overall pattern of limited effects of birds on plant growth, possibly interspersed with hotspots of trophic cascades.

An increase in the biomass of plants due to predator consumption or inhibition of herbivores is an example of a trophic cascade (Pace et al. 1999). The strength and prevalence of trophic cascades appear to vary widely across ecosystems, and much recent attention has been devoted to explaining this variation. A theme frequently emerging from reviews is that trophic cascades are less likely to occur in complex, species-rich terrestrial food webs, particularly when they are dominated by large, long-lived, nutrient-poor autotrophs such as trees (Polis and Strong 1996, Polis et al. 2000, Shurin et al. 2006). Indeed, a number of studies have failed to find a positive effect of predators on tree growth or biomass (Sipura 1999, Strong et al. 2000, Lichtenberg and Lichtenberg 2002, Gruner 2004). Nevertheless, trophic cascades have been reported from complex forested ecosystems (Marquis and Whelan 1994, Dyer and Letourneau 1999). Why trophic cascades occur in some forested settings, but are seemingly absent from others remains uncertain. One possible explanation is that trophic cascades occur in forested ecosystems only under particular environmental conditions that are simultaneously conducive to control of herbivores by predators and control of plants by herbivores. However, most trophic cascade

research in forests has been conducted at a single location, sometimes for only a single year, making it difficult to determine how trophic interactions are affected by variation in climate and other environmental factors. Recently, several studies from non-forested settings have found that annual variations in climate and seasonal fluctuations in weather can markedly alter trophic cascades (Boyer et al. 2003, Meserve et al. 2003, Ovadia and Schmitz 2004, Preisser and Strong 2004). Two studies in forests also examined climate effects upon predator-mediated top–down interactions by comparing effects across rainfall gradients (Mazia et al. 2004, Van Bael and Brawn 2005). Each study found that the strength of predation by birds and extent of herbivory were affected by climatic conditions; however, neither was designed to examine plant growth or biomass responses, and therefore whether trophic cascades were operating is unclear. Thus, the extent to which climatic variation accounts for disparate findings about trophic cascades in forests is not well understood.

To address these uncertainties, we studied how both temporal and spatial variation in environmental conditions affect trophic interactions at the Hubbard Brook Experimental Forest (HBEF), Woodstock, New Hampshire, USA.

We considered temporal variation by assessing abundance of insectivorous birds, biomass of both herbivorous and non-herbivorous arthropods, and growth responses of tree saplings over three years. We evaluated spatial variation by replicating the experiment at three sites spanning an elevational gradient of approximately 450 m a.s.l. In central NH, mean annual temperature decreases by approximately 0.6°C for every 100 m increase in elevation (Richardson et al. 2006). Vegetation phenology and composition also change along the elevational gradient: spring leaf-out is delayed approximately 2.7 days per 100 m elevation increase, and canopy height, aboveground biomass, and biomass production of the forest decrease (Whittaker et al. 1974, Richardson et al. 2006). Elevation also affects the abundance and distribution of both tree and bird species at HBEF (Doran 2003, Schwarz et al. 2003). We used this environmental gradient, coupled with experimental manipulation of bird and herbivore access to saplings, to address the following questions: 1) Do herbivorous insects affect rate of tree growth? 2) Do birds affect herbivore biomass and thereby affect tree growth? 3) How do trophic interactions change under different environmental conditions? We predicted that herbivore effects on tree growth would be positively correlated with herbivore abundance. We also predicted that birds would reduce herbivore biomass, and, that effects would be strongest where and when birds were most abundant relative to available foraging substrate. Finally, we predicted that the strength of the trophic cascade from birds to plants would vary due to climate-based influences on the food web, with climatic conditions that favored greater bird abundance relative to arthropod abundance leading to stronger effects on plant growth.

Methods

Study system

The HBEF is a forested valley in the central White Mountains of New Hampshire. We established three 4-ha plots to represent a range of environmental conditions: a low elevation (290–350 m a.s.l.), a mid-elevation (440–500 m a.s.l.) and a high elevation (740–780 m a.s.l.) plot. Plots were delineated into 25 × 25 m grids with flagging tape to facilitate mapping of bird territories. Consistent with patterns reported for the entire valley, sugar maple *Acer saccharum*, yellow birch *Betula alleghaniensis* and American beech *Fagus grandifolia* were abundant in the two lower elevation plots whereas red spruce *Picea rubens*, balsam fir *Abies balsamea*, and paper birch *Betula papyrifera* were found almost exclusively in the high elevation plot (Schwarz et al. 2003). Eastern hemlock *Tsuga canadensis* also occurred in patches in the low elevation plot, and white ash *Fraxinus americana* was relatively common in the low and mid-elevation plots.

We chose striped maple for study because it was a common understory species across the elevational gradient and had been observed to support a relatively high biomass of caterpillars at Hubbard Brook (Rodenhouse and Holmes 1992). Striped maple is a small tree that can persist as a sapling under a closed-forest canopy, and then rapidly grow to reproductive size in small canopy gaps such as those caused by tree-falls (Hibbs 1979, Hibbs et al. 1980). As in Virginia (Marquis and Passoa 1989), we found that striped maple supported a suite of generalist, leaf-chewing Lepidoptera larvae (caterpillars). Other herbivorous insects included Hymenoptera (sawfly) larvae, Coleoptera and Hemiptera. Birds that were potential predators of herbivorous insects on understory striped maple trees on the study plots included primarily ground-feeding species such as the ovenbird *Seiurus aurocapilla*, understory and sub-canopy foragers such as the black-throated blue warbler *Dendroica caerulescens*, and largely canopy feeders such as the red-eyed vireo *Vireo olivaceus* (Sabo 1980, Holmes 1986, Holmes and Robinson 1988). Collectively, these species consume arthropods from many taxa found on striped maple at HBEF, including leaf-chewing Lepidoptera (Robinson and Holmes 1982, Holmes and Robinson 1988).

