

A conditional trophic cascade: Birds benefit faster growing trees with strong links between predators and plants

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Abstract. Terrestrial systems are thought to be organized predominantly from the bottom-up, but there is a growing literature documenting top-down trophic cascades under certain ecological conditions. We conducted an experiment to examine how arthropod community structure on a foundation riparian tree mediates the ability of insectivorous birds to influence tree growth. We built whole-tree bird exclosures around 35 mature cottonwood (*Populus* spp.) trees at two sites in northern Utah, USA, to measure the effect of bird predation on arthropod herbivore and predator species richness, abundance, and biomass, and on tree performance. We maintained bird exclosures over two growing seasons and conducted nondestructive arthropod surveys that recorded 63 652 arthropods of 689 morphospecies representing 19 orders. Five major patterns emerged: (1) We found a significant trophic cascade (18% reduction in trunk growth when birds were excluded) only at one site in one year. (2) The significant trophic cascade was associated with higher precipitation, tree growth, and arthropod abundance, richness, and biomass than other site–year combinations. (3) The trophic cascade was weak or not evident when tree growth and insect populations were low apparently due to drought. (4) Concurrent with the stronger trophic cascade, bird predation significantly reduced total arthropod abundance, richness, and biomass. Arthropod biomass was 67% greater on trees without bird predation. This pattern was driven largely by two herbivore groups (folivores and non-aphid sap-feeders) suggesting that birds targeted these groups. (5) Three species of folivores (Orthoptera: *Melanoplus* spp.) were strong links between birds and trees and were only present in the site and the year in which the stronger trophic cascade occurred. Our results suggest that this trophic system is predominately bottom-up driven, but under certain conditions the influence of top predators can stimulate whole tree growth. When the most limiting factor for tree growth switched from water availability to herbivory, the avian predators gained the potential to reduce herbivory. This potential could be realized when strong links between the birds and plant, i.e., species that were both abundant herbivores and preferred prey, were present.

Key words: *bird predation; bottom-up; community effects; foundation species; herbivory; limiting factor; Populus; predator removal; strong interactors; top-down; trophic cascade.*

INTRODUCTION

Several reviews of empirical studies in terrestrial systems suggest that community-level trophic cascades are rare, that species-level cascades are widespread, and that bottom-up forces largely determine the distribution of biomass among trophic levels (Oksanen et al. 1981, Polis and Strong 1996, Pace et al. 1999, Schmitz et al. 2000, Halaj and Wise 2001). Predator effects on herbivores rarely extend to net effects on biomass of primary producers (Strong 1992), but a growing number of observational studies (e.g., McLaren and Peterson 1994, Ripple et al. 2001, Terborgh et al. 2001, Ripple and Beschta 2006) and experiments (e.g., Atlegrim 1989, Marquis and Whelan 1994, Mooney and Linhart 2006,

Schmitz 2008) refute this generality and suggest that certain ecological conditions may strengthen cascading effects. Identification of these conditions is necessary to develop general ecological principles, and to better understand the roles of top predators and the implications of their addition or removal (Schmitz et al. 2000).

Predator removal experiments offer the greatest potential for strong inference about mechanisms that affect trophic cascade strength. Most studies of terrestrial cascades manipulate invertebrate predators (Schmitz et al. 2000), ignoring predation by endothermic vertebrates on invertebrates that can produce strong trophic cascades (Borer et al. 2005). Birds are a ubiquitous class of top vertebrate predators. We found eight studies that excluded birds and measured plant biomass (or a surrogate response by primary producers), to potentially detect a strong top-down trophic cascade (Polis et al. 2000, Shurin et al. 2002). Of these eight studies, three found a strong trophic cascade, i.e., bird

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removal reduced plant biomass (Marquis and Whelan 1994, Boege and Marquis 2006, Mooney and Linhart 2006); three found a weak cascade, i.e., bird exclusion increased leaf damage but did not reduce biomass (Sipura 1999, Strong et al. 2000, Norrdahl et al. 2002); one found no effect by birds on plants (Gruner 2004); and one found greater plant biomass in bird exclosures (Lichtenberg and Lichtenberg 2002). Both studies that reported strong trophic cascades involved prey species that were strong interactors; i.e., species or species groups that link predators and plants because they are abundant herbivores highly susceptible to bird predation. For Boege and Marquis (2006) and Marquis and Whelan (1994), the strong interactors were lepidopteran larvae. For Mooney and Linhart (2006), the strong interactors were aphids as important herbivores, and their mutualist ants as the important bird prey. All studies that found weak or no cascades cited the lack of strong interactors or other characteristics of the prey community, and variable plant response to herbivory, as explanations for the attenuation of the top-down effects.

Bottom-up factors may affect bird-driven trophic cascades. For example, increased plant growth should increase herbivore consumption rates, leading to herbivory becoming a stronger limiting factor to growth (Leibold 1989, Polis 1999). This response sets the stage for predators to reduce herbivory and benefit the plant. Only four studies manipulated bottom-up factors: soil fertility (Sipura 1999, Gruner 2004, Boege and Marquis 2006), sunlight (Lichtenberg and Lichtenberg 2002), and plant chemical defense (Sipura 1999); and all weakly or inconsistently affected the trophic cascades.

Takekawa and Garton (1984), Holling (1988), Folke et al. (1996), Niemi et al. (1998), Whelan et al. (2008) and others claim that forest birds provide the ecological service of pest control in complex, natural ecosystems. However, others predict that species-rich communities are unlikely to support trophic cascades because the associated complex species interactions disperse and attenuate top-down forces (Strong 1992, Polis and Strong 1996, Polis 2000). To date, only two studies excluded birds from whole adult trees with species-rich arthropod communities and measured plant biomass response (Gruner 2004, Boege and Marquis 2006). These mixed results and a lack of a demonstrable effect of arthropod herbivore control by birds that benefits the tree beg for additional investigation.

