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The direct and indirect effects of insectivory by birds in two contrasting Neotropical forests

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Abstract A goal among community ecologists is to predict when and where trophic cascades occur. For example, several studies have shown that forest birds can limit arthropod abundances on trees, but indirect effects of bird predation (i.e. decreased arthropod damage to trees) are not always observed and their context is not well understood. Because productivity is one factor that is expected to influence trophic cascades, we compared the extent to which birds indirectly limit herbivore damage to trees in two lowland Neotropical forests that differed in seasonality of leaf production and rainfall. We compared the effects of bird predation on local arthropod densities and on damage to foliage through a controlled experiment using bird exclosures in the canopy and understory of two forests. We found that birds decreased local arthropod densities and leaf damage in the canopy of the drier site during periods of high leaf production, but not in the wetter forest where leaf production was low and sporadic throughout the year. Birds had no effect on arthropod abundances and leaf damage in the understory where leaf production and turnover rates were low. In support of these experimental interpretations, although we observed that arthropod densities were similar at the two sites, bird

densities and the rate at which birds captured arthropods were greater at the drier, seasonally productive site. The influence of top-down predation by birds in limiting herbivorous insects appears to be conditional and most important when the production and turnover of leaves are comparatively high.

Keywords Arthropods · Canopy · Herbivory · Multitrophic Interactions · Predation

Introduction

A central question in community ecology is whether herbivores are limited more by predators or by resource availability. These alternatives are formalized in food chain models that describe how “top-down” and “bottom-up” forces (predators and primary productivity) can limit or regulate herbivore population abundances (Hairston et al. 1960; Fretwell 1977; Oksanen et al. 1981). These models predict that increasing primary productivity supports greater populations at the top trophic level and at alternate trophic levels below (Hairston et al. 1960; Fretwell 1977; Oksanen et al. 1981). For example, in a food chain with three levels, increasing plant productivity is expected to increase predator biomass but not herbivore biomass; excess herbivores are limited by the predator increase. When populations at the top trophic level are reduced or removed, increased biomass at alternately lower trophic levels may produce a “trophic cascade” (Paine 1966, 1980).

While food chain and trophic cascade models have been tested and observed in aquatic systems (Power et al. 1985; Carpenter et al. 1987; Wootton and Power 1993; Brett and Goldman 1996), the incidence of trophic cascades and their role in structuring terrestrial communities has been debated (Strong 1992; Polis and Strong 1996; Persson 1999; Polis 1999; Schmitz et al. 2000; Dyer and Coley 2001; Halaj and Wise 2001;

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Walker and Jones 2001). Some theoretical work has suggested that food webs, rather than food chains, better characterize terrestrial communities, and the reticulate nature of food webs, their high species diversity, intra-guild predation, and omnivory have been cited as potential buffers from strong trophic cascades (Hunter and Price 1992; Strong 1992; Polis and Strong 1996; but see Chase 2000). A further complication occurs because plants use defensive strategies to make themselves unpalatable to herbivores: thus, increases in primary productivity may not directly translate to greater resource levels for consumers and predators (Murdoch 1966; Ehrlich and Birch 1967). Despite these arguments, trophic cascades have been observed in a diverse assemblage of terrestrial communities (reviewed by Schmitz et al. 2000; Dyer and Coley 2001; Halaj and Wise 2001; Walker and Jones 2001) although cascades appear to have stronger effects on the plant community in marine and aquatic systems (Shurin et al. 2002). Given the existence of cascading interactions in terrestrial systems, a current focus is on determining what factors promote their occurrence and affect their strength (Hunter and Price 1992; Halaj and Wise 2001).

Along with playing important roles as seed-dispersers and pollinators, birds are pervasive predators of herbivorous arthropods. Foliage-gleaning birds can limit herbivorous arthropod densities and their damage to plants in temperate forests (Atlegrim 1989; Marquis and Whelan 1994; Murakami and Nakano 2000; Sanz 2001; Sipura 1999; Strong et al. 2000), tropical forests (Van Bael et al. 2003) and in agricultural systems (Greenberg et al. 2000; Mols and Visser 2002). Although nearly all studies document decreases in arthropod abundance due to bird predation, indirect effects on the plant community are not observed in all systems or for all plant species (Wiens et al. 1991; Sipura 1999; Forkner and Hunter 2000; Lichtenberg and Lichtenberg 2002). Because birds may maintain forest productivity by limiting insect damage to trees (Marquis and Whelan 1994), understanding where and when to expect strong trophic cascades with birds as predators has implications for conservation and community ecology.