Experimental design

At each of the three plots, we selected 45 naturally occurring striped maple saplings for inclusion in a randomized block split-plot design. Saplings ranged in height from 1.3 to 3.3 m and bore at least 20 buds at the inception of the experiment. Selection criteria were that: 1) saplings could be assigned to a block with two other saplings of similar size, form and growth condition, 2) saplings were ≥3 m apart, and 3) it was feasible to construct exclosures around saplings without excessive disturbance of surrounding vegetation. Following selection, we randomly assigned one tree in each block to bird exclusion treatment, herbivore removal treatment, or control, resulting in 15 blocks at each elevation. Treatments were applied from 2004 to 2006. The bird exclusion treatment consisted of an exclosure surrounding the sapling to prevent access by birds while permitting passage by insects. The rectangular frame of each exclosure was covered with translucent nylon monofilament netting (mesh size 3.8 × 3.8 cm) in April or May of each year, prior to leaf-out and arrival of most migratory birds. Netting was removed between late August and October each year to prevent damage to the netting and saplings from falling debris and winter buildup of snow. The herbivore removal treatment consisted of two components. First, saplings were sprayed regularly with spinosad, a biologically-derived insecticide. Second, after each arthropod survey all herbivores on leaves or bark were removed by hand.

Data collection

Arthropod surveys
Six to nine arthropod surveys were conducted each year from early June to late August. The numbers, lengths, and identity (order or family) of all arthropods ≥2 mm on the leaves, branches, and trunks of every tree were recorded, except for aerial insects briefly alighting on vegetation (e.g. adult dipterans and hymenopterans); those <2 mm in length were not recorded because they contributed little to overall arthropod biomass. Subsequently, we estimated the mass of each arthropod using published length-weight regressions specific to family or order (Sample et al. 1993, Gruner 2003). For analysis, we classified each arthropod into one of four categories based upon morphology, behavior, or published descriptions: 1) leaf-chewing herbivores, 2)

phloem-feeding herbivores, 3) carnivores, and 4) omnivores, detritivores, and other species resting on plant substrate for extended periods, such as adult moths.

Plant growth

For each tree we measured the growth of the shoot with the greatest length extension (the leader) to the nearest mm after conclusion of annual shoot production. In addition to experimental years 2004–2006, we obtained a baseline measurement for 2003 and a final measurement for 2007 based on the presumption that each year's growth depended at least in part on conditions and photosynthetic assimilation in previous years. We considered leader shoot growth to be an integrator of the overall performance of the plant (Sipe and Bazzaz 2001); annual growth typically was concentrated in one or a few shoots near the apex, with shoot growth being much smaller in lower, subordinate shoots. Measurements of leader shoot growth were also much more precise than measurements of tree height or stem diameter growth given the sprawling growth form and small diameter of the trees.

Magnitude of insect herbivory

The amount of annual herbivory by leaf-chewing insects was estimated based on the proportion of leaf area missing from a 10-leaf sample collected from each tree in September 2004, 2005 and 2006. Each leaf was placed under a transparent grid with grid-points spaced at 5 mm intervals, and the number of grid-points that either intersected actual leaf material or that were within the leaf margin but did not intersect leaf material was recorded. When large sections of leaf margin were missing, silhouettes of undamaged leaves were used to infer potential leaf margin and hence leaf area in the absence of herbivory. Percent herbivory for the entire tree was estimated by dividing the total count of missing-leaf grid-points by the total count of grid-points within the leaf margins.

Understory light availability

Because striped maple growth rate has been reported to be strongly influenced by light conditions (Wilson and Fischer 1977, Hibbs et al. 1980), we estimated light availability for each tree based on methods of Messier and Puttonen (1995) and Parent and Messier (1996). Light availability was used as a covariate in shoot growth analyses. On an overcast day with the sun's disk fully obscured, we used a hand-held LI-190SB quantum sensor to measure photosynthetic photon flux density (PPFD) reaching each tree. Simultaneously, we used a LI-COR quantum sensor fixed on a tripod in the nearest open area to estimate PPFD above the canopy. Mean %PPFD for each tree was calculated by dividing understory PPFD by the open sky PPFD corresponding to that time. Measurements were taken between 21 July and 2 September 2006. Although minor changes in the canopy occurred near some trees during the three years of the study, we assumed that the percent light transmission estimates we obtained were reasonably representative of growing conditions during the study (Messier and Puttonen 1995, Comeau et al. 1998).

Bird abundance

We mapped bird territories on each study plot as a basis for comparing the potential intensity of bird predation on arthropods across years and elevations. During the peak nesting season (June to early July), weekly surveys of all bird species that prey upon foliage-feeding herbivores were conducted by two to three observers who thoroughly traversed each plot for several h. The locations of birds observed (by sight or sound) were mapped, with particular emphasis on recording territorial interactions. From these data, we calculated the total number of territories/species, including partial territories that straddled plot boundaries. Species that were observed on occasion but insufficiently for defining territory boundaries were assigned a value of 0.1 territories.

