

Contrasting cascades: insectivorous birds increase pine but not parasitic mistletoe growth

KAILEN A. MOONEY* and YAN B. LINHART

University of Colorado, Department Ecology and Evolutionary Biology, Boulder, CO 80309-0334, USA

Summary

1. Intraguild predation occurs when top predators feed upon both intermediate predators and herbivores. Intraguild predators may thus have little net impact on herbivore abundance. Variation among communities in the strength of trophic cascades (the indirect effects of predators on plants) may be due to differing frequencies of intraguild predation. Less is known about the influence of variation within communities in predator–predator interactions upon trophic cascade strength.

2. We compared the effects of a single predator community between two sympatric plants and two herbivore guilds. We excluded insectivorous birds with cages from ponderosa pine *Pinus ponderosa* trees parasitized by dwarf mistletoe *Arceuthobium vaginatum*. For 3 years we monitored caged and control trees for predatory arthropods that moved between the two plants, foliage-feeding caterpillars and sap-feeding hemipterans that were host-specific, and plant damage and growth.

3. Excluding birds increased the abundance of ant-tended aphids on pine and resulted in an 11% reduction in pine woody growth. Mutualist ants protected pine-feeding aphids from predatory arthropods, allowing aphid populations to burgeon in cages even though predatory arthropods also increased in cages. By protecting pine-feeding aphids from predatory arthropods but not birds, mutualist ants created a three-tiered linear food chain where bird effects cascaded to pine growth via aphids.

4. In contrast to the results for tended aphids on pine, bird exclusion had no net effects on untended pine herbivores, the proportion of pine foliage damaged by pine-feeding caterpillars, or the proportion of mistletoe plants damaged by mistletoe-feeding caterpillars. These results suggest that arthropod predators, which were more abundant in cages as compared with control trees, compensated for bird predation of untended pine and mistletoe herbivores.

5. These contrasting effects of bird exclusion support food web theory: where birds were connected to pine by a linear food chain, a trophic cascade occurred. Where birds fed as intraguild predators, the reticulate food webs linking birds to pine and mistletoe resulted in no net effects on herbivores or plant biomass. Our study shows that this variation in food web structure occurred between sympatric plants and within plants between differing herbivore guilds.

Key-words: bird exclusion, community ecology, effect size, food web structure, indirect effect, intraguild predation, predator exclusion, top-down, tri-trophic interaction

Journal of Animal Ecology (2006) **75**, 350–357

doi: 10.1111/j.1365-2656.2006.01054.x

Introduction

The long-standing debate over whether terrestrial plants are protected from herbivores by predators has now

progressed to the task of determining when and where top-down control is likely to be important (Matson & Hunter 1992; Schmitz, Hamback & Beckerman 2000; Halaj & Wise 2001). Trophic cascade theory is predicated on the assumption of neatly tiered trophic levels where organisms interact through linear food chains (Hairston, Smith & Slobodkin 1960; Polis & Strong 1996). Yet when predators prey upon both herbivores and other predators, the resultant network of direct

and indirect interactions causes predator effects to attenuate before herbivore abundance and plant growth are affected (Polis & Strong 1996). Variation among communities in the commonness of intraguild predation has been proposed to be responsible, in part, for variation in the strength of trophic cascades (Shurin *et al.* 2002).

Considerably less attention has been given to the potential for trophic structure to be variable within communities (but see Sipura 2002; Moon & Stiling 2004). Among-study variation in the impacts of predators has been attributed, at least in part, to characteristics of the herbivores and plants involved (Schmitz *et al.* 2000; Halaj & Wise 2001). Furthermore, there are reasons to predict within-community variability in trophic cascades as a function of the specific characteristics of the plants and herbivores involved. Plants influence rates of herbivore damage directly through constitutive (Fritz & Simms 1992) and induced (Karban & Baldwin 1997) resistance traits, and indirectly via predators (Turlings, Tumlinson & Lewis 1990; Marquis & Whelan 1996). Likewise, herbivore characteristics such as concealed vs. exposed feeding modes (e.g. Fritz 1983), sequestration of plant secondary compounds (e.g. Dyer & Bowers 1996) and predator avoidance behaviours (Preisser, Bolnick & Benard 2005) influence rates of predation.

We compared the effects of insectivorous birds between two sympatric plants, and between two guilds of herbivores. For 3 years we excluded birds (top predators) from ponderosa pine *Pinus ponderosa* Laws. *scopulorum* and its angiosperm parasite the south-western dwarf mistletoe *Arceuthobium vaginatum* (Willd.) Presl ssp. *cryptopodum* (Engelm.) Hawksw. & Wiens. Pine and mistletoe are each fed upon by separate species of foliage-chewing and sap-feeding herbivores. These are in turn preyed upon by arthropods (intermediate predators) that move freely between the two plants. By studying a gymnosperm and a parasitic angiosperm, we sought to increase the taxonomic and ecological diversity of the plants for which bird effects on plant growth have been measured. By comparing the effects of this single predator community between two herbivore guilds and between two sympatric plants, we sought to test whether trophic cascades vary within this community, and to associate the differing effects of birds with characteristics of the herbivores and plants involved.