Here we extend the results of Van Bael et al. (2003) and present results of an enclosure experiment conducted at two forest sites to explicitly compare the extent to which birds limit arthropod densities and consequent herbivore damage. We use data from Van Bael et al. (2003) (a seasonally dry site) to compare the effects of bird predation in a dry and wet forest at each end of a rainfall gradient in Panama. Because the two sites differed in the extent of rainfall seasonality, we were able to directly assess the importance of spatial and temporal differences in leaf productivity for the limitation of herbivore densities. We predicted that bird predation would be most important in the seasonally dry forest where leaf productivity was high (during the rainy season) and leaf longevity was low. Basic food chain models predict that the removal of predators will have strong effects where productivity is high and weak effects where

productivity is low (Oksanen et al. 1981). Moreover, anti-herbivore defenses in plants likely influence trophic cascades. Leaf longevity is one of many characteristics described as being part of a life-history trade-off between fast growth (i.e. competition) and anti-herbivore defense (Coley et al. 1985). By this scenario, fast-growing trees can produce “cheap,” short-lived leaves, with few anti-herbivore defenses. In this case, the trees are expected to “out-run” their herbivores (Coley et al. 1985), most likely with the help of predators and parasitoids (Leigh 1999). In contrast, long-lived leaves are expected to be better defended from herbivores.

We conducted an enclosure experiment in the canopy and understory of two contrasting sites. For 1 year, we observed how bird predation affected the local density (number/m² leaf area) and taxonomic composition of the arthropod community and also assessed changes in herbivore damage. We estimated and compared these quantities on control branches and saplings where birds had access to foliage and on branches and saplings in experimental enclosures where foliage was inaccessible to birds. We also estimated bird abundances at each site and observed bird foraging behavior in the canopy.

Materials and methods

Study sites

Canopy cranes provided access to the forest canopy in two lowland forests in the Republic of Panama. Each canopy crane has a tower (50 m) with an effective reach of 35–40 m, covering approximately 0.7–0.88 ha of forest. A gondola attached to the boom transports researchers and equipment through the canopy.

One site, Parque Natural Metropolitano (PNM), is a dry, semi-deciduous forest near the Pacific coast (8°59'N, 79°33'W). Mean annual rainfall is 1,850 mm and nearly all rainfall occurs in the wet season (May–December.) (<http://www.stri.org/tesp>). The forest has not been logged for approximately 100 years (Parker et al. 1992), so that canopy composition is representative of a mature, seasonally dry forest (Croat 1978). Over 50 tree and liana species occur within the 0.7 ha area covered by the crane boom (Parker et al. 1992). The most common tree species under the crane is *Anacardium excelsum* (Anacardiaceae), with canopy cover of ~25%. Other common canopy tree species include *Cecropia longipes* (Cecropiaceae), *C. peltata* (Cecropiaceae), *Cordia alliodora* (Boraginaceae), *Ficus insipida* (Moraceae) and *Luehea seemannii* (Tiliaceae). The canopy is approximately 30–35 m tall.

The other site, Fort Sherman (FTS), is located 70 km north on the Atlantic side of the Panamanian isthmus in the San Lorenzo Protected Area (9°17'N, 79°58' W). This forest is classified as moist evergreen forest, as annual rainfall averages 3,400 mm (<http://www.stri.org/tesp>). The forest has not been intensively logged for 200 years and the canopy represents mature, moist

Table 1 Sample sizes and leaf area for enclosure experiment in the canopy and understory at both sites

