Ecology, 88(8), 2007, pp. 2005–2014

TRITROPHIC EFFECTS OF BIRDS AND ANTS ON A CANOPY FOOD WEB, TREE GROWTH, AND PHYTOCHEMISTRY

KAILEN A. MOONEY[1]

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

Abstract. Insectivorous birds and ants co-occur in most terrestrial communities, and theory predicts that emergent properties (i.e., nonadditive effects) can determine their combined influence on arthropods and plants. In a three-year factorial experiment, I investigated whether the effects of birds on pine and its arthropods differed based on the presence of ants that were predators of most arthropods, but mutualists with tended aphid species. Birds and ants reduced the abundance of most herbivorous and carnivorous arthropods in an additive fashion, with the effects of ants being stronger than those of birds. In sharp contrast, the opposing influences of birds and ants on tended aphid species interacted strongly; ants only increased tended aphid abundance in the absence of birds, while birds only reduced their abundance in the presence of ants. This interaction was mirrored in total herbivore abundance because tended aphids dominated the herbivore community. I develop a novel lexicon to discuss the emergent properties from these effects of opposing sign (predation, mutualism). Despite having emergent effects on herbivores, birds indirectly increased pine wood and foliage growth to a similar extent whether or not ants were present, while ants had no detectable effects. Birds also indirectly increased the abundance of some pine phloem monoterpenes, but these effects differed based on the presence or absence of ants. Thus, I report on a novel yet possibly widespread indirect interaction between intraguild predators, herbivore mutualists, and plant traits (growth, secondary chemistry) mediated through a species-rich community of arthropods.

Key words: ant–aphid mutualism; Cinara; *emergent property;* Formica podzolica; *indirect effect; multiple predator effect; negative-biased interaction; phloem monoterpenes;* Pinus ponderosa; *positive-biased interaction; tritrophic interaction; trophic cascade.*

INTRODUCTION

It is well recognized that predators can enhance plant growth by reducing herbivore abundance (Schmitz et al. 2000, Halaj and Wise 2001). Yet the strength of such trophic cascades has been found to be quite variable both within (Moon and Stiling 2004, Mooney and Linhart 2006) and among communities (Shurin et al. 2002). The dynamics of a tritrophic interaction are thus not constant, but rather are modified by, or dependent on, the biotic and abiotic context in which the interaction is embedded. Having recognized such complexities, community ecology has progressed from asking whether trophic cascades occur, to asking what factors determine cascade strength.

The effects of a focal predator species on herbivores and plants can depend on its interactions with other predator species (Fig. 1a–c; Sih et al. 1998). Emergent multiple predator effects can be synergistic, enhancing herbivore suppression, when predator species forage in separate microhabitats and eliminate enemy-free space (e.g., Losey and Denno 1998). Alternatively, multiple predator effects can be antagonistic, reducing the suppression of herbivores, when predators prey upon or interfere with each other (e.g., Ferguson and Stiling 1996). Consequently, predicting the effect of a focal predator on herbivores and plants requires knowing both the identity of sympatric predator species and the emergent properties from the combined effects of these multiple predators (Rosenheim 1998).

In contrast to predator–predator interactions, little attention has been given to other attributes of food web structure that may modulate trophic cascade strength (Mooney 2006). For instance, mutualisms between ants and hemipterans are common in terrestrial communities and can substantially increase herbivore abundance (Way 1963). Yet it is unknown what consequences such mutualisms have for trophic cascades. When ants protect hemipterans from predators, trophic cascades should be weak. Alternatively, when predators prey upon ant-tended hemipterans or otherwise disrupt the mutualism, those predators may have especially strong top-down effects by keeping the mutualism in check. Mooney (2006) showed that insectivorous birds had stronger effects on total herbivore biomass when they disrupted an ant–aphid mutualism than when they foraged on pine trees with ants excluded. This experi-

Manuscript received 26 June 2006; revised 8 December 2006; accepted 12 January 2007. Corresponding Editor: D. H. Feener, Jr.

[1] Present address: Department of Ecology and Evolutionary Biology, University of California, Steinhaus Hall, Irvine, Californa 92697 USA.
E-mail: kailen.mooney@tritrophic.org

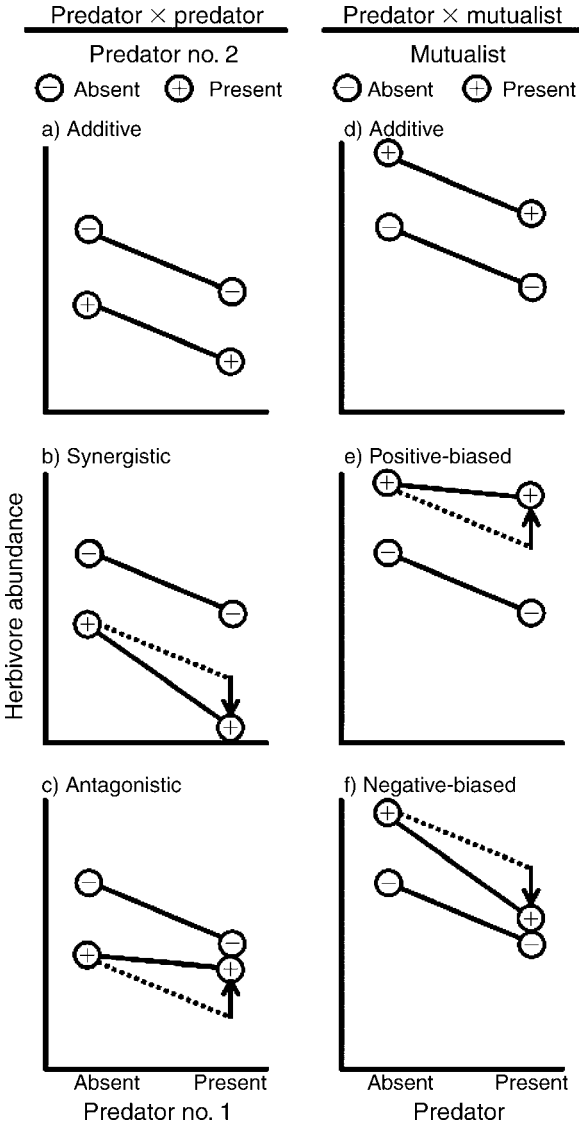

FIG. 1. Schematic diagram of additive and interactive effects of two predators or a predator and a mutualist on herbivores. Left column: multiple predator effects on herbivore abundance. The combined effects can be (a) additive, (b) synergistic (super-additive), or (c) antagonistic (sub-additive). Right column: effects of a predator and a mutualist on herbivore abundance. The combined effects can be (d) additive, or (e, f) nonadditive. Circles represent hypothetical means for herbivore abundance in each treatment. The slopes of solid lines represent effects of predators in each scenario. Where there are nonadditive (interactive) effects of multiple predators (b, c) or predators and mutualists (e, f), dashed lines show the expected effects under additivity, and arrows show departure from additivity. For nonadditive effects I employ the following terminology: (e) a positive-biased interaction occurs when the strength of the positive effect is increased at the expense of the negative effect, while (f) a negative-biased interaction occurs when the strength of the negative effect is increased at the expense of the positive effect.