Materials and methods

FIELD SITE AND STUDY SYSTEM

This work was conducted at the Manitou Experimental Forest in Woodland Park, Colorado, U.S.A. (39°06'N, 105°05'W) at an elevation of 2400 m. The field site was in a pure stand of ponderosa pine parasitized by south-western dwarf mistletoe. Dwarf mistletoes *Arceuthobium* spp. (Viscaceae) are leafless, dioecious

parasites that tap into host xylem and phloem to obtain water, minerals and photosynthates (Hawksworth & Wiens 1996).

At Manitou, mistletoe is fed upon by three specialist herbivores: caterpillars of *Dasyphyga alternosquamella* Ragonot (Pyrilidae, Lepidoptera) and *Promylea lunigerella glendella* Dyar (Pyrilidae, Lepidoptera), and the sap-feeding *Neoborella tumida* Knight (Miridae, Hemiptera) (Mooney 2001; Mooney 2003). A more diverse herbivore community feeds upon pine: caterpillars (three species of Geometridae, and two from other unidentified families), leaf- and plant-hoppers (Homoptera, suborder Auchenorrhyncha; 36 species), and the aphid *Cinara schwarzii* Wilson (Aphididae, Homoptera). *Cinara schwarzii* is a facultative mutualist with wood ants *Formica* spp. (Formicidae), but the hoppers at this site are not. Mistletoe and pine tissues damaged by caterpillars are easily recognizable, but feeding by sap-feeders is not. Based on extensive observations conducted with this community, we are certain that these herbivores are host-specific, and that no herbivore feeds upon both pine and mistletoe.

Ninety-five per cent of bird foraging on pine and mistletoe is performed by insectivorous chickadees *Parus* spp. (Paridae), nuthatches *Sitta* spp. (Sittidae) and warblers *Dendroica* spp. (Parulidae) (Mooney, in press). The arthropod predator community is dominated by generalists that move freely between pine and mistletoe (Mooney, in press), including ants, hunting spiders and web-spinning spiders. Ladybird beetle larvae and adults (Coccinellidae), lacewings (Neuroptera, Chrysopidae), and some hemipterans are most commonly associated with aphids, but also prey upon other arthropods opportunistically (Dixon 2000; Wheeler 2001).

BIRD EXCLOSURES

In late June 1999, 32 understorey pines were selected. Each was 1–3 m tall (mean $\pm$ 1 SE: 2.6 ± 0.07), and heavily parasitized by mistletoe. Ring counts of trunks showed them to be 71 ± 4 years old. Sixteen trees each were assigned to bird exclusion (cage) and control treatments. Cages consisted of a frame of four metal bars (1.25 cm diameter) and a polyvinyl chloride plastic tubing roof wrapped in 2.5 cm mesh monofilament netting (Marquis & Whelan 1994).

EFFECTS ON ARTHROPOD COMMUNITY

Visual searches were used to quantify the abundance of pine herbivores and the arthropod predators that moved between both pine and mistletoe. Mistletoe-feeding herbivores were small and extremely cryptic in their coloration, and mistletoe morphology made them difficult to detect. Consequently, data on these arthropods were not collected. Our understanding of bird effects on mistletoe herbivores is thus limited to inference from data on herbivore damage to mistletoe

tissues (see below). At this site, mistletoe caterpillars were very common (as high as 2.5 per plant in 1999; Mooney 2001, 2003) while *N. tumida* was relatively less common (0.3 per plant, Mooney unpublished data).

Fourteen separate 12-min searches were conducted for arthropods over three summers: four in 1999 and five in 2000 and 2001. This nondestructive method for measuring arthropod abundance has the advantage of not disturbing populations that are to be monitored for extended periods of time. Each search was limited to pine branches and foliage. While observations were recorded for predators foraging on mistletoe, no specific effort was made to search mistletoe shoots. The 2.8 h of observation per tree did not constitute a census all arthropods, but provide an indication of relative arthropod abundance on bird exclusion and control trees.

In each visual search, arthropods were counted as belonging to seven categories: (1) ants; (2) aphids; (3) aphid-specialist predators (coccinellids, neuropterans, *Phytochoris* spp. (Miridae, Hemiptera), *Daerocoris* spp. (Miridae, Hemiptera)); (4) pine-feeding caterpillars; (5) hoppers; (6) hunting spiders (Salticidae, Anyphaenidae); and (7) web-spinning spiders (Theridiidae). Individual tree counts were low. Counts were summed across all trees and sampling periods within year and treatment for six totals per arthropod group (exclusion and control for 1999, 2000 and 2001). Separate tests were performed with χ^2 for effects of: (1) bird exclusion across all years; (2) year *per se*, i.e. combining exclusion and control trees; and (3) the interaction between year and bird exclusion (Zar 1999). In tests for year effects, annual total arthropod counts for 2000 and 2001 were each multiplied by 0.8 to account for unequal sampling effort among years (i.e. a χ^2 comparison of three values for each arthropod group: $\Sigma 1999$, $\Sigma 2000 \cdot 0.8$, $\Sigma 2001 \cdot 0.8$). This transformation reduced the size of the counts upon which the χ^2 were calculated, thus lowering statistical power and making this a conservative test (Zar 1999). The table-wide false positive rate was controlled with a sharpened step-up Bonferroni (Garcia 2004).