	Understory saplings		Canopy branches	
	Exclosure	Control	Exclosure	Control
PNM tree species				
<i>C. longipes</i> ^a	3	3	7	7
<i>A. excelsum</i>	8	8	8	8
<i>C. peltata</i>	6	6	7	7
Total	17	17	22	22
Average leaf area ± 1 SE ^b				
Per arthropod sample ^c	0.33 \pm 0.05	0.36 \pm 0.06	1.19 \pm 0.15	1.39 \pm 0.15
Per herbivory sample ^c	0.26 \pm 0.02	0.34 \pm 0.02	0.77 \pm 0.06	0.89 \pm 0.06
FTS tree species				
<i>B. utile</i>	6	6	6	6
<i>M. bidentata</i>	6	6	6	6
<i>P. bicolor</i> ^a	6	6	3	3
<i>C. insignis</i> ^a	6	6	0	0
Total	24	24	15	15
Average leaf area ± 1 SE ^b				
Per arthropod sample ^c	0.33 \pm 0.06	0.36 \pm 0.06	0.62 \pm 0.10	0.59 \pm 0.09
Per herbivory sample ^c	0.19 \pm 0.02	0.19 \pm 0.02	0.29 \pm 0.02	0.26 \pm 0.02

^aSample sizes for this species were limited by availability of trees at the study sites

^bUnits are m² leaf area

^cLeaf area differed between the two types of samples because herbivory was measured on new leaves only, while arthropod densities were assessed for all leaves inside of the enclosure

forest (S. Paton, personal communication). Rainfall continues throughout the “dry” season at FTS resulting in less extreme seasonality than at PNM. At FTS there are 240 species of trees and lianas within the 0.88 ha area under the crane boom (Wright 2002). The most common tree species in the area are *Brosimum utile* (Moraceae) and *Manilkara bidentata* (Sapotaceae), each of which comprise ~10% of the canopy cover. *Pourouma bicolor* (Cecropiaceae), *Tapirira guianensis* (Anacardiaceae), *Symphonia globulifera* (Clusiaceae), *Vochysia ferruginea* (Vochysiaceae), and *Guatteria dumetorum* (Annonaceae) are also present under the crane. The canopy is approximately 35–40 m tall.

Previous research at both sites has revealed predictable differences in leaf traits and phenology of canopy trees. Relative to leaves from PNM, FTS leaves had longer life-spans, greater structural defense, lower nitrogen per unit mass (N_{mass}) and lower photosynthetic rates per unit mass (P_{mass}) (Santiago et al. 2004; S.J. Wright, unpublished data). Nutrient poor soils at FTS (due to greater rainfall and leaching) may require that leaves need to live longer and exhibit greater defense in order to conserve nutrients (Santiago et al. 2004). In contrast, leaf life-span may be limited by the more severe dry season at PNM. At PNM, canopy leaf flush for most tree species occurs just after the onset of the rainy season in May, while canopy leaf flush occurs in a more temporally diffuse pattern throughout the year at FTS (personal observation, S.J. Wright, unpublished data).

Field experiment methods

We excluded birds on foliage of three tree species at PNM and four tree species at FTS (Table 1). The same tree species were not available at the two sites. The tree species were chosen because they were common in each of the crane areas. In the canopy, we installed exclosures on randomly chosen treatment branches for each of six

species and paired them to control branches on the same crown (Table 1). After 1 month of the experiment, two *P. bicolor* exclosure and control pairs were lost to a tree fall, reducing the sample size to three branch pairs for this species (Table 1). In the understory along trail edges, we installed exclosures on saplings of seven species (Table 1), pairing treatment and control saplings by height and proximity to the forest edge. Mean sapling height at the start of the experiment was 1.17 m for exclosures and 1.19 m for controls. Overall, the experiment included 74 canopy branches on 34 individual trees and 82 saplings (Table 1). Finally, we only selected *Cecropia* spp. branches and saplings that were inhabited by *Azteca* spp. ants.