We evaluated the strength of bird-driven trophic cascades on cottonwoods (*Populus* spp.); a foundation species (sensu Dayton 1972) that dominate many riparian zones of the western United States. A species-level trophic cascade affecting a foundation species would have community-level implications (Polis 1999). We designed a predator removal study that used whole mature trees (up to 7 m tall) that naturally supported species-rich bird and arthropod communities. Because insect population dynamics occur on a larger than single-tree scale, the optimal design might be replicates

of multiple-tree half-hectare exclosures to buffer a central focal tree response. However, we chose a single-tree exclosure design to limit costs despite the likelihood of underestimating bird effects. Our hypotheses were: (1) Bird predation would reduce arthropod herbivory enough to increase tree growth in at least some experimental settings. (2) The relative strength of the trophic cascade would vary based on variations of tree growth, arthropod diversity, and presence of species that are strong interactors. We know of no other study conducted in North America that has tested for an avian-dominated trophic cascade in adult foundation tree species.

METHODS

Study sites

We conducted this study in 2006 and 2007 in two common gardens of naturally occurring hybrid cottonwoods (*P. angustifolia* × *P. fremontii*) planted in 1991 in northern Utah, USA, ~14 km apart. Both sites were in the lower Weber River watershed in the same semi-arid climate zone (normal precipitation 420 mm; Western Regional Climate Center, data *available online*),⁴ but one was an upland site with drier growing conditions due to well-drained soils, depth to water table >2 m, and low available water capacity. The other (valley) site had wetter growing conditions due to poorly to moderately well drained soils, depth to water table ~1.3 m, and high available water capacity (National Resources Conservation Service [NRCS] Web Soil Survey, Weber-Davis Area, Utah, *available online*).⁵ The valley site (elevation 1370 m) was more shaded due to larger trees, and the understory was dominated by perennial grasses. The upland site (elevation 1390 m) had a more diverse understory of grasses, forbs, and xeric plants such as sagebrush (*Artemisia* spp.). The valley site was flat, and had 380 trees on 1.4 ha, with adjacent large patches of natural second growth trees of several species. The upland site was gently sloping, had 306 trees on 1 ha, and fewer adjacent trees.

Tree selection and treatment assignment

All trees used in this study were F1 hybrid backcrosses to the narrowleaf parent (*P. angustifolia*), and were phenotypically similar to it. All trees of this dioecious species used in this study were sexually mature, and ranged from 4 m to ~7 m tall. We ranked 100 trees based on crown height, volume, and density, and divided the ranked list into triplets of trees closest in crown dimensions at each site. After removing outliers, we were left with 92 experimental trees. We initially randomly assigned members of each triplet to one of three treatments: control (full bird access), bird exclosure, and insecticide treatment. We were unable to

⁴ <http://wrcc.dri.edu/summary/climsmcslc.html>

⁵ <http://websoilsurvey.nrcs.usda.gov>

implement the insecticide treatment (no trees were ever treated), so we reassigned those trees to the control group. We fenced all control trees to prevent ungulate browsing that could confound bird effect on tree growth. We eliminated two trees that were damaged in a storm, yielding a sample of 35 trees with bird exclosures (15 at valley site, 20 at upland site) and 55 trees accessible to birds (18 at valley site, 37 at upland site).

Bird exclosures

We attached commercial black polyethylene bird netting with 2.5-cm square mesh size to wooden frames built around each tree in the bird exclusion treatment (Fig. 1). The net allowed almost all common arthropods to pass through, but excluded birds. On about 12 occasions we observed birds (mostly House Finches *Carpodacus mexicanus*, and Black-capped Chickadees *Parus atricapillus*) inside an exclosure attempting to escape. On two occasions we observed birds squeeze through the net into an exclosure, immediately seem to realize that they were enclosed, and promptly escape without foraging. We found no dead or injured birds inside nets. We installed nets before leaf-out (mid-May) both years of the study, and took them down after leaf senescence in the fall (mid-October) to prevent snow damage.

We tested for net effects on the trees by measuring photosynthetically active radiation (PAR) levels to the nearest micromoles per square meter per second using a Sunfleck PAR Ceptometer (Decagon Devices, Pullman, Washington, USA) and leaf photosynthetic rate on fully expanded outer canopy leaves to the nearest micromoles of CO₂ per square meter per second using a LI-COR 6400 portable photosynthesis system (LI-COR, Lincoln, Nebraska, USA) with 6-cm² clear cuvette under full sun vs. net shading. Averaged across 39 paired measurements on 13 trees with the net approximately perpendicular to the sun angle, the net reduced PAR about 14%, but reduced net photosynthetic rate only 2.2%. These results suggest that the nets had a negligible effect on tree growth.

Tree measurements

Four tree vigor characteristics were measured as treatment responses. We measured trunk circumference and installed dendrometer bands 1–1.5 m high (depending on location with no branch or bark lesion interference) in April 2006 for precise measurement of trunk growth after each treatment season. We calculated cross-sectional area (basal area) from circumference data assuming a circular trunk. In July 2005, we measured shoots on five sunlit leaders per tree, using end bud scars to estimate elongation for the three pre-treatment growing seasons. After the two treatment years, we measured shoot elongation on 10 sunlit leaders per tree. Cottonwoods flower before leaf-out in the spring using stored energy from the previous growing



FIG. 1. Two technicians conducting an arthropod survey on a cottonwood (*Populus* sp.) tree in a bird exclosure at the upland site in northern Utah, USA.

season, so we estimated seed production on the female trees each spring after the treatment seasons (2007 and 2008). Following the hierarchical sampling procedure of Schweitzer et al. (2002), we counted major flowering branches (generally flowers are clustered on the uppermost branches; low branches with just a few catkins were not “major”), the total number of catkins on a typical (visually estimated to be representative) branch, capsules on a subsample of 20 catkins, and seeds in a subsample of 15 capsules. We then multiplied seed number by each higher order count to estimate total seeds on each tree.