EFFECTS ON PINE NEEDLE HERBIVORY

Herbivore damage on 40 pine needles produced in each year was measured in early June the year after the needles were produced. Needles were selected haphazardly across the entire canopy, and damaged needles were compared with other needles in their fascicles to estimate original length. Percentage needle tissue damaged was the dependent variable in statistical tests for the effects of bird exclusion on herbivory (see *Estimating effect size* below).

EFFECTS ON PINE GROWTH

In June of 2002, 15 branch tips were collected from each tree and cut at the nodes to isolate the pre-experimental wood and foliage (1997–98) from the wood and foliage of the experimental internodes (1999–2001) and the

unopened 2002 buds. The pre-experimental internodes, which were free of foliage, were measured for the fresh mass of wood alone. For the 1999–2002 internodes, the fresh mass of foliage, wood and buds combined was measured. The wood and bud lengths and diameters from these experimental internodes were recorded to calculate volume. Regression equations were derived from 100 nonexperimental branch tips relating wood and bud volume to mass. Experimental wood and bud mass were then estimated for each branch section with these equations (wood mass (g) = $-0.027 + 0.0037 \times \text{wood volume (mm}^3\text{)}$, $R^2 = 0.89$; bud mass (g) = $-0.0255 + 0.0015 \times \text{bud volume (mm}^3\text{)}$, $R^2 = 0.92$). Finally, this estimated wood and bud mass were subtracted from the measured combined mass of wood, bud and foliage to get an estimate for foliage mass alone. This procedure thus generated mass values for production of pre-experimental wood, experimental wood and experimental foliage. Within each branch tip, wood and foliage growth during experimental years were each significantly correlated with pre-experimental wood growth (foliage, $r = 0.64$, $n = 480$, $P < 0.0001$; wood, $r = 0.79$, $n = 480$, $P < 0.0001$). Relative growth rates ('RGR') were calculated for wood and foliage production by dividing the mass produced during the experiment by pre-experimental wood growth. The mean wood RGR and foliage RGR for each tree were the dependent variables in statistical tests for the effects of bird exclusion on pine growth (see *Estimating effect size* below).

EFFECTS ON MISTLETOES

In September 1999 and June 2002 the total number of mistletoe plants on each pine and the proportion of those plants with signs of caterpillar herbivory were recorded. For each tree the 2002 counts were divided by 1999 counts and λ , the annual population growth rate, was calculated as $\lambda = (n_{2002}/n_{1999})^{1/3}$ (Hastings 1997). For each tree, the total proportion of mistletoe plants with herbivore damage was calculated for 1999 and 2002 combined. Per cent herbivory and λ were the two dependent variables used in tests for the effects of bird exclusion on mistletoe (see *Estimating effect size* below).

ESTIMATING EFFECT SIZE

To test for the effect of bird exclusion on the five plant variables, effect sizes (Hedges, Gurevitch & Curtis 1999; Osenberg, Sarnelle & Goldberg 1999) were calculated as the natural log of the ratio of exclusion mean to control mean ($= \ln(\bar{x}_{\text{exclusion}}/\bar{x}_{\text{control}})$). Ninety-five per cent confidence intervals ('95% CI') were calculated by bootstrapping with 999 replications (Potvin & Roff 1993). Means and confidence intervals were back-transformed from log ratios to the proportional change in each dependent variable caused by bird exclusion ($= \bar{x}_{\text{exclusion}}/\bar{x}_{\text{control}}$). The proportions were multiplied by control tree mean to express effect sizes in original units.

Table 1. Statistical tests for effects of bird exclusion (cage), year and the interaction between the two on pine canopy arthropods

Arthropod group	Cage		Year		Cage*Year	
	$\chi^2_{(df=1)}$	<i>P</i>	$\chi^2_{(df=2)}$	<i>P</i>	$\chi^2_{(df=5)}$	<i>P</i>
Ants	461.52	0.0001	158.63	0.0001	118.06	0.0001
Aphids	251.45	0.0001	133.16	0.0001	56.82	0.0001
Caterpillars	0.13	0.72	1.34	0.52	3.10	0.68
Hoppers	2.15	0.15	11.78	0.0027	2.23	0.82
Aphid-specialist predators	6.91	0.0086	22.78	0.0001	9.00	0.11
Hunting spiders	9.57	0.0019	54.51	0.0001	2.46	0.78
Web-spinning spiders	0.99	0.32	17.33	0.0002	1.09	0.95

Note: Analyses performed on total counts of all trees within a treatment ($n = 16$ per treatment) across all sampling periods within a year (1999 = 4, 2000 = 5, 2001 = 5). For tests of year effect, the 2000 and 2001 counts were multiplied by 0.8 to equalize with the 1999 sampling effort. The table-wide false-positive rate is protected with a sharpened step-up Bonferroni adjustment, and significant results (corrected $\alpha = 0.0051$) are shown in bold.

An effect whose 95% confidence interval does not include a zero effect is significant ($P < 0.05$). Failure to reject the null hypothesis can occur because (1) treatment effects are weak and of little biological relevance (the conclusive null result), or (2) the experiment has low statistical power and biologically relevant treatment effects may or may not exist (the inconclusive null result) (Steidl, Hayes & Schaubert 1997). The confidence intervals around nonsignificant effects provide an estimate – with 95% certainty – of the maximum and minimum effects that could have been missed (Type II error) by the conducted experiment. The confidence intervals of nonsignificant results can then be interpreted in light of the biology of the system to make a qualitative evaluation of whether the null result is conclusive or inconclusive (Steidl *et al.* 1997).