Index of bird foraging intensity

To compare the plot-level likelihood across years and elevation that subject trees would be used by birds for foraging, and to examine whether this likelihood was related to the observed magnitude of bird predation, we constructed an index of bird foraging intensity. The index yielded a single value indicative of potential predation pressure on understory trees by the entire bird community. For each plot j (low, mid- and high elevation) and year k (2004–2006), the index was expressed as equivalents of territories of the black-throated blue warbler (BTBW), the species anticipated to forage the most in the height range of study trees (0.5 to 3.0 m):

$$\text{BTBW equiv}_{j,\,k} = \sum_{i=1}^{n} \frac{F_i}{F_{BTBW}} * \frac{L_{mid}}{L_j} * \frac{V_{mid}}{V_j} * T_{ijk}$$

for foliage-gleaning bird species $i = 1$ to n, where F_i = the estimated proportion of foraging effort from 0.5 to 3.0 m for species i, L_j = the leaf area index for plot j (applied only to species foraging at least partly in the canopy; Table 1), V_j = vegetation density in the understory of plot j, and T_{ijk} = the number of territories for species i in plot j and year k. Published analyses of bird foraging behavior at Hubbard Brook and elsewhere in the White Mountains (Holmes 1986, Holmes and Robinson 1988, Sabo 1980, Steele 1993, Holmes et al. 1978, Holmes et al. 1979a) were used to estimate F (Table 1). We calculated L using plot-averaged %PPFD data described previously (Bréda 2003) and calculated V based on counts of woody shrubs and saplings >0.5 m in height in 40 randomly located 1-m^2 quadrats in each plot. L and V were included based on the premise that a greater foliage density would decrease the likelihood of foraging on control trees.

Statistical analysis

Arthropod, herbivory, and shoot growth response variables were analyzed separately using generalized linear mixed models for repeated measures (PROC GLIMMIX, SAS Inst. 2006). Experimental treatment, elevation and year were fixed factors (predictor variables). Blocks and individual subject trees were random effects. Information criteria (AIC_c values) were used to select a covariance structure for

Table 1. Insectivorous bird species with appreciable use of understory shrubs and saplings for foraging, the number of territories on each 4 ha experimental study plot, and number of territories expressed as 'black-throated blue warbler (BTBW) equivalents' from 2004–2006 at HBEF. For a given species, BTBW equivalents are the % foraging in the 0.5–3.0 m zone for each species divided by the percent foraging by the BTBW, the species that spends the most time foraging there. Total BTBW equivalent territories for the low and high elevation plots also reflect adjustments for vegetation density relative to the mid-elevation plot. The dense understory of the high elevation plot resulted in a reduction in estimated BTBW equivalent territories relative to the other plots. Species that were observed on occasion but for which plot usage could not be quantified were assigned a value of 0.1 territories. "—" denotes species that were absent from the plot in that year. Understory foraging predicted based on the following behavioral analyses: [a]Sabo (1980), [b]Holmes (1986), [c]Holmes et al. (1979a), [d]Holmes and Robinson (1988), [e]Steele (1993), [f]Holmes et al. (1978). [g]Species presumed to feed exclusively on the ground or in the understory.

Species	0.5–3.0 m	Number of territories								
		Low elevation			Mid-elevation			High elevation		
	Foraging (%)	2004	2005	2006	2004	2005	2006	2004	2005	2006
Blue-headed vireo *Vireo solitarius*	5[a]	0.5	0.5	0.5	—	—	—	0.5	1	0.5
Red-eyed vireo *V. olivaceus*	5[b]	2	2.5	2	2	3	3	0.1	0.1	0.5
Black-capped chickadee *Poecile atricapillus*	5[c]	0.5	1	0.5	0.1	0.1	0.25	0.5	1	0.5
Winter wren *Troglodytes troglodytes*[g]	30[a,d]	0.5	0.5	0.5	0.5	0.1	0.1	1	1	0.5
Veery *Catharus fuscescens*[g]	25[d]	—	—	0.1	2	1	1	—	—	—
Swainson's thrush *C. ustulatus*[g]	25[a,d]	0.1	0.5	0.1	—	—	—	1	0.5	1
Hermit thrush *C. guttatus*[g]	25[d]	1	1	0.5	0.5	0.5	0.5	—	—	—
Nashville warbler *Vermivora ruficapilla*	20[a]	—	—	—	—	—	—	0.25	0.1	—
Magnolia warbler *Dendroica magnolia*	15[a]	—	—	—	—	—	—	0.1	—	0.5
Black-throated blue warbler *D. caerulescens*	35[b,e]	0.1	1.5	1	0.1	1.5	1.5	2	1.5	1.5
Yellow-rumped warbler *D. coronata*	15[a]	—	—	—	—	—	—	0.5	0.25	0.5
Black-throated green warbler *D. virens*	5[a,b]	1	2	1	2	2.5	2	3.5	2	2
American redstart *Setophaga ruticilla*	25[a,b,f]	—	—	—	0.5	1	1.5	—	—	—
Ovenbird *Seiurus aurocapilla*[g]	10[d]	1	2	2	2	3	3	1	0.5	0.5
Canada warbler *Wilsonia canadensis*	30[a]	—	—	—	—	—	—	0.5	1	1
Rose-breasted grosbeak *Pheucticus ludovicianus*	10[b]	—	—	—	—	0.25	0.5	—	—	—
Scarlet tanager *Piranga olivacea*	5[b]	0.5	0.5	0.5	0.1	0.5	0.25	—	—	—
Dark-eyed junco *Junco hyemalis*[g]	25[a,d]	—	—	—	—	—	—	0.1	0.1	0.25
Total number of territories		7.2	12	8.7	9.8	13.5	13.6	11.1	9.1	9.3
Index of potential predation pressure:										
Total number of BTBW equivalent territories		3.1	6.0	4.2	3.8	5.2	5.5	1.7	1.4	1.5

the repeated measures and to determine whether to retain random blocks in each model (Littell et al. 2006). Arthropod response variables were mean annual biomass (total and by feeding guild) per 100 leaves for each tree calculated using all the surveys per year. Baseline (2003) shoot growth and percent transmittance of light (both log-transformed) were covariates in shoot growth models. Pre-planned differences of least square means were used to compute effect sizes and compare mean responses. To ensure that model residuals met assumptions of normality and homogeneity of variances, arthropod and shoot growth response models were fit with a lognormal error distribution and an arcsine cube root transformation was applied to percentage of leaf area missing.