We also measured total nonstructural carbohydrate (TNC) concentration in sunlit shoots at the end of the second growing season. TNC concentration represents stored carbohydrates available for metabolic use by the tree before the next leaf-out (Kolb and McCormick 1991, Reichenbacher et al. 1996). We collected three vigorous leaders from east, west, and south sides in the upper canopy on each tree and froze them immediately for later analysis in the laboratory. We ground the oven-

TABLE 1. Repeated-measures MANOVA and ANOVA results for tree performance factors and leaf damage by site showed a strong year effect on shoot elongation and trunk growth of cottonwoods (*Populus* spp.) at both sites in northern Utah, USA.

Site and treatment	Shoot elongation			Trunk growth			Total nonstructural carbohydrates†		
	df	F	P	df	F	P	df	F	P
Valley site									
Bird treatment	1, 31	0.928	0.343	1, 30	0.073	0.789	1, 31	2.364	0.134
Year	1, 31	44.481	<0.001	1, 30	31.044	<0.001		...	
Year × treatment	1, 31	0.160	0.692	1, 30	0.655	0.425		...	
Upland site									
Bird treatment	1, 54	2.130	0.150	1, 54	3.942	0.052	1, 54	0.171	0.681
Year	1, 54	259.252	<0.001	1, 54	145.499	<0.001		...	
Year × treatment	1, 54	0.907	0.345	1, 54	0.693	0.409		...	

Note: Only trunk growth (cube-root transformed) at the upland site showed a bird-exclusion treatment effect ($P = 0.052$).

† ANOVA results.

dried terminal 10-cm shoot sections with buds removed in a Wiley mill until they passed through a 40-mesh sieve, and dissolved the carbohydrates by autoclaving the grounds in distilled water at 125°C for 30 min. The filtered sample solutions were analyzed for total carbon in an automated analyzer (Shimadzu TOC-VCSH with a TNM-1 unit; Shimadzu, Kyoto, Japan), and the values were adjusted for dilution to yield a standardized parts per million of TNC per sample.

To sample insect damage, we collected 60 leaves from throughout the crown of each tree in late July of 2006 and 2007. Leaves were pressed and dried, and then scanned to obtain images for a leaf analysis software program (WinFOLIA Pro 2006a; Regent Instruments 2006). Each image was manually edited so the software could discriminate insect damaged leaf area, and calculate a ratio of leaf “holes” to total leaf area. We then calculated the average percent leaf area lost to insect damage per tree.

Arthropod and bird surveys

We nondestructively surveyed arthropods on each tree three times in each growing season: early June, late June, and early July. Previous studies in these common gardens found that arthropod diversity typically peaks in early to mid July (Wimp et al. 2007). We sampled trees in the same order each sample period, resulting in a 14- to 18-day interval between samples of the same tree. Analyses presented in this report are based on combined totals of morphospecies and abundance over each respective season per year. Two technicians spent 30 min recording morphospecies (Oliver and Beattie 1996), length in millimeters, and numbers of individuals observed. One technician worked from the ground and focused on low branches, while the second surveyed higher branches accessible from a 5-m orchard ladder. In late July, concurrent with our leaf damage survey, we sampled leaf modifier species (gallers, leaf-rollers, leaf-tiers, and leaf-miners), which had not been counted in the earlier surveys.

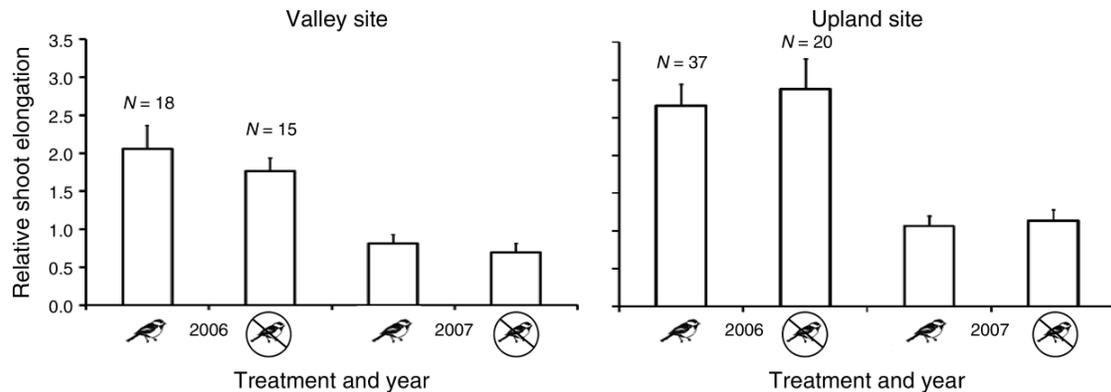


FIG. 2. Cottonwood shoot elongation (mean ± SE) during the two study years (2006, 2007) relative to the average of the three years before the study by site and bird treatment. There was no significant bird effect, but note the large yearly difference ($P < 0.0001$ at both sites), and greater yearly difference at the upland site. Bird icons indicate trees fully accessible to bird predation; no-bird icons indicate trees with birds excluded.

TABLE 1. Extended.

Seeds			Leaf damage		
df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>
1, 13	0.256	0.621	1, 31	0.450	0.507
1, 13	1.698	0.215	1, 31	0.585	0.450
1, 13	0.810	0.385	1, 31	1.388	0.248
1, 30	0.037	0.850	1, 55	0.177	0.675
1, 30	0.052	0.821	1, 55	0.635	0.429
1, 30	2.403	0.132	1, 55	0.885	0.351

Arthropod morphospecies were all placed in mutually exclusive functional groups based on feeding mode and likely interaction with the tree or its dependent community. Arthropod predators were divided into specialists or generalists based on whether they typically fed upon a single type (e.g., aphids), or a broad variety of prey. Species that had no apparent interaction with the tree or its dependent community (e.g., Ephemeroptera, carrion-feeding Diptera) were classified as vagrants and excluded from analyses. Ants were classified as omnivores.