Exclosures were constructed with untreated wooden dowels wired together and covered with agricultural netting (Bird-X, <http://www.bird-x.com>, 2x2 cm mesh size). Each exclosure surrounded a volume of approximately 1 m³ and an average leaf area of 0.95 m² in the canopy and 0.35 m² in the understory. Procedural control (sham) exclosures, where materials were in the canopy but were open on the sides to bird foraging, were constructed and monitored throughout the year. The sham controls were compared to exclosures and controls in a previous analysis, and the exclosure materials on sham branches did not appear to attract arthropods, did not damage leaves or branches, and did not significantly reduce light (Van Bael 2003). Moreover, large Orthoptera and larvae of large Lepidoptera were routinely observed inside the exclosures, suggesting that the netting did not prohibit access to these large herbivores. Parasitic wasps were also observed moving in and out of the netting.

The exclosures effectively excluded insectivorous birds, but allowed access to *Anolis* spp. lizards. Changes in arthropod density and damage are attributed primarily to bird predation, while acknowledging that some canopy bats may glean arthropods from leaves. One leaf-gleaning bat species, *Lamproncyteris brachyotis* may

have been present in the canopy at both sites (E. Kalko, personal communication), but densities are unknown.

We non-destructively censused arthropod densities at approximately 3-week intervals between April 2000 and March 2001. We censused by visually inspecting all leaf surfaces on experimental branches and saplings, accessing the leaves through a small door in the netting with as little disturbance as possible. For each arthropod observed, we recorded Order and feeding guild (predator, chewer, phloem-feeder). Colonial arthropods (ants and aphids) were not included in counts. We report all arthropod densities as the number of arthropods per m² leaf area. Leaf area was estimated by counting leaves, establishing a mean leaf length for each sapling/branch, and using the mean in species specific allometric equations (Van Bael 2003) to sum over the number of leaves present.

We conducted non-destructive censuses of leaf damage at 6-week intervals between April 2000 and March 2001. Leaf damage was determined for all leaves using a plastic grid (1.0×1.0 cm squares) to estimate total leaf area and a smaller grid (0.5×0.5 cm) to estimate the amount of missing area. We measured damage only for enclosure and control leaves that flushed after the experiment began; we distinguished leaves that were present previously by a small mark with a permanent, water-based, odor-free pen.

We estimated rates of new leaf production (leaf area time 2–leaf area time 1/number of days) on control saplings and canopy branches during the month of maximum leaf flush. These rates express the amount of leaf area produced in a volume of canopy or understory space that measured ~ 1 m³ (Table 2). An additional comparison in

leaf productivity between the sites and strata was the average leaf area per herbivory sample throughout the year (Table 1), since we only measured herbivory on leaves produced since the enclosure experiment began. The control data show that new leaf production (per 1 m³) decreased from PNM canopy > PNM understory > FTS canopy > FTS understory (Table 1). Thus, throughout the text, when we refer to differences in “leaf productivity” we refer to the combined estimates of new leaf production during the month of maximum leaf flush (Table 2) and throughout the year (Table 1). We used these branch-level estimates because they fit the scale of the experiment and represented the amount of new leaf area available to chewing insects (nearly all leaf damage occurs while leaves are young and soft; S. Van Bael, personal observation; Coley and Barone 1996). We estimated leaf life spans using long-term measurements of marked leaves at both sites (S.J. Wright, unpublished. data).

Bird census and foraging observations

We conducted timed counts of foliage-gleaning birds in the canopy at each of the crane sites, approximately once a week for the whole year. All censuses were between 0600 and 0730 hours. Each census consisted of two counts (5 min each) with the crane gondola parked at the opposite, extreme ends of the crane boom (~80 m apart). The counts occurred at a fixed location above the canopy that allowed full view of the canopy surface (~0.70–0.88 ha). During each count, we recorded birds that were seen and heard within the half circle of area under the crane boom, so that the combined counts covered the entire circle of area under the crane.

In addition to censuses, ad hoc observations of foraging birds were collected from the gondola and from the crane tower. Bird foraging observations were generally initiated if a bird or flock was foraging within 3–4 m of the gondola or 5–10 m of the tower. The gondola was usually parked during observations, but was sometimes moved in order to follow birds. Foraging observations were described as they occurred on a hand-held tape-recorder (Remson and Robinson 1990). The tapes were later transcribed using a stopwatch so that foraging rates could be determined for each sequence. The observations included all movements, including attacks and captures, and food identification. Successful captures were sometimes difficult to determine, so capture rates (the number of visible food items/minute) are likely underestimated in this study. The average length of foraging sequences was 89 ± 15 s (mean ± SE).