ment did not identify the indirect effects of birds and ants on pine, leaving open the question of how ant–hemipteran mutualisms affect trophic cascade strength.

Birds and ants are often important predators of arthropods in temperate and tropical communities (Warrington and Whittaker 1985, Gruner 2004, Mooney and Linhart 2006), while ants may simultaneously be mutualists with some hemipterans (Way 1963). The influence of birds and ants directly on arthropods and indirectly on plants is likely to be determined by the emergent properties of their combined effects. With respect to shared prey, net predation pressure will depend on whether their combined predatory effects are additive, antagonistic, or synergistic (Fig. 1a–c). With respect to ant-tended hemipterans, the negative effects of birds and the positive effects of ants may also be nonadditive (Fig. 1d–f). Here the effects act in opposing directions and the two possible outcomes for nonadditivity do not fit within this synergism–antagonism lexicon. When the strength of the positive effect is increased at the expense of the negative effect, I refer to this as a "positive-biased" interaction. This would occur where ants can protect mutualists from predation. Alternatively, a "negative-biased" interaction occurs when the strength of the negative effect is increased at the expense of the positive effect. This would occur when predators prey upon hemipterans or otherwise disrupt the ant–hemipteran mutualism. The net effects of predation and mutualism on ant-tended herbivores will thus be determined by whether their combined effects are additive, positive-biased, or negative-biased.

I studied the effects of birds (chickadees, nuthatches, warblers) and the ant *Formica podzolica* Francour on the ponderosa pine (*Pinus ponderosa* Laws. *scopulorum*) food web in a three-year factorial experiment (see Plate 1). In this diverse community of nearly 300 arthropod species, birds and ants each feed as intraguild predators in that they consume both herbivorous and predatory arthropods. Because ants are chemically defended against predation (Hölldobler and Wilson 1990), these birds and ants interact with each other primarily as competitors (Haemig 1996). At the same time, birds and ants have opposing effects on two species of ant-tended *Cinara* aphids that are the most abundant pine herbivores, making this ant–aphid mutualism a key element of the pine food web (Mooney 2006).

While a handful of studies have documented birds increasing the woody growth of deciduous trees by removing caterpillars (e.g., Marquis and Whelan 1994), this study documents a trophic cascade in a coniferous forest that is mediated by sap-feeding aphids. In addition to affecting plant growth, I also document a novel interaction where predators shape plant quality; by reducing herbivore density and changing herbivore species composition, birds indirectly affected plant secondary chemistry and in so doing potentially altered future plant attack through effects on altered resistance. This work provides a novel investigation into how

predators and mutualists, both individually and in combination, directly structure an arthropod community and indirectly affect pine growth and defensive chemistry.

Materials and Methods

Field site and experimental trees

I conducted this work at the Manitou Experimental Forest in Woodland Park, Colorado, USA (39°06′02″ N, 105°05′32″ W) in mature stands of ponderosa pines at an elevation of 2400 m. Ninety-five percent of pine foraging by birds at this site is by chickadees, nuthatches, and warblers (Mooney 2006). *Formica podzolica* is a predator of most arthropods, but engages in a mutualism with several aphids (Aphididae: Hemiptera; Way 1963). The feeding ecology of *F. podzolica*, the bird community, and the interactions between birds and ants have been described elsewhere (Mooney and Tillberg 2005, Mooney 2006).

During the first week of June 2001 I selected 21 sets of four pine trees associated with *F. podzolica* mounds. Trees within sets were <8 m apart, and the sets were distributed over an area of 750 ha. I excluded ants from two randomly selected trees in each set with sticky paste (Tanglefoot, Grand Rapids, Michigan, USA), and applied a similar amount of paste to half the trunk diameter of control trees. I selected three branches on each tree ranging from 0.5 to 6.0 m from the ground (2.4 ± 0.8 m, mean ± SE). On one ant-exclusion and ant-control tree each I excluded birds from these three branches with 2.5-cm opening monofilament netting bags.

Effects on pine arthropods

During the first week of each month from June to September in 2001 and June to August in 2002 I collected arthropods, alternating between two of the three experimental branches. The June 2001 sampling was immediately prior to bird and ant exclusion. I beat branches with a padded bat to dislodge arthropods into a 1.5×1.5 m fabric tub (0.5 m deep) and preserved them in 70% ethanol (Mooney and Tillberg 2005). While this sampling method may under-represent arthropods that are able to escape or cling pine branches, such uneven sampling is consistent among experimental treatments. I identified each arthropod, measured its length to the nearest millimeter and calculated dry biomass from a published length–biomass algorithm (Rogers et al. 1976). I then cut and weighed the pine branches at the conclusion of the experiment. I analyzed these data as milligrams arthropod dry mass per kilogram pine branch fresh mass (wood and foliage combined), or arthropod loads (sensu Root 1996).

I divided the pine canopy arthropod community into four predator and four herbivore categories. Predators consisted of: (1) web-spinning spiders (Araneae, 14 species from five families); (2) hunting spiders (Araneae, 13 species from five families); (3) specialist aphid predators (larval and adult Coccinellidae beetles, four species; larval Neuroptera, two species; mirids [Miridae, Hemiptera], five species from genera *Daerocoris* spp., *Pilophoris* spp., *Phytochoris* spp.); and (4) ants (*F. podzolica*).