We expanded a voucher collection of specimens that is maintained by the Colorado Plateau Biodiversity Center at Northern Arizona University. We also photographed the most common species to train survey technicians and maintain consistent morphospecies names within and between seasons. We transformed morphospecies lengths into (air-dried) biomass using published allometric equations for the various taxa (Rogers et al. 1977, Sage 1982, Sample et al. 1993), although we modified some equations based on dry weights obtained from our voucher collection.

We recorded the numbers of birds of each species seen or heard during each visit to our study sites. In 2007, to compare the study site bird communities to that of a natural riparian forest, we conducted two surveys (morning point counts at three locations each survey) on a 2-ha portion of a cottonwood forest located on the Weber River between the two study sites.

Data analysis

Three of the four growth measurements, percentage of leaf damage, and arthropod species richness data met the parametric assumptions of equal variances and normality, but percentage of basal area increment, arthropod abundance, and arthropod biomass data were significantly non-normal. Cube-root transformation of basal area increment data, and log transformations of the arthropod abundance and biomass data were normally or approximately normally distributed and met the homoscedasticity assumption, and therefore were used in MANOVAs and *t* tests.

Due to the many differences between the two study sites (i.e., growing conditions, understory characteristics, tree genotypes) we tested for treatment effects at each site separately. For three of the four growth measurements (shoot annual elongation, seed production, and cube root of annual basal area increment) and leaf damage measurement, we conducted repeated-measures MANOVA with three fixed effects; namely, treatment (birds or no birds), year (2006 or 2007), and treatment \times year. Total nonstructural carbohydrate was measured only once, and analyzed for treatment effect with a one-way ANOVA. We used the same analytical approach to test for treatment effects on arthropod abundance, richness and biomass. If there was a significant treatment \times year interaction, we conducted ANOVA to discover the source of the variation. We compared means using Student's *t* tests to evaluate our a priori hypotheses that birds would improve tree growth, reduce leaf damage, and reduce arthropod species and numbers. When we compared multiple means, we used a Bonferroni adjustment (Rice 1989). We used JMP 7.0 Fit Model platform (SAS Institute 2007) for all MANOVA and ANOVA and Microsoft Office Excel 2007 for means tests.

To test our conceptual model of the trophic relationships and identify which arthropod functional groups linked bird predation to a tree growth response, we constructed a structural equation model (Amos 16.0.1, *available online*)⁶ for the upland site in 2006 (the site-year combination for which our data were most consistent with a trophic cascade). Bird treatment was a binary exogenous variable, functional group biomass values were endogenous variables, and the significant growth response was the dependent variable of the model. A chi-square test of model fit with the data was used, with $\alpha = 0.05$. In this context, *P* values greater than α indicated good model fit.

RESULTS

Treatment and year effects on tree growth and leaf damage

There were significant year effects on shoot elongation and trunk growth at both sites, but not on the other performance measures or leaf damage (Table 1). In 2006 there was 2.5 times more shoot elongation than in 2007 (Fig. 2), and trunk basal area increment was 1.75 times greater in 2006 than 2007 (Fig. 3). This difference was primarily driven by precipitation: In the first six months of 2006, precipitation was 93% of the 30 year mean for the region, and in the same period of 2007, it was 56% of the mean (The Western Regional Climate Center, see footnote 4). In 2006, the upland site exhibited relatively more growth than the valley site (Fig. 2).

The only tree performance measure that responded strongly ($P = 0.052$) to bird treatment was trunk growth

⁶ (<http://amosdevelopment.com>)

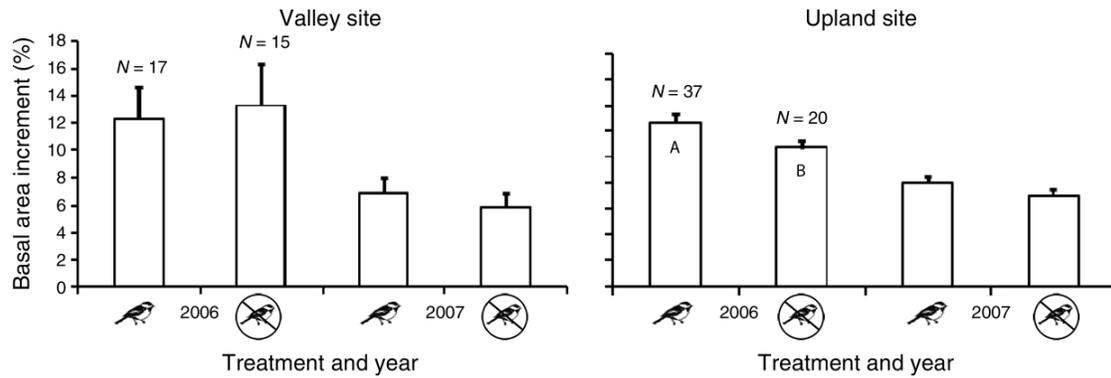


FIG. 3. Cottonwood annual basal area increment (mean + SE) during the two study years (2006, 2007) as a percentage of the initial basal area. The year difference at both sites is significant ($P < 0.0001$). Presence of avian predators had the greatest effect at the upland site in 2006, with a significant (indicated by letters A, B) 17.7% increase in trunk growth ($P = 0.038$). Symbols are as in Fig. 2.

at the upland site (Table 1), where trees with bird access grew more in both years, indicating a strong trophic cascade. Trees at the upland site with bird access grew 17.7% more in 2006, 13.9% more in 2007, and 18.3% more over both years compared to trees with birds excluded (Fig. 3). Although there was no significant treatment \times year interaction ($P = 0.409$) at the upland site, we tested the treatment effect on trunk growth each year to see if it was stronger in 2006, because the arthropod response to bird treatment was consistently stronger there in 2006, suggesting a mechanistic linkage. These tests showed a stronger effect of bird exclusion at the upland site in 2006 ($P = 0.038$) than in 2007 ($P = 0.168$). There was no significant treatment effect on TNC or seed production (Table 1). Leaf damage averaged $\sim 2.75\%$ of total leaf area and varied little among sites, years, and treatments (range 2.5% to 3.3%,

with highest damage on bird-excluded trees at the valley site in both years: 3.3% in 2006 and 3.2% in 2007).