Results

EFFECTS ON ARTHROPOD COMMUNITY

The 5004 arthropods observed (66% on caged trees) were 41% ants, 16% tended aphids, 15% hunting spiders, 12% aphid-specialist predators, 9% web spinning spiders, 6% hoppers and 1% caterpillars. Excluding birds with cages caused significant increases in ants, tended aphids, and hunting spiders (Table 1, Fig. 1). Bird effects on hunting spiders were constant among years (20% reduction) but there were interactions with year for effects on ants and tended aphids. Birds affected ants in each year (1999 $\chi^2_{(1)} = 42.7$, $P < 0.0001$, 47% reduction; 2000 $\chi^2_{(1)} = 30.1$, $P < 0.0001$, 37% reduction; 2001 $\chi^2_{(1)} = 480.4$, $P < 0.0001$, 81% reduction). Aphid abundance was lower in the presence of birds the later 2 years (2000 $\chi^2_{(1)} = 38.5$, $P < 0.0001$, 56% reduction; 2001 $\chi^2_{(1)} = 247.6$, $P < 0.0001$, 87% reduction) but not in the first year (1999 $\chi^2_{(1)} = 4.0$, $P = 0.047$ not significant at adjusted $\alpha = 0.017$). There was no effect of birds or bird-by-year interaction on aphid-specialist predators or hoppers, but in 2001 the patterns in the means among the five sampling dates suggested the possibility of real treatment effects that were missed in our

original analysis (Fig. 1). *Post-hoc* χ^2 analysis for 2001 showed an effect of birds on aphid-specialist predators ($\chi^2_{(1)} = 15.6$, $P < 0.0001$, 30% reduction) but not on hoppers ($\chi^2_{(1)} = 3.76$, $P = 0.0525$).

EFFECTS ON PINE HERBIVORY AND GROWTH

Pine needle herbivory (mean ± 1 SE) across all trees and years was $4.1 \pm 0.3\%$. There was no bird effect (Fig. 2, 'foliage damage'). Ninety-five per cent confidence intervals for this null result did not include a level of herbivory likely to be of biological significance to pine, making this a conclusive null result (95% CI: +2.0% to -0.3% change in herbivory). There was no detectable bird effect on foliage growth (Fig. 2), but this null result was inconclusive because the large confidence interval (95% CI: +23% to -22% change in foliage RGR) meant this experiment had insufficient statistical power to address this question. Bird exclusion significantly reduced wood RGR by 11% (95% CI: -21% to -2% change in wood RGR) (Fig. 2).

EFFECTS ON MISTLETOES

Averaged across 1999 and 2002 there were 65 ± 7 mistletoe plants per host pine and $18 \pm 1.4\%$ of mistletoe plants had herbivore damage. There was no bird effect on caterpillar damage to mistletoe tissues (Fig. 2), and the relatively narrow confidence interval makes this a conclusive null result (95% CI: +5% to -7%). Averaged across both treatments, λ was 1.05 ± 0.03 and unaffected by bird exclusion (Fig. 2). This null result, presented as percentage change in mistletoe abundance per year ($= (\lambda - 1) * 100$), was somewhat inconclusive given the range of possible effects that we may have failed to detect (95% CI: +11% to -17%).

Discussion

The presence of birds in pine canopies was associated with increased pine wood growth, and this was likely a direct result of birds having negative effects on