Results

Arthropod responses

Taxa recorded
Leaf-chewing herbivores dominated arthropod biomass, constituting 30% to nearly 90% of the biomass recorded on control and exclosure trees; biomass of carnivores and other non-herbivores each ranged from about 5–35% of total biomass per plot, while phloem-feeders comprised a minor percentage of total biomass (Fig. 1). Free-living geometrid and noctuid caterpillars were the most abundant leaf-chewers. Virtually all caterpillars and sawfly larvae lacked spines, hairs, or warning coloration, and we presume that they were highly palatable to birds. Leaf-chewing curculionids and chrysomelids also were relatively common, though the latter family was observed only on the high elevation plot. Phloem-feeders consisted primarily of small aphids, leafhoppers, and treehoppers. Most carnivores were small (2–5 mm), web-building spiders that we believe primarily preyed upon small flying insects and rarely captured leaf-chewing insects. The spined soldier bug *Podisus maculiventris* was a far less common carnivore, but we observed it feeding upon caterpillars on multiple occasions. Syrphid and neuropteran larvae were uncommon predators occasionally observed feeding upon caterpillars. Among other (not herbivorous or carnivorous) arthropods, psocopteran nymphs and adults were common, but because of their small size they probably were not preferred by insectivorous birds. Non-leaf-chewing beetles were also common; moths and ants were recorded occasionally.

Treatment effects
The effects of the herbivore removal treatment were strong and consistent; the effects of the exclosure treatment were less uniform (Fig. 1; treatment effect on herbivores $F_{2,126} = 65.2$, $p < 0.001$). Herbivore biomass was consistently much lower on herbivore removal trees than control ($t = 9.2$, $p < 0.001$) or bird exclosure trees ($t = 10.4$, $p < 0.001$). Overall, total arthropod biomass was significantly greater on exclosure trees than control trees (Table 2). Average biomass was approximately 20% greater on exclosure trees than on control trees (17.1 mg/100 leaves vs 14.2 mg/100 leaves, based on back-transformation of modeled biomass). Herbivore biomass, which accounted for the majority of arthropod biomass, was also greater on
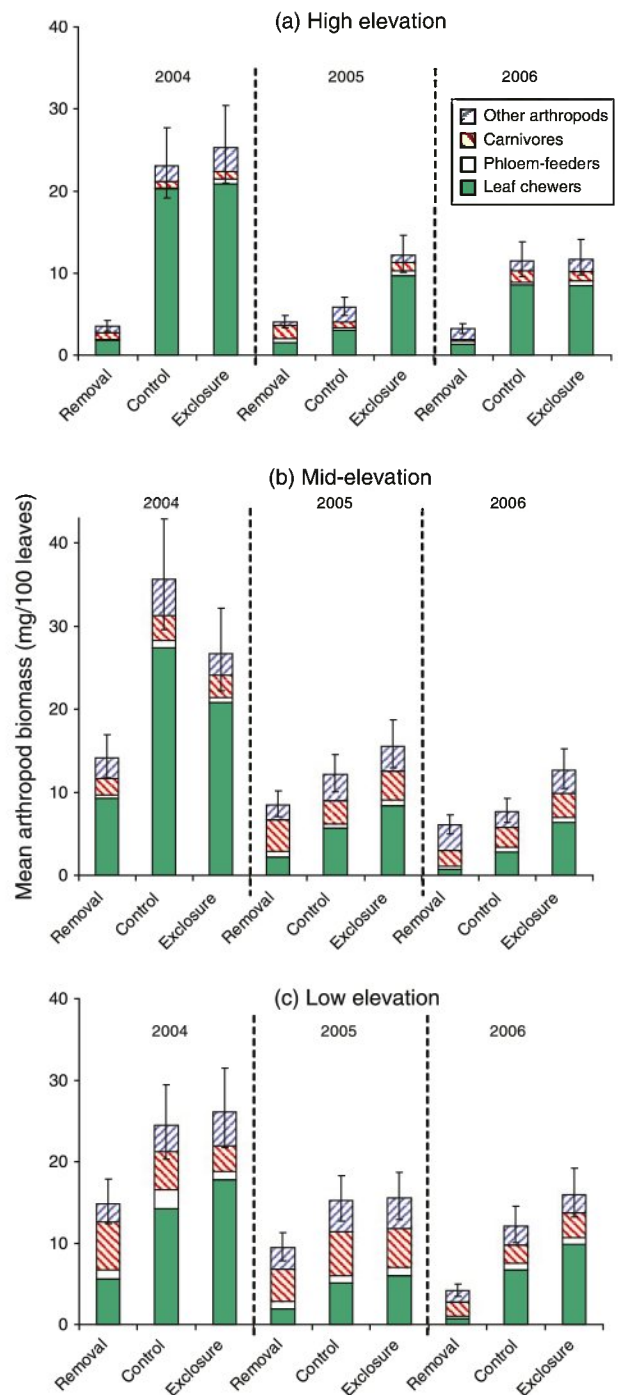

Figure 1. Arthropod biomass by feeding guild, at HBEF for striped maple saplings, 2004–2006 (geometric mean ± SE total arthropod biomass) on a) high, b) mid- and c) low elevation plots.

exclosure trees on average, though not statistically significant (Table 2). Although exclosure effects were not completely consistent across plots or years (Fig. 1), biomass of all arthropod categories tended to be greater inside exclosures (Fig. 2).