Bird and arthropod surveys

The valley and upland sites were similar to each other and to the natural riparian forest in numbers of canopy foraging birds and bird species in both years (Table 2). The number of species ranged from 8 to 10 across sites, and the maximum numbers of individuals of each species seen at one time totaled from 19 to 27; the upland site consistently had more species but fewer individuals (Table 2). Although the bird communities were similar at the site scale, we observed that birds were not evenly distributed across trees within the sites, likely due to locations of bird territory boundaries and nest locations, adding to variation of bird predation effects among those trees.

TABLE 2. Maximum numbers of each bird species seen or heard at one time on the two study sites (valley, upland) and the riparian forest comparison site.

Bird species	2006		2007		Riparian
	Valley	Upland	Valley	Upland	
<i>Carduelis tristis</i> (American Goldfinch)	3	2	2	3	6
<i>Poecile atricapilla</i> (Black-capped Chickadee)	4	2	7	5	4
<i>Pheucticus melanocephalus</i> (Black-headed Grosbeak)	5	2	4	2	4
<i>Selasphorus platycercus</i> (Broad-tailed Hummingbird)		1	1	1	1
<i>Spizella passerina</i> (Chipping Sparrow)				1	
<i>Picoides pubescens</i> (Downy Woodpecker)	1	1	2	1	
<i>Picoides villosus</i> (Hairy Woodpecker)					1
<i>Carpodacus mexicanus</i> (House Finch)	2	2	3	3	
<i>Troglodytes aedon</i> (House Wren)					2
<i>Passerina amoena</i> (Lazuli Bunting)		2		2	
<i>Colaptes auratus</i> (Northern Flicker)		1			
<i>Icterus bullockii</i> (Bullock's Oriole)	5	5	5	4	3
<i>Vireo gilvus</i> (Warbling Vireo)		1		1	
<i>Piranga ludoviciana</i> (Western Tanager)	1				
<i>Dendroica petechia</i> (Yellow Warbler)	3		3		5
<i>Wilsonia pusilla</i> (Wilson's Warbler)	1				
Total individuals	25	19	27	23	26
Total species	9	10	8	10	8

Note: Only birds observed spending some foraging time in tree canopies are included.

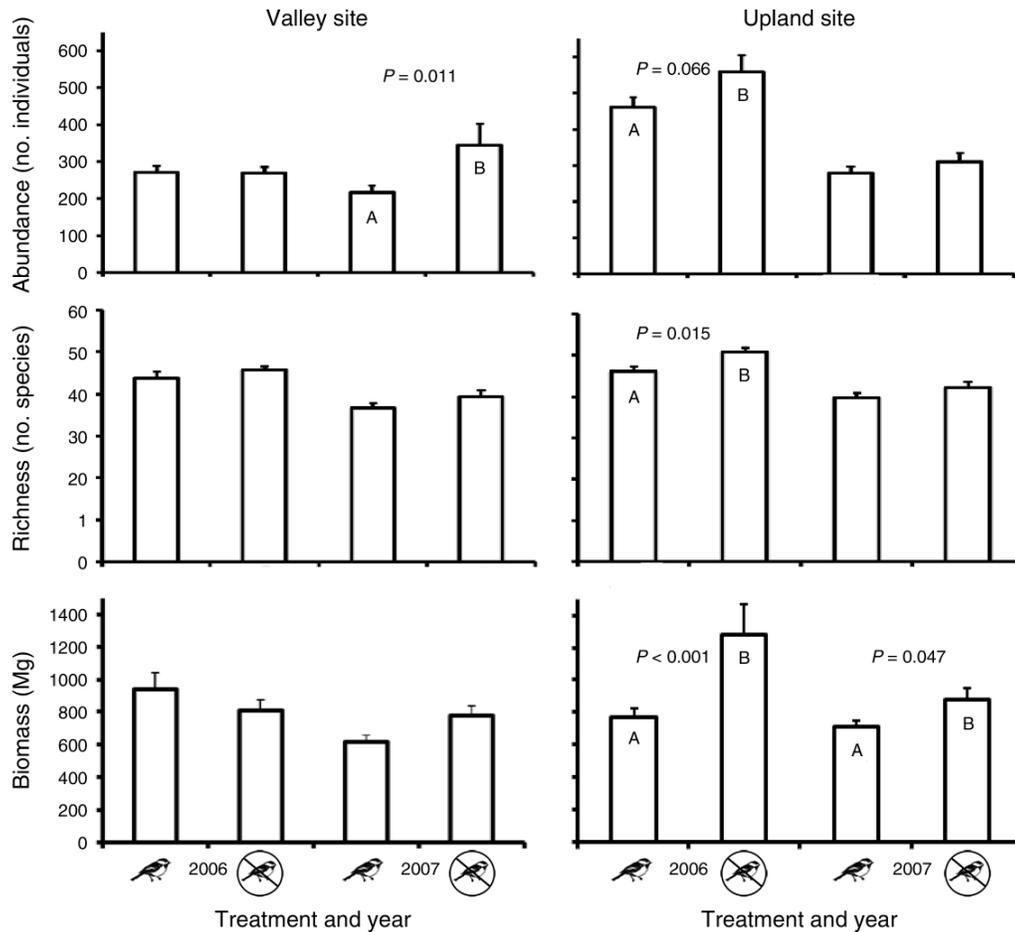


FIG. 4. Bird treatment effects (mean + SE) on arthropod community parameters by site and year (2006, 2007). Significant bird treatment effects are indicated by different letters, with P values as shown. Treatment effects were consistently stronger at the upland site in 2006. Symbols are as in Fig. 2.