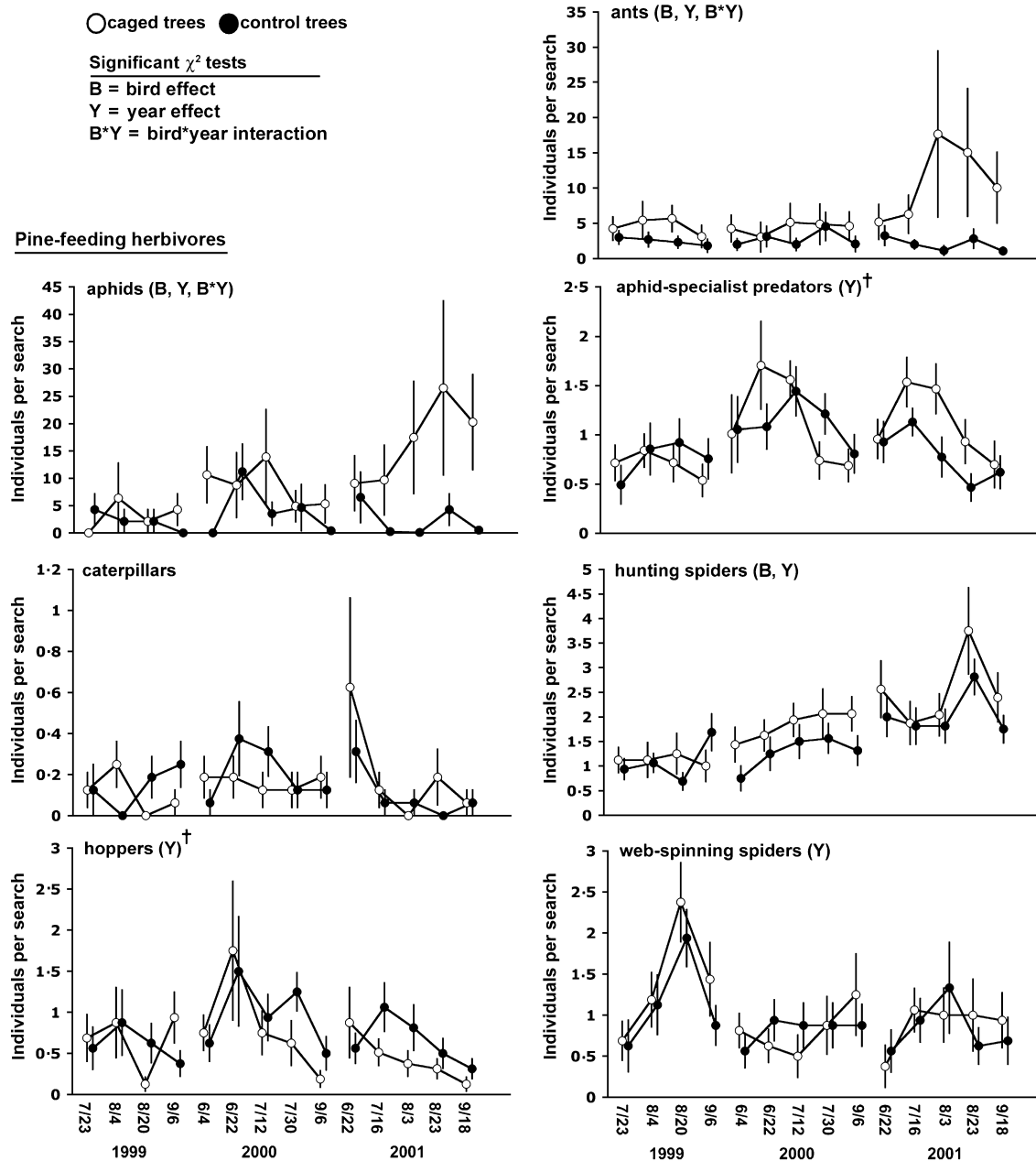


Fig. 1. Arthropod abundance on bird exclusion (solid circles) and control trees (hollow circles) from 1999 to 2001. Predator data were collected from both pine and parasitic mistletoes. Data on herbivores are exclusively from pine. Mean (± 1 SE) arthropods per 12-minute search are shown on the Y-axis. Letters next to arthropod group in each panel indicate significant ($P < \text{adjusted } \alpha \text{ of } 0.0051$) effects of bird exclusion ('B'), year ('Y') and their interaction ('B*Y'). See Table 1 for detailed statistics. '†' indicates a *posthoc* tests was conducted; bird exclusion affected aphid-specialist predators in 2001 ($P < 0.0001$) but not hoppers ($P > 0.05$).

ant-tended aphids in 2000 and 2001. Aphids have been shown to affect the wood growth of other tree species as well (Dixon 1971b,a). Aphid feeding has also been shown to reduce foliage growth of trees in other settings (e.g. May & Carlyle 2003; see review in Dixon 1998), but the high variance of foliage mass in our experiment meant we had inadequate statistical power to resolve this question (Steidl *et al.* 1997). The variability we observed was likely because foliage mass was a function not only of growth, but also of subsequent needle abscission. In contrast to the effects of bird

exclusion on ant-tended aphids, there were not detectable effects on untended pine herbivores (hoppers and caterpillars), nor were there indirect effects of bird exclusion on damage to pine foliage. As a result, we assume that the mechanism for the indirect impact of birds on pine growth was via direct effects on ant-tended aphids.

This stark difference in the effects of bird exclusion between ant-tended and untended pine herbivores suggests there was within-community variation in food web structure (Fig. 3). The negligible impact of bird exclusion on untended herbivores is consistent with

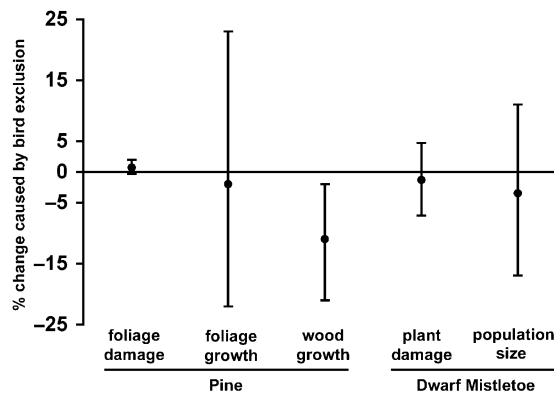


Fig. 2. Effects of birds on pine and mistletoe. Effect sizes (back-transformed $\log[\bar{x}_{\text{exclusion}}/\bar{x}_{\text{control}}]$) were multiplied by control tree means to report effects ($\pm 95\%$ confidence interval) in original units. Pine foliage damage = % needle tissue damaged. Pine foliage and wood growth = % change in relative growth rates. Mistletoe plant damage = % change in the number of plants fed upon by caterpillars. Mistletoe population size = % change per year in number of mistletoe plants per host tree ($= (\lambda - 1) * 100$). Effects with confidence intervals spanning zero are not significant.