Year effects
Year strongly influenced the magnitude of arthropod biomass on control and bird exclosure trees (Table 2, Fig. 1).

Table 2. Generalized linear mixed model results for the effects of bird exclosure treatment, elevation, and year on a) total herbivore biomass and b) total arthropod biomass (In(mg)/100 leaves) on striped maple saplings at 3 elevations (~300, 500, and 750 m a.s.l.) at Hubbard Brook Experimental Forest (HBEF), NH, 2004–2006. Estimate represents the mean for the first fixed effect minus the mean for the second fixed effect. This analysis does not include the herbivore removal treatment. Bold denotes $p<0.05$. DF = 84 for exclosure and elevation comparisons, 168 for year comparisons, 241.6 for herbivore treatment×year comparisons, 248.6 for total biomass treatment×year comparisons (Kenward–Roger DF approximations).

Fixed effect 1	Fixed effect 2	a) Total herbivore biomass			b) Total arthropod biomass		
		Estimate ± SE	t	p	Estimate ± SE	t	p
Bird exclosure	Control	0.209 ± 0.129	1.6	0.109	0.185 ± 0.086	2.2	**0.033**
Exclosure 2004	Control 2004	-0.074 ± 0.196	-0.4	0.707	-0.043 ± 0.137	-0.3	0.751
Exclosure 2005	Control 2005	0.491 ± 0.196	2.5	**0.013**	0.333 ± 0.137	2.4	**0.015**
Exclosure 2006	Control 2006	0.209 ± 0.196	1.1	0.288	0.264 ± 0.137	1.9	0.054
Mid-elev.	Low elev.	-0.012 ± 0.158	-0.1	0.941	-0.085 ± 0.104	-0.8	0.412
High elev.	Low elev.	0.181 ± 0.158	1.2	0.254	-0.274 ± 0.104	-2.6	**0.010**
High elev.	Mid-elev.	0.193 ± 0.158	1.2	0.225	-0.190 ± 0.104	-1.8	0.072
2004	2005	1.154 ± 0.128	9.0	**<0.001**	0.785 ± 0.092	8.5	**<0.001**
2004	2006	1.124 ± 0.128	8.8	**<0.001**	0.824 ± 0.092	8.9	**<0.001**
2005	2006	-0.030 ± 0.128	-0.2	0.816	0.039 ± 0.092	0.4	0.675

Herbivore and total arthropod biomass per 100 leaves were greatest in 2004 across elevations and treatments, largely due to an abundance of geometrid and noctuid caterpillars. Carnivore biomass was significantly greater in 2005 than 2004 (t = 3.7, p < 0.001) or 2006 (t = 2.2, p = 0.027). Biomass of other non-herbivorous arthropods was significantly greater in 2004 than 2006 (t = 2.6, p = 0.012), with biomass intermediate in 2005.

Elevation effects

Arthropods varied in their responses to elevation. Carnivores (particularly spiders) and other non-herbivorous arthropods were significantly less abundant at the high elevation than the other plots (Fig. 1; elevation effect for carnivores $F_{2,84} = 58.1$, p < 0.001, for other arthropods $F_{2,84} = 21.9$, p < 0.001). Caterpillar biomass was greatest at the mid-elevation during 2004 and 2005 but lowest in
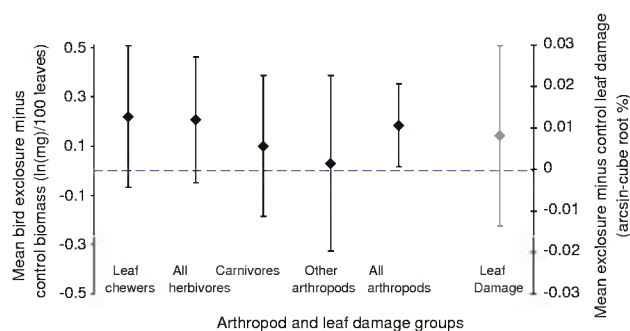

Figure 2. Summary of the differences in arthropod biomass and leaf damage between bird exclosure treatments and controls for striped maple saplings at three elevations from 2004–2006 at HBEF. Diamonds represent the mean difference between exclosure and controls for responses, thick bars represent 90% confidence intervals for each response, and thin bars represent 95% confidence intervals. 'All herbivores' includes leaf-chewing herbivores + phloem-feeding herbivores. 'Other arthropods' includes detritivores, omnivores, and other species that are not primarily herbivores or carnivores. Horizontal dashed line denotes no difference between treatments. Total arthropod biomass was significantly greater on exclosure trees; other responses were greater for exclosure trees but not statistically significant based on 95% confidence intervals.

2006, a pattern reflected in herbivore and total arthropod biomass (Fig. 1; elevation × year interaction for herbivores $F_{4,168} = 5.2$, p < 0.001, for total biomass $F_{4,168} = 3.4$, p = 0.010). Despite relatively high herbivore biomass at the high elevation, the reduced biomass of carnivores and other arthropods meant that overall arthropod biomass was significantly less than in the low elevation plot (t = 2.6, p = 0.010) and contributed to a significant elevation effect on total arthropod biomass ($F_{2,84} = 3.6$, p = 0.031).