Over the two years of the study, we identified 63 652 individual arthropods of 689 morphospecies representing 19 orders. This total includes some immature forms (eggs, pupae, and nymphs) of species that were not necessarily identified with the adults of the same species, and possibly includes variants within a life stage, and is therefore an overestimate of the actual species richness. The arthropod community was overwhelmingly composed of morphospecies that were counted fewer than six times within a year, but these 428 rare species contributed only 1.6% of total abundance and 9.8% of total arthropod biomass. Our analyses excluded these species because their rarity precludes them from being important links between birds and plants. We also excluded an additional 27 species of vagrants because they were unlikely to directly interact with the tree or its herbivores. The reduced list included 173 species in 2006 (the wetter year) and 152 in 2007, of which 93 species were common to both years.

Total arthropod abundance (excluding rare species) was 31% lower in 2007 than 2006, and biomass was 22% lower in 2007. Non-aphid sap-feeders (dominated by leafhoppers and planthoppers) were the most abundant herbivores and had the largest biomass, constituting 52% of the herbivore biomass in 2006, while folivores amounted to 30%. In 2006 the upland site had twice as much folivore biomass per tree as the valley site. In 2007 sap-feeders became even more dominant as they made up 75% of herbivore biomass, while folivores were only 15% and evenly distributed by site.

The removal of birds significantly increased arthropod abundance at the valley site in 2007, and richness and biomass on trees at the upland site (Fig. 4). There was a significant year \times treatment interaction for arthropod abundance at the valley site ($P = 0.010$), and for arthropod biomass at the upland site ($P = 0.038$), so we tested for treatment effect by year in those cases. Birds reduced abundance ($P = 0.011$) only in 2007 at the valley

TABLE 3. Mean biomass per tree (milligrams, with SE in parentheses) of arthropod functional groups found on treatments (B, birds; NB, no birds) at each site (valley, upland) and year (2006, 2007).

Functional group	2006				2007			
	Valley B	Valley NB	Upland B	Upland NB	Valley B	Valley NB	Upland B	Upland NB
Herbivores								
Non-aphid sap-feeders	390 (99)	283 (31)	191 (35)	347 (97)	287 (35)	342 (44)	292 (26)	375 (46)
Aphids	57 (9)	54 (14)	71 (5)	81 (7)	21 (4)	25 (7)	30 (3)	30 (4)
Folivores	139 (20)	157 (35)	90 (11)	322 (52)**	83 (18)	98 (16)	35 (5)	82 (19)*
Subtotal†	590 (95)	496 (43)	377 (42)	843 (143)**	400 (39)	477 (53)	370 (27)	493 (52)*
Predators								
Generalists	104 (19)	98 (33)	73 (9)	103 (18)	70 (13)	93 (26)	89 (13)	83 (15)
Specialists	133 (28)	161 (34)	223 (21)	257 (57)	80 (11)	120 (21)	184 (14)	212 (26)
Parasitoids	3 (1)	6 (3)	6 (2)	4 (2)	12 (3)	12 (8)	4 (1)	5 (2)
Subtotal	240 (38)	266 (42)	302 (22)	365 (59)	163 (18)	223 (42)	276 (18)	299 (31)
Omnivores								
Ants	7 (2)	6 (1)	27 (6)	29 (6)	1 (1)	0.5 (0.2)	10 (5)	17 (7)
Total arthropods	936 (107)	808 (71)	765 (51)	1284 (184)**	612 (48)	775 (66)*	710 (32)	874 (75)*

Notes: Asterisks indicate that there was a significantly greater biomass in the no-bird treatment.

* $P < 0.05$; ** Bonferroni-adjusted alpha $P < 0.003$.

† The subtotal includes some minor herbivore functional groups not listed.

site, but reduced biomass both years at the upland site ($P = 0.0006$ in 2006, $P = 0.047$ in 2007). This 68% greater biomass on the bird-excluded trees in 2006 prompted us to test whether there was a corresponding effect on arthropod richness and abundance even though there were no significant year \times treatment interactions for these at the upland site. We found a marginally significant reduction of abundance ($P = 0.066$), and a significant reduction of richness ($P = 0.015$) by birds at the upland site in 2006 (Fig. 4).

Trees with birds had significantly reduced biomass of folivores and all herbivores only at the upland site in 2006 ($P < 0.003$) compared with trees without birds (Table 3). Three species of folivorous grasshoppers (*Melanoplus* spp.) contributed most of the difference in biomass between treatment groups at the upland site, and these same species were virtually absent from the trees in 2007. Birds were associated with decreased arthropod biomass in every site-year combination except the valley site in 2006, where sap-feeder biomass was greater on trees with bird access (Table 3).

Birds were associated with nonsignificant decreases in biomass of arthropod predators in both years at both sites (Table 3). Specialist predators, consisting mostly of aphid predators, were consistently more abundant (1.5 to almost three times more biomass) than generalist predators, which were mostly spiders. Ants made up a small proportion of the total community, and were not affected by bird predation (Table 3).

Structural equation model

We applied this model to our data for the upland site in 2006 (Fig. 5). We modeled biomass of the two large herbivore functional groups (folivores, sap-feeders) at the upland site in 2006 as the mediators between the birds and the trees, using trunk growth as the dependent