Herbivore categories consisted of: (1) ant-tended aphids (*Cinara schwarzii* Wilson and *C. arizonica* Wilson), (2) untended aphids (*C. solitaria* [Gillette and Palmer], *C. glabra* [Gillette and Palmer], *Essigella fusca* [Gillette and Palmer], and *Schizolachnus piniradiatae* [Davidson]), (3) non-aphid sap feeders (plant and leaf hoppers [Homoptera, suborder Auchenorrhyncha], 36 species not tended by ants; herbivorous Hemiptera, 15 species from five families), and (4) tissue-damaging herbivores (caterpillars [larval Lepidoptera, five species], thrips [Thysanoptera, one species], adult herbivorous beetles [Coleoptera excluding Coccinellidae, 102 species]) hereafter referred to as "chewing herbivores."

I tested whether trees differed significantly in their arthropod communities prior to my exclusion of birds and ants (June 2001 sampling) using the MANOVA feature of PROC GLM in SAS 8.1 (SAS Institute 2001). I analyzed data from the experimental months as a two-factor repeated-measures design with birds and ants treatments as within-subject effects, month as an among-subject effect. Both birds and ants had large effects on arthropod abundance, and my experimental design did not prevent prey depletion. In such situations, a multiplicative null model is needed to test for interactions, requiring the use of log-transformed data (Sih et al. 1998, Hambäck and Beckerman 2003). I first tested for the multivariate response of all arthropods (MANOVA) followed by univariate mixed-model analyses (PROC MIXED), in which each set of four trees was included as a random block. In these univariate analyses I only tested for those effects that were significant in the multivariate model.

Effects on pine

Pine growth and damage.—I used the third (undisturbed) experimental branch on each tree to measure pine growth and foliage damage. Pine branches function as physiologically autonomous units (Sprugel 1991), making the branch-level study of pine responses a reasonable proxy for whole-tree manipulations. In fall 2003 I collected five haphazardly selected tips from each branch, and cut each tip at the nodes to isolate the preexperimental internodes (2000) and each of the three years of growth since imposing the treatments (2001–2003). I randomly selected six pine needles from each 2001 internode to measure percentage damage by chewing herbivores. I measured the fresh mass of wood in the preexperimental internodes, which were free of foliage, and the combined fresh mass of foliage and wood for internodes from each of the experimental years. I then recorded the wood volume of each experimental internode (length $\times \pi \times$ radius^2). I derived a regression equation from 100 nonexperimental branch

tips to relate mass (g) to wood volume (in mm^3): (wood mass $= -0.027 + 0.0037 \times$ wood volume; $R^2 = 0.89$). Using this equation, I estimated the wood mass and subtracted this from the measured combined mass of wood and foliage. This procedure gave mass values for wood produced in the preexperimental year, and wood and foliage mass produced during each of the experimental years. For each branch tip I thus calculated relative growth rates (RGR) by dividing the experimental wood and foliage mass by the preexperimental (2000) wood mass. The RGR for each branch was the experimental observation. I analyzed percentage herbivory, wood RGR, and foliage RGR according to the same statistical methods as the arthropod data.

Pine phloem chemistry.—In December 2003 I measured the indirect effects of birds and ants on phloem monoterpenes from a branch adjacent to the three branches used for collecting arthropods and measuring pine growth and damage. Pine phloem monoterpenes have been widely implicated in resistance to a diversity of parasites and herbivores (Mitton and Sturgeon 1982, Snyder 1992, Paine and Hanlon 1994, Snyder et al. 1996). Monoterpenes in phloem have not previously been shown to be inducible, but those in needle tissues are inducible following herbivory (Litvak and Monson 1998, Thoss and Byers 2006). While ant exclusion was at the whole-tree level, this branch was not within the bird exclusion treatment and thus provided an estimate of the systemic effects of birds on tree chemistry. I measured the content of nine phloem monoterpenes (see *Results*) by gas chromatography according to the methods of Latta et al. (2000). I performed a factor analysis using PROC FACTOR with a PROMAX rotation in SAS 8.2 (SAS Institute 2001). This procedure takes a data set of multiple, correlated dependent variables and reduces its dimensionality to fewer "factors" that explain some portion of this overall multivariate variance. With PROMAX rotation, the produced factors are allowed to correlate to a limited extent, thus increasing the explained variation. I accepted all factors with eigenvalues >1.0, and tested for bird and ant effects on factor scores according to the same statistical methodology described for arthropods.

Results

Effects on pine arthropods

I collected 111 756 arthropods for a collection of 190 $\pm$ 16 arthropods/branch (mean $\pm$ SE). Total canopy arthropod load (milligrams arthropod/kilogram pine, averaged across all treatments and sampling periods) was 17% ants, 22% predators, and 61% herbivores. Herbivore load was 55% tended aphid species, 24% untended aphid species, 2% non-aphid sap feeders, and 19% chewing herbivores. The trees assigned to each of the four bird and ant exclusion treatments did not differ in arthropod community composition prior to my exclusion of birds and ants (based on Wilks' λ: bird, $F_{8,72} = 0.59$, $P = 0.78$; ant, $F_{8,72} = 0.56$, $P = 0.81$; bird $\times$ ant, $F_{8,72} = 1.48$, $P = 0.18$). Arthropod community composition was affected by bird exclusion, ant exclusion, and sampling month, and by interactions between bird and ant effects and between ant and sampling month (see MANOVA; see Appendix). While the abundance of predatory and herbivorous arthropods changed substantially over the course of the experiment (Fig. 2), all interactions with month were due to differences in the strength, but not direction, of bird and ant effects. As a result, the effects of birds and ants on each arthropod group are displayed in Fig. 3 without respect to sampling month.

Predatory arthropods.—Birds reduced the abundances of hunting spiders by 24% but had no effects on web-spinning spiders (Fig. 3, Appendix). Ants reduced the abundances of these predator groups by 46% and 18%, respectively (Fig. 3, Appendix). These effects of birds and ants were additive. In the case of aphid specialist predators, there was a weak but significant antagonistic interaction: individually, birds and ants reduced the density of these predators by 44% and 57%, respectively, but their combined effect was only 73%, less than the 76% that is predicted by the multiplicative null model (Fig. 3, Appendix). On trees with ants, birds reduced ant density by 49%, and this effect of birds varied among sampling months (Fig. 3, Appendix).