Statistical methods

The two response variables from the enclosure experiment, average leaf damage/branch and arthropod density, were log transformed and these values were subjected to repeated measures analysis using a mixed model test in

Table 2 Leaf-life span, months of maximum leaf flush, and leaf production rates at the two study sites

Site, level, tree species	Median leaf life span (days)	<i>n</i> (leaf life span)	Month(s) of maximum flush	Average ± 1 SE leaf production rate (cm ² /day) ^a
PNM, canopy				
<i>A. excelsum</i>	257	200	December/June	92 ± 32
<i>C. longipes</i>	87	147	June	142 ± 20
<i>C. peltata</i>	114	247	June	185 ± 36
PNM, understory				
<i>A. excelsum</i>	–	–	May	17 ± 7
<i>C. longipes</i>	158	26	June	72 ± 8
<i>C. peltata</i>	147	110	June	87 ± 29
FTS, canopy				
<i>B. utile</i>	306	92	February/June	24 ± 47
<i>M. bidentata</i>	414	163	September	24 ± 16
<i>P. bicolor</i>	219	77	July	42 ± 96
FTS, understory				
<i>B. utile</i>	718	64	September	2.5 ± 3
<i>M. bidentata</i>	783	30	September	1.3 ± 1.1
<i>P. bicolor</i>	339	129	July	23 ± 17
<i>C. insignis</i>	–	–	June	10 ± 13

^aCalculated during the month of maximum leaf flush. For species with two major flushes, the wet season month was used. Rates of leaf area production were calculated on a per enclosure basis, which includes the amount of leaf area in ~1 m³ volume of canopy or understory space

SAS (2000). This procedure allows for unbalanced data and unrestrictive assumptions about the structure of variance-covariance matrices (Littell et al. 1996). The factors in the model were treatment (α), census period (τ), host tree species (β), host tree (d) and all two-way interactions. All three-way interactions were non-significant and were removed from the models. The model was:

$$y_{ijkm} = \mu + \alpha_i + \beta_j + \tau_k + (\alpha\tau)_{ik} + (\beta\tau)_{jk} + (d\beta)_{ijkm} + e_{ijkm}$$

The random effect in the model was the individual host tree nested within host species ($d\beta$). We ran a separate model for each site and each stratum. We calculated effect sizes for leaf damage as the ratio of exclosure to control means x_e/x_c using least-squares means (adjusted means) generated by the models at each site and strata. For arthropod Order and guild comparisons, we compared branch averages of arthropod density using paired permutation tests (Sprent 1993) with Monte Carlo resampling (10,000 randomization tables per test) to estimate P values (Gajjar et al. 1998). For these tests, the mean arthropod density/branch (averaged over all time periods) was an independent data point. We paired exclosure and control branches within the same tree crowns. The paired permutation test statistic is calculated using the ranks of the sign and magnitude of the paired differences.

We used four seasonal divisions to summarize the bird census observations. Rainfall patterns during the 1-year study period were categorized as early dry season (January–February), late dry season (March–April), early wet season (May–August) and late wet season (September–December). Census data were subjected to repeated measures analysis with the number of birds as the dependent variable and site, time and their interaction as independent variables. Foraging observations of unmarked birds in a small area are potentially dependent, because the same bird may be observed in subsequent days. In general, we use statistics only to describe medians, means and standard errors of rates due to the potential non-independence of the foraging sequences.

Results

Observed differences between sites

Leaf seasonality

The phenology of leaf production and the frequency of leaf turnover differed between the two sites. The month of maximum leaf flush was similar for all tree species at PNM, in the canopy and understory (Table 2). This pulse in new leaf production followed the onset of the rainy season in May. In contrast, FTS trees showed greater interspecific variation in the timing of maximum leaf production (Table 2). In general, canopy leaves at PNM had shorter life spans and greater leaf area pro-

duction rates relative to the understory and FTS foliage (Table 2). Turnover for canopy leaves was therefore greater at PNM than at FTS (Table 2).