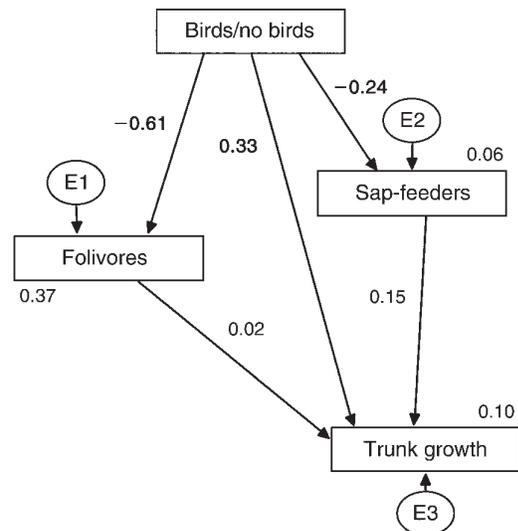


FIG. 5. A structural equation model of path strengths between the presence or absence of bird predation, biomass of the two major herbivore functional groups, and tree trunk growth at the upland site in 2006. All values are standardized to standard deviations of the respective variables. The values associated with the path arrows are partial correlation coefficients representing the strength of the connections, and only those in boldface type are significant ($P = 0.06$ for difference in abundance at upland site in 2006; included because it is consistent with the overall pattern). Numbers next to boxes represent the amount of the respective variation explained by the model. The ovals represent error terms. The model illustrates significant negative effects of birds on the herbivores and a positive bird effect on trunk growth but shows no direct effect of the herbivores on the trees (chi-square test of model fit, $\chi^2 = 2.529$, $df = 1$, $P = 0.112$).

variable. As expected from the univariate analyses, there was a significant negative relationship between bird presence and folivores and sap-feeders, and a positive relationship between bird presence and tree growth. Contrary to expectation, there was no significant path from either herbivore group to tree growth.

DISCUSSION

Conditional trophic cascade

We define a strong trophic cascade as an increase in net biomass (rather than merely a decrease in plant herbivore damage) of a plant resulting from top predators. We found an avian-dominated strong trophic cascade where birds increased trunk growth at one of our study sites more in the year with the greatest tree growth and the highest arthropod abundance, richness, and biomass. We interpret the large between-year differences in tree growth as evidence that tree growth was determined mainly by soil water availability, especially at the upland site where the lack of a water table and low available water capacity of the soils made those trees more dependent on timely precipitation. The magnitude of the trophic cascade was greater in 2006, indicated by the ~18% significantly ($P = 0.038$) greater trunk growth by trees subjected to bird predation compared with the nonsignificant ($P = 0.168$) 14% growth in 2007.

Recent studies have discovered that foliage-gleaning bats could add to the effect of removal of bird predation by net enclosures in place overnight (Kalka et al. 2008, Williams-Guillén et al. 2008). There are at least four species of foliage-gleaning bats that were potentially present at our study sites (Oliver 2000, Johnson 2008), and although they are likely less abundant than such bats in tropical areas where the above studies were conducted, we acknowledge that bats may have amplified the bird effects we observed.

This strong trophic cascade also correlated with the highest biomass of folivores on the bird-excluded trees. The three species of grasshoppers that almost wholly contributed to the higher folivore biomass on the netted trees at the upland site in 2006 were not abundant at the valley site in 2006, and were absent from both sites in 2007. Thus, these apparent strong interactors were transitory members of the tree herbivore community. We hypothesize that high populations of these grasshoppers, which are generalist herbivores usually foraging on herbaceous plants, resulted in their spreading onto the cottonwoods to forage in 2006. Despite this evidence that transitory folivores increased the herbivory load at the upland site in 2006 enough to affect tree growth (three species of grasshopper comprised 17% of all herbivore biomass), we did not detect a corresponding significant increase in leaf damage. (Leaf damage was highest at the upland site in 2006, but not significantly so.) We suggest three reasons why our measure of folivore damage did not correlate more strongly with grasshopper biomass. First, our method of

a single leaf collection in late July was not able to detect complex tree responses to leaf damage, such as premature dehiscence or stimulation of new leaf growth, nor could it detect leaves that were completely consumed, so we probably underestimated overall leaf damage (Lowman 1984, Sand-Jensen et al. 1994). Second, we may have under-sampled severely damaged leaves (likely more abundant on trees with high herbivory) simply because they were smaller, and less likely to be picked during our “blind” sampling procedure, when we reached for leaves without looking. Third, many of the grasshoppers had not reached maturity by late July, and therefore continued to forage in the cottonwoods after we collected leaves, and later instar herbivores can consume much more food per individual than early instars (Schoonhoven et al. 1998).

The strong tree response to bird predation at the upland site in 2006 was correlated with reductions in arthropod abundance, richness, and biomass. We acknowledge the risk of spurious significance in reduced model statistical analyses when no significant interactions were found in the MANOVA whole models (in the cases of abundance and richness). In this case, however, we assert that spurious significance is unlikely because of the multiple lines of evidence that converge on the uniqueness of the upland site in 2006, and their logical coherence (Moran 2003). Birds had the greatest effects on the arthropods and the trees where and when tree growth was greatest, and arthropods were most abundant. Furthermore, the arthropods most affected by the birds (i.e., grasshoppers) were likely important herbivores, making them plausible strong links between the birds and the trees, and only present in that site-year. It seems quite improbable to us that all these phenomena would converge by chance (Moran 2003).

We acknowledge that the mechanistic link between the birds and the arthropod community effects we observed would be strengthened if we had direct observations of bird foraging patterns and diet. However, the effort required to obtain large numbers of bird feeding observations on large numbers of trees spread over several hectares was beyond our available resources, and we believe that our experimental design is a practical compromise for researching the effects of birds on arthropods.

Our finding of a strong cascade when tree growth was high is generally consistent with trophic theory that high primary productivity and high standing biomass tend to promote top-down regulation of primary production (Polis 1999, Polis et al. 2000, Borer et al. 2005). These authors gave overviews of factors and processes that influence the probability of trophic cascades. Complex and reticulate food webs characteristic of species-rich systems are predicted to suppress top-down influence, and the trophic cascade we document here occurred in the site-year situation with the highest arthropod richness and abundance. Our findings suggest that even in a speciose system, the presence of a few strong

interactors (e.g., grasshoppers) can overwhelm the cascade-dampening effects of processes such as intraguild predation and interference competition likely to be present in complex communities (Polis and Strong 1996). There may have been other idiosyncrasies of this community that suppressed cascade-dampening effects; for example, contrary to many other bird exclusion studies (reviewed by Gunnarsson 2008), we did not find significant evidence of intraguild predation on spiders or other arthropod predators by birds.