Herbivorous arthropods.—There was a strong antagonistic interaction between the effects of birds and ants on untended aphid species: individually, birds and ants reduced the density of these herbivores by 34% each, but their combined effect was only 37%, much less than the 56% reduction that is predicted by the multiplicative null model (Fig. 3, Appendix). Birds and ants reduced the density of non-aphid sap feeders by 36% and 46%, respectively, and these effects were additive (Fig. 3, Appendix). Neither birds nor ants affected chewing herbivore density (Fig. 3, Appendix). The negative effects of birds and the positive effects of ants interacted for tended aphid species (Fig. 3, Appendix). Birds reduced the abundance of tended aphid species more on trees with than without ants, with 85% and 61% reductions, respectively. Ants increased the abundance of tended aphid species by 196% in the absence of birds but only by 15% in their presence. The effects of birds and ants on total herbivore abundance mirrored these results for tended aphid species (Fig. 4, Appendix). Birds reduced total herbivore abundance by more on trees with than without ants, with 66% and 40% reductions, respectively. Ants increased total herbivore abundance by 41% in the absence of birds but reduced it by 5% in their presence.

Effects on pine

Pine growth and damage.—Neither birds nor ants affected foliage damage by chewing herbivores (Fig. 3, Appendix). By fall 2003 chewing herbivores had removed only 5.0% $\pm$ 0.4% of the foliage that flushed in 2001. The bivariate analysis (MANOVA) of wood

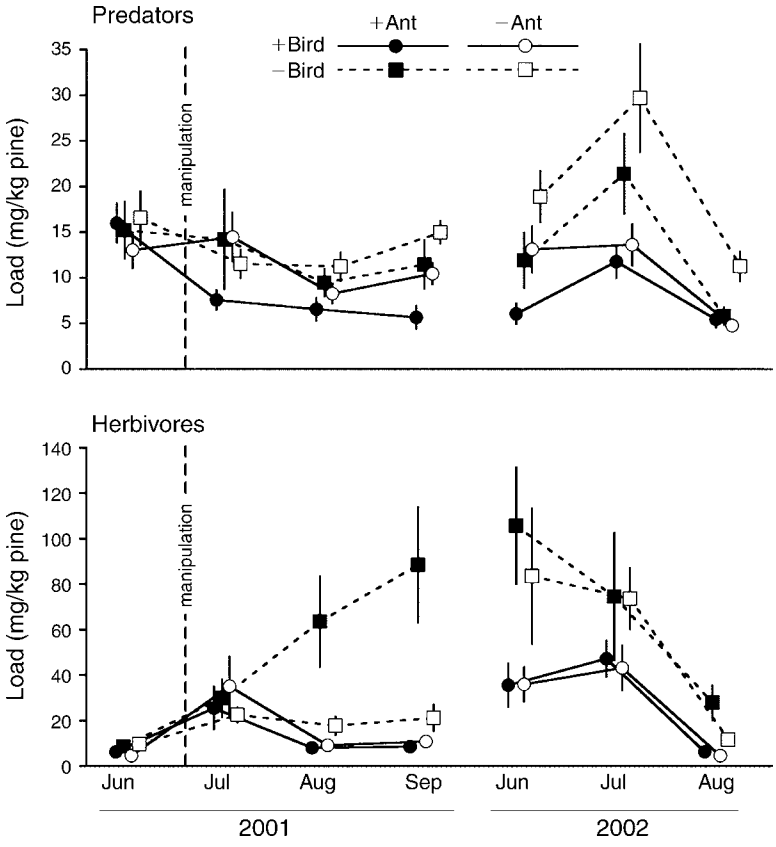

FIG. 2. Pine canopy predator and herbivore density (mean ± SE, $N = 21$) in 2001 and 2002 for pines in control (with birds and ants), bird exclusion, ant exclusion, and dual exclusion treatments. Herbivore and predator density are expressed as loads, i.e., milligrams of arthropod biomass per kilogram of pine branch biomass of wood and foliage combined (see *Methods: Effects on pine arthropods*). The June 2001 sampling was conducted immediately prior to the installation of treatments. For predators, the effects of bird exclusion, ant exclusion, and sampling month were significant (Appendix). For herbivores, the effects of bird exclusion, sampling month, bird exclusion × sampling month interaction, and ant exclusion × sampling month interaction were significant (Appendix).

RGR and foliage RGR showed significant effects of year, birds, and a bird-by-year interaction, but no effects of, or interactions with, ants (Appendix). Subsequent univariate tests showed significant effects of birds and year for both wood RGR and foliage RGR, and there was a bird-by-year interaction for wood RGR. The effect of birds on foliage growth, averaged across experimental years, was an 18% increase in growth from 23 ± 1.7 g (per branch tip) to 27 ± 1.8 g (Fig. 3). I inspected the effects of birds in each year because wood RGR interacted with year. Wood growth was 3.5 ± 0.1 g (per branch tip) in 2001 and was not affected by birds ($F_{1,55} = 0.39$, $P = 0.54$). Birds increased wood growth in 2002 by 21% from 1.70 ± 0.13 g to 2.05 ± 0.12 g ($F_{1,55} = 5.35$, $P = 0.0244$), and in 2003 by 34% from 0.88 ± 0.1 g to 1.18 ± 0.06 g ($F_{1,55} = 9.86$, $P = 0.0027$; Fig. 3).

Pine phloem chemistry.—I detected nine monoterpenes and there were two factors with eigenvalues >1.0 that together explained 59% of the total variation in phloem chemistry. Myrcene, δ3-carene, and γ-terpinene loaded heavily on factor 1 (hereafter F1), while camphene, β-phellandrene, and β-pinene loaded heavily on factor 2 (hereafter F2). Limonene, α-pinene, and terpinolene loaded moderately on both factors. The effects of birds and ants were not significant for F1, but there was a significant bird effect and bird-by-ant interaction on F2 (Appendix). Birds had little effect on the concentration of F2 monoterpenes in the absence of ants (2% reduction from 3.2 ± 0.4 mg/g to 3.1 ± 0.5 mg/g) but increased their concentration by 83% from 2.2 ± 0.3 mg/g to 4.0 ± 0.6 mg/g in the presence of ants.