Arthropod seasonality

Arthropod densities on branches that were accessible to bird foraging reflected the differences in seasonality between the two sites. Concurrent with the wet season leaf flush at PNM, chewing arthropod densities on canopy foliage were 90% greater in the wet season than in the dry season (Fig. 1a,b). In contrast, phloem-feeding insects were greater in the dry than wet season (Fig. 1a,b). In the FTS canopy, average chewing and phloem-feeding arthropod densities were less seasonal and increased by 9 and 35%, respectively in the wet season relative to the dry season (Fig. 2a,b). Chewing arthropod densities were similar at the two sites during the wet season, but were greater at FTS relative to PNM during the dry season (Figs. 1, 2). Throughout the year, average densities of predatory arthropods, primarily spiders, were greater in the canopy at FTS ($1.97 \pm 0.30/\text{m}^2$ leaf area on control branches) than at PNM ($0.94 \pm 0.20/\text{m}^2$ leaf area on control branches).

Exclosure experiment

Between canopy comparison

We observed significant effects of excluding birds in the canopy at PNM but not at FTS. In the canopy at PNM, overall arthropod densities were significantly greater on branches that were inaccessible to bird foraging (an overall increase of 20%, Table 3). This increase only occurred during the wet season, coinciding with the general increase of chewing arthropods (Fig. 1). In contrast, in the canopy at FTS, we did not observe experimental effects of bird predation on overall arthropod density (overall 3% decrease, Table 3) or for most arthropod Orders (Fig. 2). Only Blattaria and Orthoptera increased on inaccessible foliage in both the wet and dry seasons (Fig. 2). With respect to feeding guild, chewing and predatory arthropods were greater where foliage was inaccessible at PNM (Fig. 1), but there were no significant differences at FTS (Fig. 2).

We observed greater herbivore damage on inaccessible foliage of canopy branches at PNM but not at FTS. At PNM, increased densities of chewing arthropods resulted in greater leaf damage (Table 4, Fig. 3). Besides a significant treatment effect, the effects of time and tree species by time interaction were significant sources of variation for leaf damage (Table 4). At the end of the PNM wet season, average damage levels increased at least 86% where foliage was inaccessible to birds (Fig. 3a). The confidence interval for PNM canopy branches does not contain the ratio one, and implies with 95% certainty that leaf damage on exclosure branches is 1.1–3.42 times as much as on control branches (Fig. 3b).