compensatory predation (Polis & Strong 1996) by the hunting spiders, ants and aphid-specialist predators that were more abundant in cages. Aphid-specialist predators are most often associated with aphids, but also prey upon other arthropods opportunistically (Dixon 2000; Wheeler 2001). Evidence from other work at this field site documents that ants remove pine herbivores (Mooney & Tillberg 2005; Mooney, in press), and work from other systems documents the abilities of hunting spiders to reduce insect herbivore abundance (see review in Wise 1993). Web-spinning spiders did not respond to bird exclusion, and thus probably did not contribute to compensatory predation within cages. Our results for untended herbivores thus support the notion that reticulate food webs created by intraguild predation resulted in compensatory predation that decoupled the effects of top predators from plant growth (Polis & Strong 1996).

In contrast to the above results for untended herbivores, aphid populations burgeoned in the absence of birds on caged trees despite increases in hunting spiders and aphid-specialist predators. Ants apparently protected pine-feeding aphids from these intermediate arthropod predators but not from insectivorous birds. In this way, the ant-aphid mutualism simplified the trophic pathway between birds and pine into a three-tiered, linear food chain as envisioned by early food web theorists (Hairston *et al.* 1960). Under these conditions, we observed a trophic cascade. The food web structure linking insectivorous birds and pine thus varied between ant-tended herbivores (= linear food web structure) and untended herbivores (= reticulate food web structure) (Fig. 3): the former, but not the latter, transmitted bird effects to pine.

We measured the accumulated impact of bird exclusion on pine growth at the conclusion of the

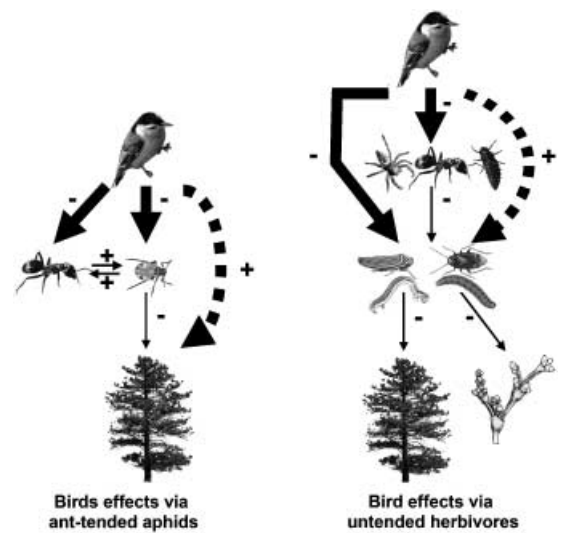


Fig. 3. Proposed food web models for the variable top-down effects of birds. Effects (+, -) are transmitted from the base to the head of each arrow, and the arrow width represents interaction strength. Solid-straight arrows are direct effects, and dashed-curved arrows are indirect effects. Left diagram: effects of birds on pine via predation of ant-tended aphids (*F. podzolica* tending *C. schwarzii*). Bird feeding upon aphids indirectly increased pine growth. We do not include predatory arthropods in this model because aphids were protected by mutualist ants. Right diagram: effects of birds on pine and mistletoe via predation on predatory arthropods (left to right: hunting spiders, ants, aphid-specialist predators) and untended herbivores of pine (top to bottom: hoppers, caterpillars) and mistletoe (top to bottom: *N. tumida* and the caterpillars *D. alternosquamella* and *P. lunigerella*). Birds had no net effects on the untended pine and mistletoe herbivores, or on pine and mistletoe biomass, due to compensatory predation of untended herbivores by ants, hunting spiders, and aphid-specialist predators. We do not include web-spinning spiders in this model because they did not increase in abundance on caged trees and thus did not contribute to compensatory predation.

experiment, but our arthropod data suggest the effect of our manipulation likely varied among years. While ants responded immediately to bird exclusion in 1999, aphid populations only increased on caged trees the subsequent year (2000). In the third year (2001), both aphid and ant populations showed dramatic peaks within cages. One explanation for this pattern is that ants benefited from bird exclusion first (1999), and only subsequently (2000) did ant-dependent aphids begin to accumulate on caged trees. In the third year (2001), aphid populations continued to increase and this attracted additional ants. While this is a coherent interpretation of our data, there are other possible explanations. Precipitation levels decreased over the 3 years of the experiment (annual total 43.9 cm in 1999, 32.1 cm in 2000, 26.1 cm in 2001), and aphid response to bird exclusion may have only occurred on drought-stressed trees. In any case, these multiyear dynamics underscore the need for long-term studies to properly characterize trophic dynamics on long-lived plants.

Caterpillar damage to mistletoe was unaffected by bird exclusion. This suggests that predatory arthropods

may have compensated for bird predation of mistletoe herbivores as we have argued they did for the untended herbivores of pine. We did not quantify the abundance of herbivores on mistletoe plants so our understanding of this food web is incomplete. Pine and mistletoe share a single community of predatory arthropods, and the higher abundance of arthropod predators in pine canopies almost certainly had implications for mistletoe herbivores. In a separate 30-day trial conducted at this site, we found that pine canopy arthropod predators reduced the survival of mistletoe-feeding caterpillars by one-third (Mooney, unpublished data). The higher abundance of predatory arthropods on and around mistletoe plants in cages thus provides an explanation for why caterpillar damage to mistletoe and mistletoe population size did not respond to bird exclusion.