DISCUSSION

Effects on pine arthropods

Birds and ants had strong negative effects on most arthropods, but the effects of birds were consistently weaker than those of ants (Fig. 3). By preying upon both predatory and herbivorous arthropod groups, birds and ants each acted as intraguild predators. Consequently, some of their direct negative effects on herbivores were likely counterbalanced by the removal of predatory arthropods. While it has been proposed that intraguild predators may have little net effect on herbivores (Polis and Holt 1992, Polis and Strong 1996), these results

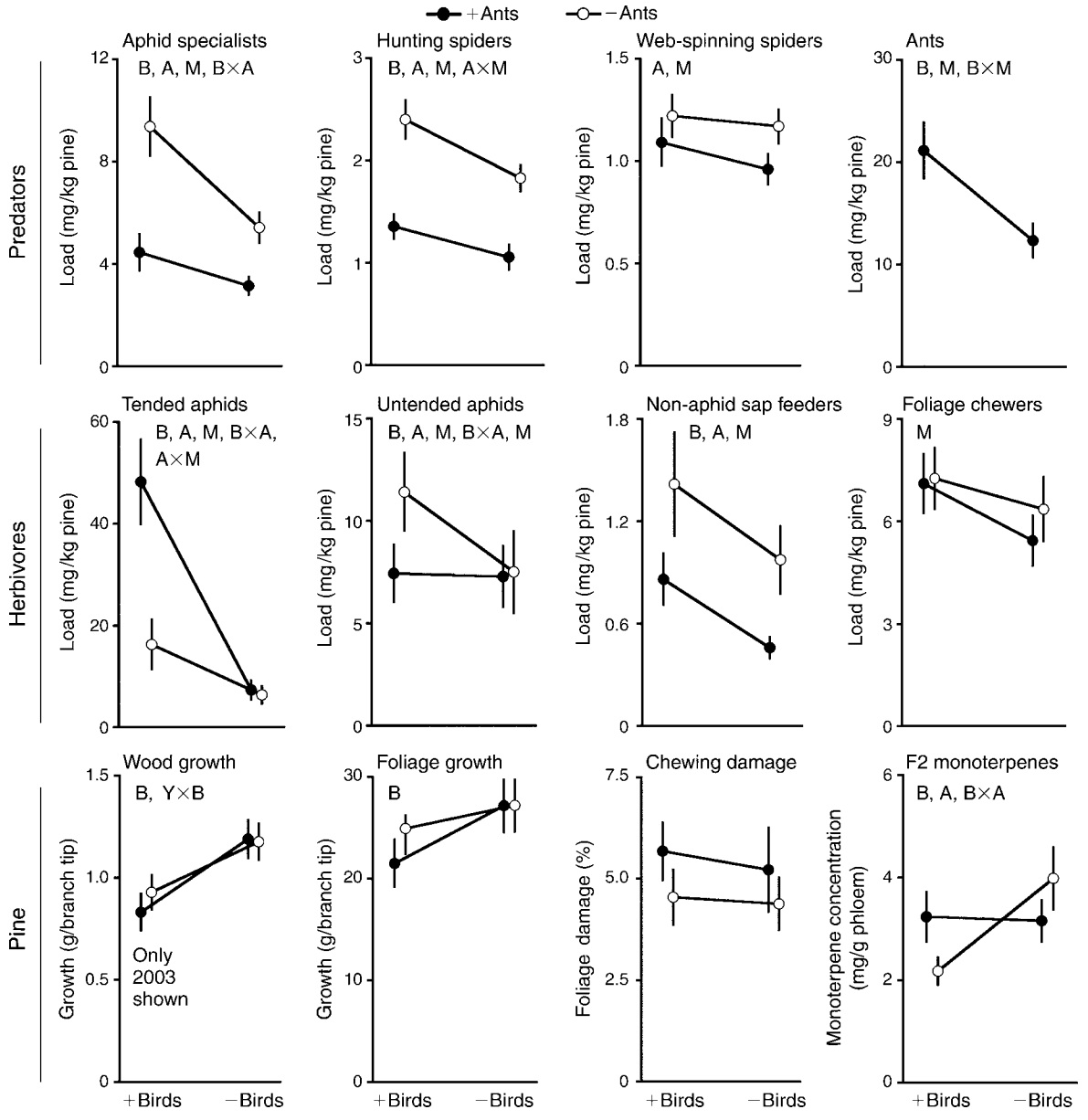

FIG. 3. Interaction graphs for the effects of birds and ants on pine canopy arthropods and on pine. The text at the top of each panel indicates the response variable and significant ($P < 0.05$) effects of birds (B), ants (A), time (month, M for arthropods; year, Y for pine response variables) and their interactions (e.g., B × A). Detailed statistical results are provided in the Appendix. Values for arthropods (means ± SE) are across six posttreatment sampling months (July 2001–August 2002). Interactions between bird and ant effects on arthropod densities and sampling month are due to temporal differences in the strength (not the direction) of the effects of birds and ants. Pine responses (means ± SE) are across three experimental years (2001–2003), except for wood growth. Bird effects on wood growth increased in strength each year (2001, no effect; 2002, 21% increase by birds; 2003, 34% increase by birds); only 2003 data are shown. All statistical tests were performed against a multiplicative null model (on log-transformed data), but untransformed data are displayed.

demonstrate that birds and ants (two taxonomically and ecologically distinct groups of predators) both reduced herbivore abundance despite also removing predatory arthropods.

The effects of birds and ants interacted strongly for ant-tended aphid species. In the absence of birds, ants doubled in density and tended aphid species nearly tripled. Past work suggested that much of this effect of birds was nonconsumptive, and due to birds disrupting the ant–aphid mutualism by inducing changes in ant behavior (Mooney 2006); ants increased their foraging to bird-exclusion branches and the per capita benefit of ants to mutualist aphids was higher in the absence of birds. As a consequence, both Mooney (2006) and the

present study demonstrate that *Formica podzolica* provides almost no detectable benefit to mutualist aphids in the presence of birds. In contrast to *F. podzolica*, aphids may in fact benefit from tending by larger and more aggressive ant species that can repel insectivorous birds (Haemig 1996, Mooney 2006).