Leaf damage

Herbivore consumption of leaves, as measured by percent of leaf area missing per tree (Fig. 3), was positively correlated with the biomass of leaf-chewing insects (Fig. 1) over years and treatments (r = 0.67, p < 0.001). Herbivore damage was greatest in 2004 (year effect $F_{2,244} = 174$, p < 0.001), and damage switched from being highest at the mid-elevation in 2004 to lowest there in 2006. Removal trees experienced significantly less damage than trees in the other treatments (Fig. 3; vs controls t = 8.3, p < 0.001, vs exclosure trees t = 9.1, p < 0.001). Overall, mean herbivore damage on exclosure and control trees were not statistically distinguishable (Fig. 2; t = 0.7, p = 0.49), but the magnitude of damage was somewhat greater on exclosure trees (5.5% vs 5.2%, based on back-transformed mean values). Damage was also greater on low and mid-elevation exclosure trees than controls.

Shoot growth responses

Light availability was positively correlated with shoot growth both within and across plots (r = 0.62, p < 0.001 across all plots in 2007). Light availability increased with elevation (mean %PPFD low elevation 1.4 ± 0.09, mid-elevation 3.9 ± 0.3, high elevation 6.9 ± 0.7); after controlling for light availability and baseline growth, shoot growth did not differ significantly by elevation ($F_{2,127} = 0.4$, p = 0.70). Shoot growth was not significantly affected by either bird exclosure or herbivore removal, contrary to our predictions (Fig. 4; $F_{2,123} = 0.08$, p = 0.92). As in the
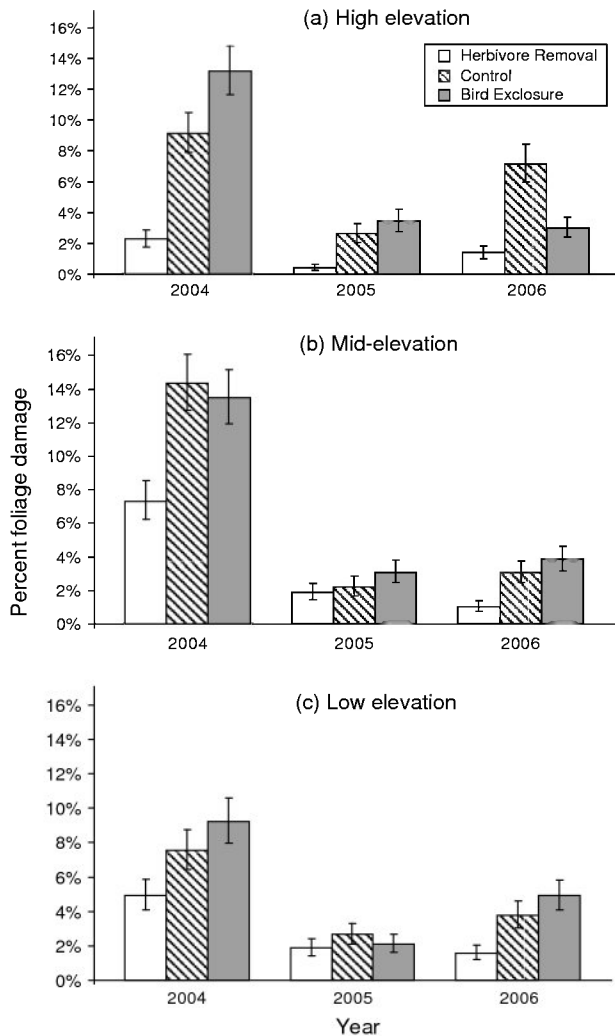
Figure 3. Foliage damage (mean ± SE) on striped maple saplings, 2004–2006 at HBEF on a) high, b) mid- and c) low elevation plots. Damage was significantly greater in 2004 than 2005 and 2006 (p < 0.001) for all three elevations. For the three years, damage was significantly less on herbivore removal trees than control trees and exclosure trees at each elevation (p < 0.05). Control and bird exclosure trees were not significantly different from each other at any elevation, averaged across the three years.

case of arthropod biomass, year had a large effect on shoot growth ($F_{2,120}$ = 5.4, p = 0.002). Growth was substantially less in 2005 and 2006 than in 2004, the same pattern apparent for arthropod biomass; growth rebounded in 2007 (Fig. 4).

Bird abundance and index of bird foraging intensity

Eighteen species of insectivorous birds that were likely to spend appreciable time foraging on striped maple saplings were documented on the study plots (Table 1). Six maintained territories across the elevational gradient (e.g. black-throated blue warbler); five were present only on the low and mid-elevation plots (e.g. scarlet tanager); four were restricted to the high elevation plot, which had substantial numbers of spruce and fir trees (e.g. magnolia warbler); and two occupied both the high elevation plot
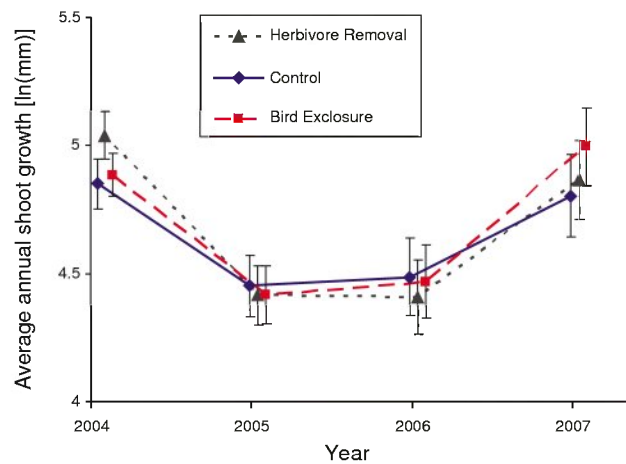

Figure 4. Annual growth of the leading shoot (mean ± SE) by treatment for striped maples at HBEF, 2004–2007. Treatment categories are offset on the x-axis for clarity. Pre-treatment growth was recorded for 2003; experimental treatments were applied in 2004, 2005 and 2006. Overall, treatments were not significantly different based on mixed models for repeated measures.

and areas with hemlocks on the low elevation plot (blue-headed vireo and Swainson's thrush). The net result was a similar number of species present at each elevation, generally from 9 to 11 per year.