The pine and mistletoe systems were linked directly by competition for resources between the two plants, and indirectly by a shared community of predatory birds and arthropods. As a result, dynamics occurring on one plant likely had consequences for the other. One scenario, in particular, seems quite plausible to us; the higher abundance of aphids on caged pines may have recruited additional ants that then preyed upon mistletoe herbivores. We have observed that ants tending pine-feeding aphids also preyed upon mistletoe herbivores and reduced mistletoe damage (Mooney, pers. ob). More generally, there is extensive evidence that both plants and herbivores interact indirectly via shared enemies (Holt & Lawton 1994). By comparison, there is relatively less known about how plants interact indirectly via shared predator communities (but see Linhart *et al.* 2005). It is almost certain that in pine canopies, and in complex communities generally, trophic cascades will be affected by dynamics that link trophic structure between plants.

The comparison of bird effects between pine and mistletoe (Fig. 2) is somewhat weakened by the fact that we used different metrics to quantify herbivore damage (proportion pine foliage with herbivory vs. proportion of mistletoe plants with herbivory) and plant growth (pine wood and foliage RGR vs. mistletoe population size). Yet this comparison is at least suggestive of two conclusions. First, the lack of a bird effect on caterpillar damage to pine and mistletoe suggests similar food web dynamics with respect to predator effects on untended herbivores on these two plants. Second, the indirect effects of birds differed between the two plants as a function of pine, but not mistletoe, having ant-tended herbivores. The fact that ant-tended aphids were present on pine but not mistletoe may ultimately be attributable to the differing plant morphology; in the Rocky Mountains, aphids on woody plants are 70% more likely to be ant-tended than aphids on herbaceous plants (Bristow 1991: analysis of their fig. 9.3, $\chi^2_{(3)} = 19$, $P < 0.0001$), and the unusual structure of mistletoe phloem (Hawsworth & Wiens 1996) may affect aphid feeding. The effects of plant morphology

on the evolution of herbivore communities could thus set the stage upon which birds currently act.

Our study documents the differing effects of a single predator community between two guilds of herbivores and two plants. This adds to a small but growing literature demonstrating that the trophic linkage between terrestrial predators and plants varies not only among, but also within ecological communities (Sipura 2002; Moon & Stiling 2004). The patterns we observed suggested these variable effects of birds were a result of differing food web structure, and these effects supported current food web theory: linear food chains resulted in trophic cascades, while the reticulate food webs associated with intraguild predation did not. Our study adds to this understanding by demonstrating that variation in food web structure occurs among sympatric plants, and even among herbivores feeding on the same plant.

Acknowledgements

This work was supported by funds from the U.S. Forest Service Rocky Mountain Research Station and the University of Colorado at Boulder. Brian Geils (U.S.D.A. Rocky Mountain Research Station) provided valuable advice on mistletoe-related matters. Kathy Thomas and Ken Keefover-Ring helped in the field. M. Deane Bowers advised the experimental design and execution. Comments from M.D.B., B.G., Sharon Collinge, Carl Bock, Michael Singer and the Plant–Animal Interaction group at Boulder improved this manuscript. Wayne Shepherd and Steve Tapia (Rocky Mountain Research Station) provided logistical assistance.

References

- Bristow, C.M. (1991) Why are so few aphids ant-tended? *Ant–Plant Interactions* (eds C.R. Huxley & D.F. Cutler), pp. 104–119. Oxford University Press, Oxford.
- Dixon, A.F.G. (1971a) Role of aphids in wood formation 1. Effect of sycamore aphid, *Drepanosiphum platanoide* (Schr) (Aphididae), on growth of sycamore, *Acer pseudoplatanus* (L.). *Journal of Applied Ecology*, **8**, 165–179.
- Dixon, A.F.G. (1971b) Role of aphids in wood formation 2. Effect of lime aphid, *Eucallipterus tiliae* L. (Aphididae), on growth of lime, *Tilia x vulgaris hayne*. *Journal of Applied Ecology*, **8**, 393–399.
- Dixon, A.F.G. (1998) *Aphid Ecology: an Optimization Approach*, 2nd edn. Chapman & Hall, London.
- Dixon, A.F.G. (2000) *Insect Predator–Prey Dynamics: Ladybird Beetles and Biology Control*. Cambridge University Press, Cambridge.
- Dyer, L.A. & Bowers, M.D. (1996) The importance of sequestered iridoid glycosides as a defense against an ant predator. *Journal of Chemical Ecology*, **22**, 1527–1539.
- Fritz, R.S. (1983) Ant protection of a host plant's defoliator – consequence of an ant-membracid mutualism. *Ecology*, **64**, 789–797.
- Fritz, R.S. & Simms, E.L. (1992) *Plant Resistance to Herbivores and Pathogens: Ecology, Evolution, and Genetics*. University of Chicago Press, Chicago, IL.
- Garcia, L.V. (2004) Escaping the Bonferroni iron claw in ecological studies. *Oikos*, **105**, 657–663.