Birds reduced ant abundance by nearly half, yet the combined predatory effects of birds and ants were additive for most arthropod groups (Fig. 3). It would seem the predatory effects of ants should be lower in the presence of birds, and consequently that the combined predatory effects of birds and ants should be less than the sum of their individual effects (i.e., an antagonistic interaction, Fig. 1c). Much of the negative effects of birds on ants was likely due to birds disrupting the ant–aphid mutualism (Mooney 2006). Birds may thus have reduced the abundance of aphid-tending ants without substantially reducing the number of prey-foraging ants. Because untended aphid species feed in the same microhabitats as ant-tended species, the benefits of bird exclusion to untended aphid species may have been negated by the simultaneous local increase in aphid-tending ants. This scenario would explain why the effects of birds and ants interacted antagonistically for untended aphid species. If birds did not affect prey-foraging ants, it would explain why bird and ant effects were additive or nearly so for hunting spiders, non-aphid sap feeders, and aphid specialist predators. In any event, these results demonstrate that the strength of multiple predator effects is determined not only by predator–predator interactions, but also by attributes of the herbivores (Sih et al. 1998), and that the combined effects of multiple predators can vary substantially within a single community.

The nonadditive effects of birds and ants on tended aphid species were mirrored in their effects on total herbivore abundance (Fig. 4) because tended aphid species constituted over half of herbivore biomass. Ants increased herbivore abundance by 41% when birds were excluded, but had little effect in the presence of birds. Likewise, birds reduced herbivore abundance more when ants were present (66%) than when they were excluded (40%). Birds and ants also affected the relative abundance of herbivore groups independent of their effects on absolute abundance (Fig. 4). Consequently, while birds reduced herbivore abundance on trees both with and without ants, ants altered the composition of the herbivore community upon which birds acted. Although ants did not affect herbivore abundance in the presence of birds, they nevertheless had strong effects on the species composition of the herbivore community.

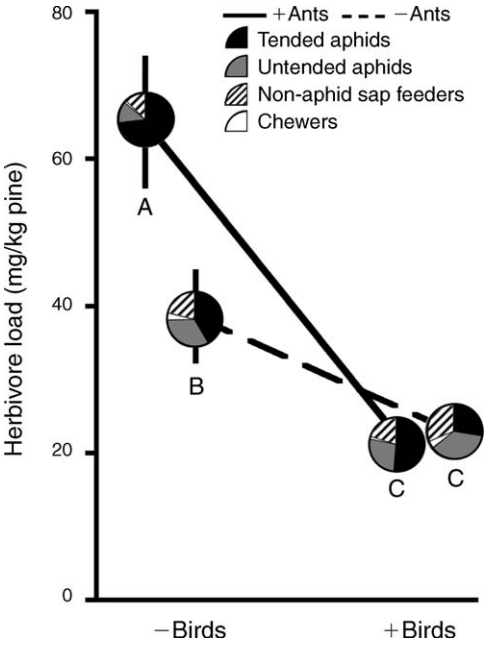

FIG. 4. Interaction graph for the effects of birds and ants on total herbivore density in pine canopies, and pie charts depicting herbivore community composition in each treatment. Herbivore densities (means ± SE) are shown across six posttreatment sampling months. Means not sharing a letter differ significantly ($P < 0.05$), and the interaction between bird and ant effects is significant ($P = 0.0318$; Appendix).

Effects on pine

Although birds and ants had interactive effects on total herbivore abundance (Fig. 4), only the effects of birds cascaded to affect pine growth. Birds increased foliage growth by 18%, while the effects of birds on wood growth increased across years, reaching 34% by 2003. Consequently, these effects of birds on pines with and without ants were indistinguishable, even though the herbivore biomass upon which birds acted was substantially higher on trees with ants. The lower herbivore biomass on ant-exclusion trees thus had an equivalent effect on pine growth as the more abundant herbivores on trees with ants. Because ants changed the composition of the herbivore community from untended to tended sap-feeding herbivores (Fig. 4), it is likely that at equivalent densities the former had stronger effects on pine growth.

In contrast to pine growth, there was a strong interaction between the effects of birds and ants on pine phloem chemistry. Birds increased the abundance of F2 monoterpenes (camphene, β-phellandrene, β-pinene) by 83% when ants were excluded but had no detectable effects in the presence of ants (Fig. 3). So as with pine growth, birds had stronger effects on the secondary chemistry of ant-excluded pine trees than would be predicted based on how they affected total herbivore abundance. These results are consistent with untended aphids being largely responsible for the effects on pine chemistry; in the presence of ants, birds had no detectable influence on either untended aphids or pine chemistry, but in the absence of ants birds had strong effects on each. While exploratory analyses did not reveal correlations between the abundance of any

PLATE 1. Birds and ants in ponderosa pine (*Pinus ponderosa*) canopies. (Left) A Mountain Chickadee (*Poecile gambeli*) perched next to pine foliage. Photo credit: Steve Holt. (Right) An ant (*Formica podzolica*) descending a pine trunk with a caterpillar in its mandibles. Photo credit: K. A. Mooney.

herbivore groups and pine secondary chemistry (K. A. Mooney, *unpublished data*), this may not be surprising because arthropods and phloem samples were collected from different pine branches.

While it may be logically predicted that predators should indirectly affect plant secondary chemistry, this is only the third study to test for such dynamics. Under seminatural conditions Griffin and Thaler (2006) found this indirect effect, while Stamp and Bowers (2000) did not. This study thus documents a novel source of phenotypic variation in pine monoterpenes and provides the first documentation of predators influencing plant chemistry in a natural community. Such dynamics can be expected, in turn, to indirectly influence interactions between pine and a diversity of its parasites and herbivores (Mitton and Sturgeon 1982, Snyder 1992, Paine and Hanlon 1994, Snyder et al. 1996).