Cottonwoods and their dependent communities possess many characteristics that would make an avian trophic cascade unlikely. Cottonwood leaves are defended by condensed tannins, salicortin, and phenolic glycosides that reduce their edibility as well as that of the herbivores that eat them (Rehill et al. 2005, 2006, Muller et al. 2006), and poor edibility weakens top-down influence (Polis et al. 2000). Cottonwood trees growing without reliable ground water in the dry western climates are frequently water-limited and stressed (Horton et al. 2001, Gitlin et al. 2006), which reduces primary productivity needed to support high herbivore populations necessary for trophic cascades (Oksanen et al. 1981). Major herbivores on our study trees were sap-feeders such as galling and free-living aphids that were not attractive prey to many birds, which made them weak links between the tree and birds. Cottonwood branch structure offers more refugia for prey species compared to simpler plants, perhaps making predation by birds less efficient, thus weakening their effects on herbivores (Polis et al. 2000). Lastly, the arthropod community is species-rich and dynamic, and community heterogeneity is thought to cause predator effects to attenuate more rapidly (Polis et al. 2000). We believe that these conditions prevent birds from causing a trophic cascade in southwestern cottonwood ecosystems in most sites and years. Conditions at the upland site in 2006 permitted a trophic cascade, and help illuminate the circumstances under which cascades can occur.

The interplay between bottom-up and top-down forces can be framed in the context of limiting factors to tree growth: Only when water availability became less of a limiting factor could herbivory become limiting, and only then could the top predators affect tree growth by reducing herbivory. The additional crucial condition was the concurrent presence of an important set of herbivores that were also important bird prey (i.e., the grasshoppers), thus mediating the trophic cascade. The importance of such strong interactors to the occurrence of trophic cascades has been postulated by many authors (e.g., Paine 1980, summarized in Polis and Strong 1996, Borer et al. 2005). We would need to know how often all of these conditions are met in this system in order to evaluate how important bird predation is to the trees over their lifetime, but any effect on this foundation species may have community implications. Is an 18% increase in growth that occurs once every two or five years biologically significant? Are there years or

places when the benefit is much greater? If some bird species were lost from the system, would others compensate for the lost predation pressure? Our study cannot answer these questions, but our results suggest that conditions promoting top-down regulation are dynamic, and perhaps predictable.

Structural equation model

The lack of a causal connection between herbivore biomass and trunk growth in our structural equation model was surprising in light of our experimental findings of a negative effect of birds on herbivorous arthropods and a positive effect of birds on tree growth (Fig. 5). We suggest four reasons why our measure of herbivore biomass was not correlated with tree growth: First, we measured instantaneous herbivore biomass, which does not reflect herbivore turnover, feeding efficiency, or growth rates. Predator avoidance behavior can reduce prey feeding efficiency (Sih 1992, Schmitz et al. 1997), so disturbance by foraging birds could result in a net reduction in herbivory and slower herbivore growth rates. Also, prey removed by birds could be replaced fairly quickly by vagile insects attracted to a vigorous tree with less intraguild competition, but the time it takes to happen would lower net feeding time.

Second, sap-feeders constituted the major herbivore functional group on our trees, and these insects' impact on the tree is disproportionate to their biomass compared to folivores because of the water and nutrient loss resulting from their feeding mode (Brodbeck et al. 1993). Sap-feeder feeding efficiency is dependent on phloem hydrostatic pressure, which varies with plant water stress (Dixon 1998). At high populations (which we observed in 2006), sap-feeders may be competing with each other as their feeding stresses the tree, and therefore removal of some individuals via predation will improve the feeding efficiency of the remaining insects (Larson and Whitham 1991). The result is a nonlinear, or threshold effect where reduction in sap-feeder biomass has no net benefit to the tree until it reaches the point at which the tree is no longer stressed.

Third, tolerance of herbivory could also weaken the correlation between herbivory and plant response. The cottonwood trees likely have a certain amount of tolerance to herbivory (Strauss and Agrawal 1999), below which there is no growth response, or possibly even an overcompensatory response (Reichenbacher et al. 1996). The growth of trees experiencing herbivory below this threshold would be determined by some factor other than herbivory. If many of our trees were below their tolerance threshold, then the bird effect we detected was driven by a few trees at each end of the growth distribution.

Lastly, numerous studies have emerged from these common gardens showing a significant genetic component to arthropod community structure, ecosystem processes and trophic interactions (reviews by Whitham et al. 2006, 2008). The two study sites shared very few genotypes, but we did not have sufficient replicates to

incorporate a genetics perspective into our trophic cascade studies and genetic variation among trees would have added additional variation that would likely make our findings conservative. Because we now know that tree genotype does influence important insect herbivores, which in turn can affect the foraging of birds (Dickson and Whitham 1996, Bailey et al. 2006), new common gardens need to be established to examine trophic cascades within a genetics framework. A study design controlling for genotype with sufficient replications would increase power to detect genetically driven tree responses to herbivory.

Our results suggest that this trophic system is predominately bottom-up driven, but under certain circumstances the influence of top predators can stimulate whole tree growth. Such conditionality is consistent with numerous studies showing how fundamental relationships may switch over time, space, or with addition of another interacting community member (e.g., review by Bailey and Whitham 2007). For example, Johnson et al. (1997) showed that mycorrhizae were plant mutualists under poor growing conditions, but could become parasitic with the addition of fertilizer. The complexity of the species interactions fits the model proposed by Hunter and Price (1992) where heterogeneity at any trophic level can affect levels above and below. In our study, it appears that abiotic growing conditions affected tree growth and herbivore populations, which in turn affected bird foraging patterns that cascaded back to the trees. This dynamic complexity may preclude predictability of ecosystem response to the addition or loss of top predators at a given place or time, but it also precludes the assumption that predators do not have a regulatory function in species-rich systems.

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