- Hairston, N.G., Smith, F.E. & Slobodkin, L.G. (1960) Community structure, population control, and competition. *American Naturalist*, **94**, 421–425.
- Halaj, J. & Wise, D.H. (2001) Terrestrial trophic cascades: How much do they trickle? *American Naturalist*, **157**, 262–281.
- Hastings, A. (1997) *Population Biology: Concepts and Models*. Springer, New York.
- Hawthornth, F.G. & Wiens, D. (1996) *Dwarf Mistletoes: Biology, Pathology, and Systematics*. U.S. Department of Agriculture Forest Service, Washington, DC.
- Hedges, L.V., Gurevitch, J. & Curtis, P.S. (1999) The meta-analysis of response ratios in experimental ecology. *Ecology*, **80**, 1150–1156.
- Holt, R.D. & Lawton, J.H. (1994) The ecological consequences of shared natural enemies. *Annual Review of Ecology and Systematics*, **25**, 495–520.
- Karban, R. & Baldwin, I.T. (1997) *Induced Responses to Herbivory*. University of Chicago Press, Chicago, IL.
- Linhardt, Y.B., Keefover-Ring, K., Mooney, K.A., Breland, B. & Thompson, J.D. (2005) A chemical polymorphism in a multi-trophic setting: Thyme monoterpene composition and food web structure. *American Naturalist*, **166**, 517–529.
- Marquis, R.J. & Whelan, C.J. (1994) Insectivorous birds increase growth of white oak through consumption of leaf-chewing insects. *Ecology*, **75**, 2007–2014.
- Marquis, R.J. & Whelan, C. (1996) Plant morphology, and recruitment of the third trophic level: Subtle and little-recognized defenses? *Oikos*, **75**, 330–334.
- Matson, P.A. & Hunter, M.D. (1992) The relative contributions of top-down and bottom-up forces in population and community ecology. *Ecology*, **73**, 723–723.
- May, B.M. & Carlyle, J.C. (2003) Effect of defoliation associated with *Essigella californica* on growth of mid-rotation *Pinus radiata*. *Forest Ecology and Management*, **183**, 297–312.
- Moon, D.C. & Stiling, P. (2004) The influence of a salinity and nutrient gradient on coastal vs. upland tritrophic complexes. *Ecology*, **85**, 2709–2716.
- Mooney, K.A. (2001) The life history of *Dasypyga alternosquamella* Raganot (Pyralidae) feeding on the Southwestern dwarf mistletoe (*Arceuthobium vaginatum*) in Colorado. *Journal of the Lepidopterists' Society*, **55**, 144–149.
- Mooney, K.A. (2003) *Promylea lunigerella glendella* Dyar (Pyralidae) feeds on both conifers and parasitic dwarf mistletoe (*Arceuthobium* spp.): one example of food plant shifting between parasitic plants and their hosts. *Journal of the Lepidopterists' Society*, **57**, 47–53.
- Mooney, K.A. (2005) The disruption of an ant–aphid mutualism increases the effects of insectivorous birds on pine herbivores. *Ecology*, in press.
- Mooney, K.A. & Tillberg, C.V. (2005) Temporal and spatial variation to ant omnivory in pine forests. *Ecology*, **86**, 1225–1235.
- Osenberg, C.W., Sarnelle, O. & Goldberg, D.E. (1999) Meta-analysis in ecology: concepts, statistics, and applications. *Ecology*, **80**, 1103–1104.
- Polis, G.A. & Strong, D.R. (1996) Food web complexity and community dynamics. *American Naturalist*, **147**, 813–846.
- Potvin, C. & Roff, D.A. (1993) Distribution-free and robust statistical-methods – viable alternatives to parametric statistics. *Ecology*, **74**, 1617–1628.
- Preisser, E.L., Bolnick, D.I. & Benard, M.F. (2005) Scared to death? The effects of intimidation and consumption in predator–prey interactions. *Ecology*, **86**, 501–509.
- Schmitz, O.J., Hamback, P.A. & Beckerman, A.P. (2000) Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. *American Naturalist*, **155**, 141–153.
- Shurin, J.B., Borer, E.T., Seabloom, E.W., Anderson, K., Blanchette, C.A., Broitman, B., Cooper, S.D. & Halpern, B.S. (2002) A cross-ecosystem comparison of the strength of trophic cascades. *Ecology Letters*, **5**, 785–791.
- Sipura, M. (2002) Contrasting effects of ants on the herbivory and growth of two willow species. *Ecology*, **83**, 2680–2690.
- Steidl, R.J., Hayes, J.P. & Schaubert, E. (1997) Statistical power analysis in wildlife research. *Journal of Wildlife Management*, **61**, 270–279.
- Turlings, T.C.J., Tumlinson, J.H. & Lewis, W.J. (1990) Exploitation of herbivore-induced plant odors by host-seeking parasitic wasps. *Science*, **250**, 1251–1253.
- Wheeler, A.G. (2001) *Biology of the Plant Bugs (Hemiptera: Miridae): Pests, Predators, Opportunists*. Comstock Publishing Associates, Ithaca, NY.
- Wise, D.H. (1993) *Spiders in Ecological Webs*. Cambridge University Press, Cambridge, MA.
- Zar, J.H. (1999) *Biostatistical Analysis*, 4th edn. Prentice Hall, Upper Saddle River, NJ.

Received 8 July 2005; accepted 20 October 2005