Predation, mutualism, and community structure

The relative importance of mutualism and predation in structuring communities depends not just on the frequency of these interactions (Stachowicz 2001, Bruno et al. 2003), but also on whether their combined influence is additive, positive-biased, or negative-biased (Fig. 1). In the ponderosa pine community, the effects of birds and ants on tended aphids and total herbivore abundance were approximately equal in magnitude when they acted alone. Yet in combination, the effects of birds trumped those of ants in a negative-biased interaction. While it is as yet unclear how common such dynamics may be, there are a number of research areas that provide insight into emergent properties from effects of opposing signs. Linhart et al. (2005) measured the beneficial effects of predators and the negative effects of plant competition on *Thymus vulgaris* and found negative-biased interactions, i.e., plants only benefited from predators in the absence of competition. The combined influences of herbivores and pollinators on plant fitness also appear to show negative-biased interactions because the fitness benefits of pollinators are reduced by herbivory (Strauss and Armbruster 1997, Strauss and Murch 2004). In contrast, the combined positive effects of ants and negative effects of herbivores on myrmecophilous plants appear to show a positive-biased interaction because predatory ants reduce herbivore damage (Agrawal and Rutter 1998). While there is currently not a framework for predicting the combined influence of mutualism and predation, past work on emergent effects in other contexts suggests that nonadditive dynamics are likely to be common (Wootton 1994, Sih et al. 1998, Hambäck and Beckerman 2003).

Emergent properties result in ecological contingency when there is temporal or spatial variation in community species composition. Here I have shown that birds had stronger effects on pine herbivores in the presence than absence of ants. Because ant abundance can vary

by orders of magnitudes among neighboring trees (K. Mooney, *personal observation*), the top-down effects of birds are also likely to vary at this fine-grained scale. Fine-grained variation in food web structure may also have evolutionary implications; emergent properties from interactions that affect a species' fitness result in diffuse selection (Inouye and Stinchcombe 2001, Linhart et al. 2005). While the evolutionary implications of such ecological contingency have been considered at the landscape scale (Thompson 1994), less attention has been given to the implications of fine-scale variation.

I documented an emergent effect of birds and ants directly on herbivores that failed to produce an emergent indirect effect on pine growth. This occurred because the influence of ants attenuated, such that only the effects of birds cascaded to pine. While the attenuation of trophic cascades has been proposed to be common in species-rich communities (Strong 1992), the implications of such attenuation for indirect emergent properties have not been considered. Studies that have manipulated multiple predators in a tritrophic context provide some insight. Morin (1995) found the predatory effects of newts and salamanders on tadpoles interacted antagonistically, but these predators each increased phytoplankton abundance indirectly and their combined indirect effects were additive. Other studies have found indirect effects that mirrored direct effects with respect to emergent properties (Spiller and Schoener 1994, Nystrom and Abjornsson 2000, Nystrom et al. 2001, Snyder and Wise 2001, Cardinale et al. 2003). No study has found indirect emergent effects arising from additive direct effects, or indirect emergent effects differing in form (i.e., synergism, antagonism, and positive and negative bias) from that of their causal direct effects. It thus appears that nonadditive direct effects either propagate as parallel nonadditive indirect effects, or attenuate to become additive; emergent properties apparently do not strengthen or change in form. As a consequence, indirect interactions may be subject to relatively less ecological contingency than their composite direct interactions. Here I showed that the effect of birds on herbivores was contingent on the presence of ants, but the indirect effect of birds on pine growth was constant whether or nor ants were present.

Birds and ants are two of the most studied groups of terrestrial animals and their importance as consumers has been well documented. The present study was motivated by the notion that characterizing the emergent properties of bird and ant effects could contribute to our understanding of how these animals influence their resident communities. In fact, emergent properties were a central component of how birds and ants influenced pine arthropods, growth, and secondary chemistry.

Acknowledgments

This research was supported by the Rocky Mountain Research Station, U.S. Department of Agriculture Forest Service, the University of Colorado Undergraduate Research Opportunities Program, and the University of Colorado Department of Ecology and Evolutionary Biology. Field assistance came from Jenny Rhors, Mark Gillilan, Riley Pratt, Jon Haloin, Chris Gocha, Kim Ballare, Jose Becerril, John Schmidt, Kunal Mandal, Colin Gotlieb, Chris Morgan, Renee Keele, and Morgan Smith. Logistical assistance came from Brian Geils, Steve Tapia, and Wayne Shepperd. This experiment and manuscript were greatly improved by comments from and discussions with the Boulder Plant–Animal Interaction group, Yan Linhart, M. Deane Bowers, Sharon Collinge, Carl Bock, Mary Power, Ken Keefover-Ring, Anurag Agrawal, and Jen Thaler.

Literature Cited

Agrawal, A. A., and M. T. Rutter. 1998. Dynamic anti-herbivore defense in ant-plants: the role of induced responses. Oikos 83:227–236.

Bruno, J. F., J. J. Stachowicz, and M. D. Bertness. 2003. Inclusion of facilitation into ecological theory. Trends in Ecology and Evolution 18:119–125.

Cardinale, B. J., C. T. Harvey, K. Gross, and A. R. Ives. 2003. Biodiversity and biocontrol: emergent impacts of a multi-enemy assemblage on pest suppression and crop yield in an agroecosystem. Ecology Letters 6:857–865.

Ferguson, K. I., and P. Stiling. 1996. Non-additive effects of multiple natural enemies on aphid populations. Oecologia 108:375–379.

Griffin, C. M., and J. S. Thaler. 2006. Insect predators affect plant resistance via density- and trait-mediated indirect interactions. Ecology Letters 9:338–346.

Gruner, D. S. 2004. Attenuation of top-down and bottom-up forces in a complex terrestrial community. Ecology 85:3010–3022.

Haemig, P. D. 1996. Interference from ants alters foraging ecology of great tits. Behavioral Ecology and Sociobiology 38:25–29.

Halaj, J., and D. H. Wise. 2001. Terrestrial trophic cascades: how much do they trickle? American Naturalist 157:262–281.

Hambäck, P. A., and A. P. Beckerman. 2003. Herbivory and plant resource competition: a review of two interacting interactions. Oikos 101:26–37.

Hölldobler, B., and E. O. Wilson. 1990. The ants. Belknap Press of Harvard University Press, Cambridge, Massachusetts, USA.

Inouye, B., and J. R. Stinchcombe. 2001. Relationships between ecological interaction modifications and diffuse coevolution: similarities, differences, and causal links. Oikos 95:353–360.

Latta, R. G., Y. B. Linhart, L. Lundquist, and M. A. Snyder. 2000. Patterns of monoterpene variation within individual trees in ponderosa pine. Journal of Chemical Ecology 26: 1341–1357.

Linhart, Y. B., K. Keefover-Ring, K. A. Mooney, B. Breland, and J. D. Thompson. 2005. A chemical polymorphism in a multi-trophic setting: thyme monoterpene composition and food web structure. American Naturalist 166:517–529.