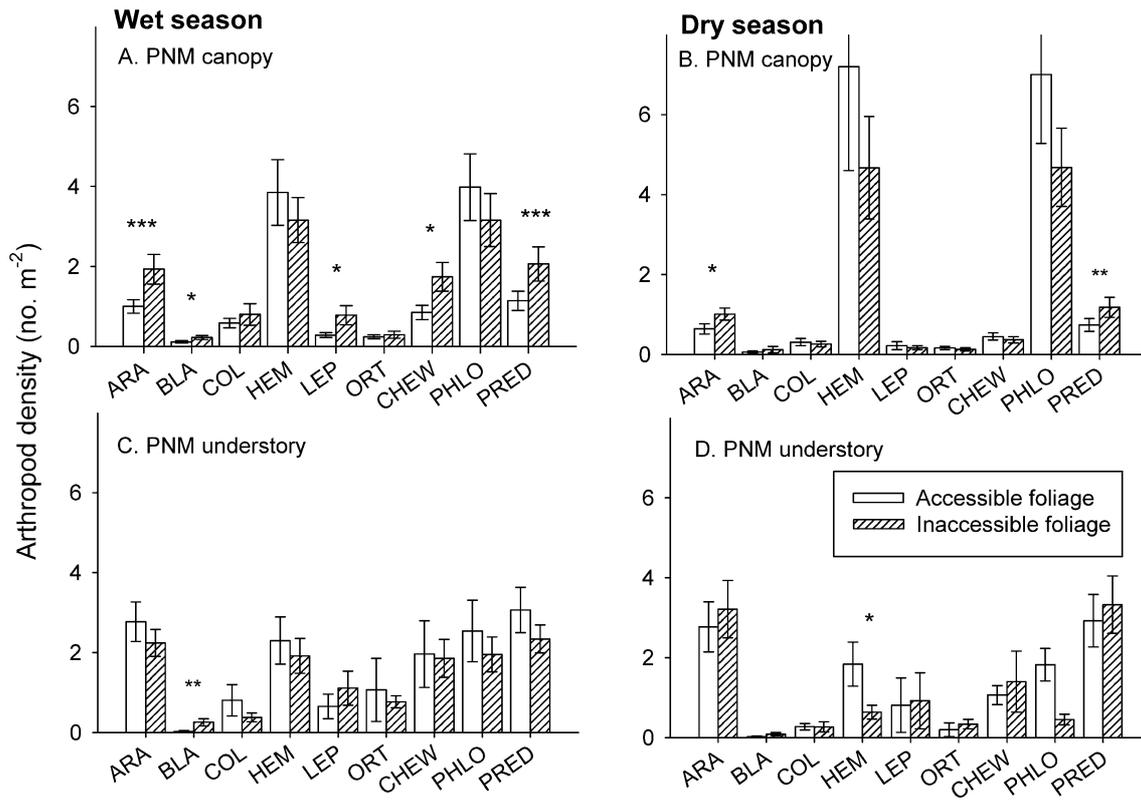


Fig. 1 [insert legend]

Canopy versus understory comparison

Rates of leaf production were lower in the understory than in the canopy (Table 2). We did not observe significant effects of bird predation on arthropod densities within either understory (Table 3). Overall and within Orders, arthropod densities were similar on accessible and inaccessible saplings (Figs. 1, 2). At PNM, Blattaria increased on inaccessible saplings during both the dry and wet seasons, but densities were extremely low (Fig. 1). Finally, we did not observe effects of bird predation on leaf damage at either site in the understory (Table 4, Fig. 3). The greatest sources of variation for herbivory in the understory were the effects of time, tree species, and their interaction (Table 4).

Canopy birds

Estimated abundances of foliage-gleaning birds were nearly 2-fold greater in the PNM canopy than in the wetter FTS canopy (Fig. 4). The difference in bird abundance between the two sites was significant (repeated measures, $F_{1,58} = 6.77$, $P = 0.01$, time and interaction effects were non-significant). Bird abundances were lowest during the early dry season of 2001 and highest during the early wet season of 2001 (Fig. 4). The most common foliage-gleaning bird species at both sites was *Hylophilus decurtatus* (Lesser Greenlet) (Electronic Supplementary Material, S1). Counts for *H. decurtatus* were similar at each site, but its density relative to other species was greater at FTS (S1). Three tanager species, *Tachyphonus*

Table 3 Results of repeated measures mixed models for overall arthropod density at both sites and in both strata

Fixed effects ^a	PNM						FTS					
	Canopy branches			Understory saplings			Canopy branches			Understory saplings		
	df	F	P	df	F	P	df	F	P	df	F	P
Bird exclusion treatment	1, 81	4.4	0.04	1, 76	0.0	0.97	1, 20	0.1	0.83	1, 49	0.6	0.46
Time	7, 201	7.7	< 0.001	7, 156	1.3	0.25	7, 139	0.5	0.83	7, 171	4.2	< 0.001
Tree species	2, 16	7.3	0.006	2, 41	9.8	< 0.001	2, 138	13.5	< 0.001	3, 49	10.7	< 0.001
Treatment × time	7, 182	0.7	0.67	7, 105	1.5	0.17	7, 22	0.5	0.85	7, 172	0.4	0.93
Tree species × treatment	2, 85	0.3	0.77	2, 43	0.9	0.99	2, 20	0.6	0.56	3, 43	1.7	0.09
Tree species × time	14, 198	3.6	< 0.001	12, 125	0.8	0.62	14, 130	2.3	< 0.001	17, 179	0.9	0.52

^a This model includes arthropod densities from the wet season only (May–December). Dry season densities did not vary significantly with bird exclusion