Expressed as BTBW-equivalent territories, adjusted for vegetation density (Table 1), the expected foraging pressure on study trees was quite different than suggested by a raw tally of the number of bird territories. Our estimates of L (leaf area index) were 8.5, 6.5 and 5.1 and V (understory vegetation) were 0.6 ± 0.2 (SE) stems m^{-2}, 0.9 ± 0.2 stems m^{-2}, and 3.5 ± 0.5 stems m^{-2} in the low, mid- and high elevation plots, respectively. The high elevation plot was estimated to have the least foraging intensity due to the high density of woody stems, particularly hobblebush *Viburnum alnifolium*. Canopy density decreased with elevation, partially offsetting the increase in shrub density. The greater density of foraging birds in the understory at the mid-elevation was counter-balanced by the lesser stem density in the low elevation, resulting in similar estimates of predation pressure.

Plot-averaged differences in arthropod biomass between bird exclosure and control trees were not related to estimated intensity of bird predation, contrary to our predictions (linear regression, $R^2 < 0.01$, n = 9 plot-year observations, p = 0.83). Neither years nor plots with high intensity of insectivorous bird foraging showed consistent evidence of greater effects of bird exclosure treatment on arthropod biomass (Table 1, Fig. 1). No clear differences in the effects of birds on arthropods were apparent between the high arthropod biomass year, 2004 and 2005–2006 (Fig. 1).

Discussion

Bird abundance and effects on arthropods

The species identities and abundance of birds differed considerably across elevation and years, and at least part of

this variation can be attributed to direct and indirect effects of climate. In particular, the dense understory and increasing prevalence of conifers at the high elevation plot, reflecting the environmental gradient, likely attracted some species (such as magnolia and Canada warblers) while deterring others (such as veery). Within a plot, the species present were consistent from year to year, but the total number of territories fluctuated considerably. These annual fluctuations could be due to both changes in population sizes as well as broad-scale settlement patterns of returning migrants across the HBEF.

The measured strength of the bird exclosure treatment on arthropods also differed annually and across elevations, but contrary to our predictions this variation was not clearly related to bird abundance, arthropod abundance or climatic effects. The range of variability, however, is informative about the capacity of birds to control biomass of their prey in this system. Arthropod abundance was greater on exclosure trees than controls in all but one of the nine year-elevation combinations, with the estimated annual amount of biomass removed from controls ranging from 2–52%. A 1978–1979 study of bird foraging on striped maple foliage at Hubbard Brook, conducted at a time of somewhat lower arthropod abundance but greater bird density, found that birds removed an even greater percentage of the standing crop of Lepidoptera larvae (Holmes et al. 1979b, Holmes 1990). Several formerly common insectivorous bird species that prefer earlier successional forest stages, such as least flycatcher *Empidonax minimus* and Philadelphia vireo *Vireo philadelphicus*, have disappeared from the study plots since the initial study (Holmes and Sherry 2001). Considering other forested systems, birds frequently reduced herbivore abundance but the magnitude of bird effects has been found to vary considerably (Marquis and Whelan 1994, Strong et al. 2000, Lichtenberg and Lichtenberg 2002, Van Bael et al. 2008).

An analysis of bird abundance relative to available foraging sites provides further evidence that birds were limited in their ability to deplete arthropod biomass during the study. For example, we estimated that the high elevation plot encompassed the foraging equivalent of about 5 black-throated blue warbler territories per year, not adjusting for vegetation. We also estimated that this 4 ha plot contained 141 000 woody stems > 0.5 m tall (all species), including 3000 striped maples. This large volume of vegetation relative to bird abundance suggests a low probability that any particular striped maple tree would be visited during a given 2-week sampling interval. Many avian tritrophic experiments have not been designed to quantify the abundance or identity of predators, in marked contrast to experiments involving arthropod predators (Ovadia and Schmitz 2004, Finke and Denno 2006). We recommend that future tri-trophic studies seek to quantify bird predation pressure as a basis for understanding the variability in the effects of forest birds on arthropods and plants.

Variation in arthropod abundance

As in the case of the bird community, we observed both similarities and differences among the arthropod community across the elevational gradient. One of the most notable differences was the species composition of the herbivore community. Leaf-chewing weevils were observed only at the lower two elevation plots, and leaf-chewing chrysomelid beetles were observed only at the highest elevation. However, we observed considerable elevational synchrony in both species composition and abundance among leaf-chewing larvae. Herbivore biomass was substantially greater in 2004 than in 2005 and 2006 at all elevations. The synchrony was consistent with large-scale, regional patterns in leaf-chewer abundance on multiple plant species that have been observed across a 400 km^2 area of central NH that may reflect regional climatic conditions (Jones et al. 2003, Reynolds et al. 2007). More localized variations in temperature and other environmental factors may explain the elevational differences in herbivore abundance that we observed, which generally were smaller in magnitude than the annual differences.

Effects of birds and herbivores on tree growth

We did not document trophic cascades due to bird predatory effects in our study. Two findings appear to explain this observation: 1) birds exerted only moderate effect on herbivores, even though herbivorous insects are a major component of their diet, and 2) herbivores usually caused only moderate damage to plants even in the absence of birds. These findings are at odds with early food-chain theories that proposed predator control of herbivores was largely responsible for observed plant productivity in systems with three trophic levels (Hairston et al. 1960, Oksanen et al. 1981). They are, however, consistent with more recent arguments that many factors other than predation determine the production and distribution of plant biomass, and that trophic cascades are unusual in complex terrestrial food webs (Polis and Strong 1996, Polis 1999, Shurin et al. 2006).