Litvak, M. E., and R. K. Monson. 1998. Patterns of induced and constitutive monoterpene production in conifer needles in relation to insect herbivory. Oecologia 114:531–540.

Losey, J. E., and R. F. Denno. 1998. Positive predator–predator interactions: enhanced predation rates and synergistic suppression of aphid populations. Ecology 79:2143–2152.

Marquis, R. J., and C. J. Whelan. 1994. Insectivorous birds increase growth of white oak through consumption of leaf-chewing insects. Ecology 75:2007–2014.

Mitton, J. B., and K. B. Sturgeon. 1982. Bark beetles in North American conifers: a system for the study of evolutionary biology. First edition. University of Texas Press, Austin, Texas, USA.

Moon, D. C., and P. Stiling. 2004. The influence of a salinity and nutrient gradient on coastal vs. upland tritrophic complexes. Ecology 85:2709–2716.
Mooney, K. A. 2006. The disruption of an ant–aphid mutualism increases the effects of insectivorous birds on pine herbivores. Ecology 87:1805–1815.
Mooney, K. A., and Y. B. Linhart. 2006. Contrasting cascades: insectivorous birds increase pine but not parasitic mistletoe growth. Journal of Animal Ecology 75:350–357.
Mooney, K. A., and C. V. Tillberg. 2005. Temporal and spatial variation to ant omnivory in pine forests. Ecology 86:1225–1235.
Morin, P. J. 1995. Functional redundancy, nonadditive interactions, and supply-side dynamics in experimental pond communities. Ecology 76:133–149.
Nystrom, P., and K. Abjornsson. 2000. Effects of fish chemical cues on the interactions between tadpoles and crayfish. Oikos 88:181–190.
Nystrom, P., O. Svensson, B. Lardner, C. Bronmark, and W. Graneli. 2001. The influence of multiple introduced predators on a littoral pond community. Ecology 82:1023–1039.
Paine, T. D., and C. C. Hanlon. 1994. Influence of oleoresin constituents from *Pinus ponderosa* and *Pinus jeffreyi* on growth of Mycangial fungi from *Dendroctonus ponderosae* and *Dendroctonus jeffreyi*. Journal of Chemical Ecology 20: 2551–2563.
Polis, G. A., and R. D. Holt. 1992. Intraguild predation: the dynamics of complex trophic interactions. Trends in Ecology and Evolution 7:151–154.
Polis, G. A., and D. R. Strong. 1996. Food web complexity and community dynamics. American Naturalist 147:813–846.
Rogers, L. E., W. T. Hinds, and R. L. Buschbom. 1976. General weight vs length relationship for insects. Annals of the Entomological Society of America 69:387–389.
Root, R. B. 1996. Herbivore pressure on goldenrods (*Solidago altissima*): its variation and cumulative effects. Ecology 77: 1074–1087.
Rosenheim, J. A. 1998. Higher-order predators and the regulation of insect herbivore populations. Annual Review of Entomology 43:421–447.
SAS Institute. 2001. SAS version 8.2. SAS Institute, Cary, North Carolina, USA.
Schmitz, O. J., P. A. Hambäck, and A. P. Beckerman. 2000. Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. American Naturalist 155: 141–153.
Shurin, J. B., E. T. Borer, E. W. Seabloom, K. Anderson, C. A. Blanchette, B. Broitman, S. D. Cooper, and B. S. Halpern. 2002. A cross-ecosystem comparison of the strength of trophic cascades. Ecology Letters 5:785–791.
Sih, A., G. Enlund, and D. Wooster. 1998. Emergent impacts of multiple predators on prey. Trends in Ecology and Evolution 13:350–355.
Snyder, M. A. 1992. Selective herbivory by Aberts squirrel mediated by chemical variability in ponderosa pine. Ecology 73:1730–1741.
Snyder, M. A., B. Fineschi, Y. B. Linhart, and R. H. Smith. 1996. Multivariate discrimination of host use by dwarf mistletoe *Arceuthobium vaginatum* subsp *cryptopodum*: inter- and intraspecific comparisons. Journal of Chemical Ecology 22: 295–305.
Snyder, W. E., and D. H. Wise. 2001. Contrasting trophic cascades generated by a community of generalist predators. Ecology 82:1571–1583.
Spiller, D. A., and T. W. Schoener. 1994. Effects of top and intermediate predators in a terrestrial food web. Ecology 75: 182–196.
Sprugel, D. G. 1991. Disturbance, equilibrium, and environmental variability: what is "natural" vegetation in a changing environment? Biological Conservation 58:1–18.
Stachowicz, J. J. 2001. Mutualism, facilitation, and the structure of ecological communities. BioScience 51:235–246.
Stamp, N. E., and M. D. Bowers. 2000. Do enemies of herbivores influence plant growth and chemistry? Evidence from a seminatural experiment. Journal of Chemical Ecology 26:2367–2386.
Strauss, S. Y., and W. S. Armbruster. 1997. Linking herbivory and pollination: new perspectives on plant and animal ecology and evolution. Ecology 78:1617–1618.
Strauss, S. Y., and P. Murch. 2004. Towards an understanding of the mechanisms of tolerance: compensating for herbivore damage by enhancing a mutualism. Ecological Entomology 29:234–239.
Strong, D. R. 1992. Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. Ecology 73: 747–754.
Thompson, J. N. 1994. The coevolutionary process. University of Chicago Press, Chicago, Illinois, USA.
Thoss, V., and J. A. Byers. 2006. Monoterpene chemodiversity of ponderosa pine in relation to herbivory and bark beetle colonization. Chemoecology 16:51–58.
Warrington, S., and J. B. Whittaker. 1985. An experimental field study of different levels of insect herbivory induced by *Formica rufa* predation on sycamore (*Acer pseudoplatanus*. II. Aphidoidea). Journal of Applied Ecology 22:787–796.
Way, M. J. 1963. Mutualism between ants and honey-dew producing Homoptera. Annual Review of Entomology 8: 307–344.
Wootton, J. T. 1994. Putting the pieces together: testing the independence of interactions among organisms. Ecology 75: 1544–1551.

APPENDIX

Statistical analyses for treatment and time effects on arthropods and on ponderosa pine (*Ecological Archives* E088-121-A1).