Why were birds not able to exert stronger control over herbivore biomass? One factor may be that the vast majority of herbivores were cryptic in appearance and engaged in behaviors that reduced the risk of being captured, such as clinging to leaf midribs (Heinrich 1993). As noted previously, another possible factor was that bird density was insufficient relative to available foraging substrate. This explanation, however, begs the question of why bird density was not greater in the first place. Previous work at Hubbard Brook has demonstrated that insectivorous bird density is regulated by multiple mechanisms, one of which is food availability (Rodenhouse et al. 2003). Combining these two factors suggests a scenario whereby the complex architecture of branches and foliage of forest trees provide sufficient refugia for small, cryptic herbivores to impede avian foraging efficiency. Consequently, appreciable numbers of herbivores escape predation.

If substantial numbers of herbivorous insects avoid predation by birds, then why were we unable to find stronger evidence that they limit tree growth? The reason appears to be that herbivore biomass and the extent of herbivory were relatively modest compared to what has been reported in experiments with bird-precipitated trophic cascades. During 2005 and 2006, all but one plot averaged less than 5% leaf area missing per tree, even within

exclosures. Plot herbivory means in 2004 ranged from about 7–14%, not including removal trees, reflecting the greater abundance of Lepidoptera larvae in that year. By contrast, Marquis and Whelan (1994) estimated that leaf-chewing herbivores on exclosure trees removed over 25% of foliage. Our findings are more similar to studies that have not found significant effects of birds on herbivore damage (Forkner and Hunter 2000, Low and Connor 2003).

Even though we did not detect trophic cascades, several sources of information allow us to draw inferences about the conditions that would be necessary for trophic cascades to occur in our system. We have examined the relationship between herbivore biomass and striped maple growth responses through correlations between shoot growth and leaf chewer biomass in the previous year (without regard to experimental treatment); correlations between shoot growth and the extent of leaf damage in the prior year; correlations between leaf chewer biomass and leaf damage; and a separate experimental study of the effect of simulated herbivory on sapling growth (Schwenk 2008). Collectively, these analyses suggest each increment of about 30–40 mg (per 100 leaves) additional leaf-chewer biomass, equivalent to one large caterpillar present for the entire season, could cause a 10% reduction in sapling growth in the subsequent growing season. Mean leaf-chewer biomass reached 30 mg/100 leaves on only a few exclosure trees in 2005 and 2006, implying that strong trophic cascades would be unlikely in those years. However, nearly one-third of exclosure trees exceeded this level in 2004. In such cases, concentrated foraging on selected saplings with high leaf-chewer biomass could readily result in removal of greater than 30 mg/100 leaves, though birds do not remove this amount of biomass across an entire plot. Thus, if bird-mediated trophic cascades occurred during the years of our study, they may have been confined to small areas or individual saplings where bird foraging removed relatively large herbivore loads.

Other climate-related effects on tree growth

Like arthropod biomass, tree growth varied both with elevation and year. Considering elevation, we expected to find reduced annual growth at higher elevation plots because cooler temperatures delay leaf emergence and shorten the growing season. We observed the opposite pattern, however, because light gaps and decreased canopy cover enhanced striped maple sapling growth, more than offsetting potential temperature effects. Canopy disturbance may have been due to combined effects of greater wind speeds and colder temperatures.

Considering temporal effect, we also observed substantial annual changes in striped maple shoot growth that were synchronized across elevations, with growth in 2004 and 2007 much greater than in the intervening years. Because these changes do not appear to be due to herbivore activity, we believe that shared climatic conditions are the most plausible explanation. The pattern of precipitation during the previous year's growing season parallel's shoot growth changes, according to meteorological data collected by HBEF scientists, and could be a mechanism responsible for the growth variability we observed (Tardif et al. 2001).

Conclusions

We found that the interactions among insectivorous birds, herbivorous insects and an understory tree species reflect a complex interplay of regional climatic synchrony and local environmental gradients that lead to myriad direct and indirect responses among this community. Regional synchronization of ecological processes, mediated by climate, may encompass tree growth rates, herbivore populations, and insectivorous birds that feed on the herbivores (Jones et al. 2003). Local conditions modify broad regional trends, affecting the identity, abundance, and interactions of plants and animals that are present. This complexity points to the difficulty in predicting future trends, such as those that could be imposed by changing climatic conditions. At the time of our study, herbivore biomass and tree growth did not appear to be tightly coupled to bird predation in this system. However, the capacity of individual components to fluctuate out of sequence with each other suggests that under the right confluence of circumstances involving localized high bird abundance and plant vulnerability to herbivory, birds might significantly affect plant biomass production. Dependence of trophic cascades upon particular climatic circumstances has been previously demonstrated in a system involving arthropod predators (Ovadia and Schmitz 2004). If such patterns apply to birds, the system could be conceived of as featuring a mosaic of top–down strengths across time and space, with an overall pattern of limited top–down control, possibly interspersed with hotspots of trophic cascades. This could also reconcile the inconsistent findings among other studies of top–down effects of birds on herbivores and plants. Long-term studies that include estimates of both the abundance of the predator community and potential predation pressure should further elucidate the strength and variability of tri-trophic interactions. Study of additional tree species could also enhance understanding of community-level trophic interactions, given that tree species differ in the abundance of arthropod species they support and the opportunities for avian foraging that they provide (Holmes and Schultz 1988).

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