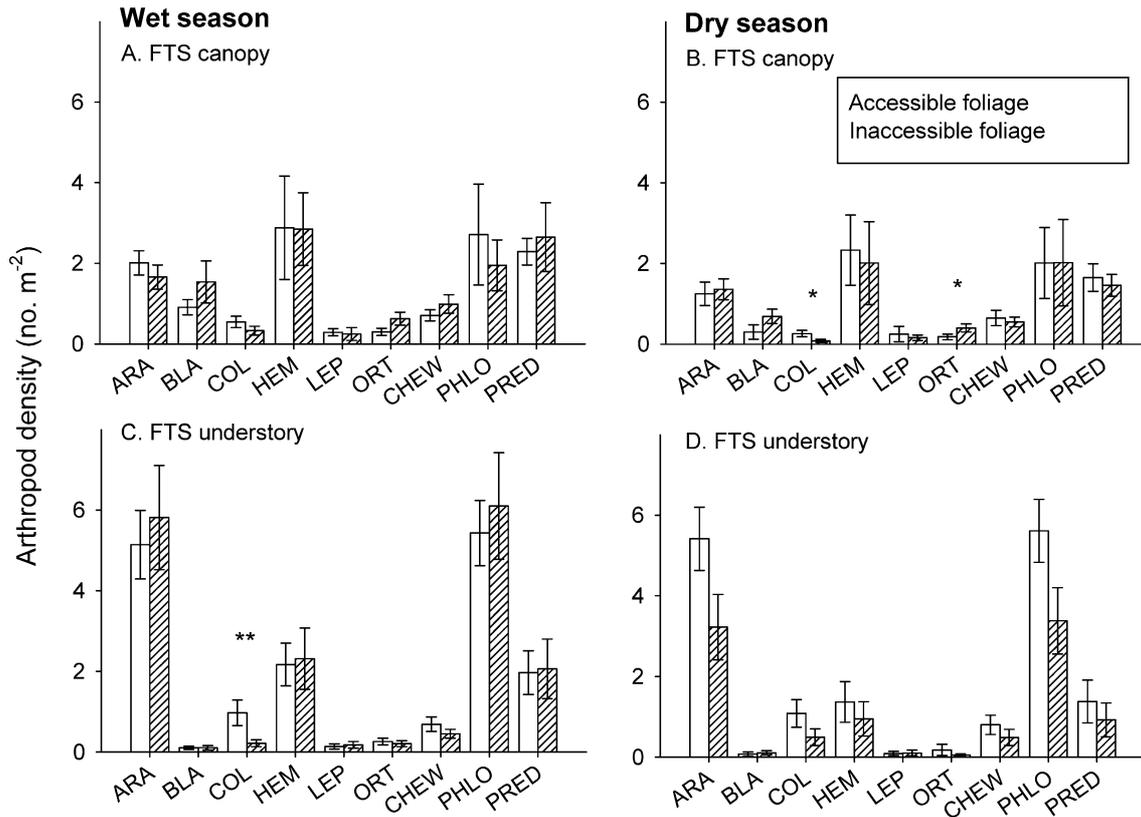


Fig. 2 [insert legend]

luctuosus (White-shouldered Tanager), *Tangara inornata* (Plain-colored Tanager), and *Thraupis episcopus* (Blue-gray Tanager) were common at PNM but not at FTS (S1). These three species were observed moving in large flocks through the PNM canopy, sometimes accompanied by *H. decurtatus* and other tanager species. Differences in abundances of foliage-gleaning birds between PNM and FTS were mostly due to the increased abundance of resident tanagers and passage migrants at PNM (S1).

Three foliage-gleaning bird species were common enough at both sites to compare their foraging behavior (Table 5). Movement rates were faster for all three species at FTS relative to PNM, but attack rates were equal or greater for all three species at PNM relative to

FTS (Table 5). Moreover, mean (\pm SE) capture rates were higher at PNM (0.70 ± 0.11 captures/min) relative to FTS (0.38 ± 0.13 captures/min) for the three species (Table 5). Thus, these bird species apparently exerted less effort and captured more food items at PNM than at FTS. In total, 520 attacks on arthropods were observed by 12 foliage-gleaning bird species (see S1 for bird species). Arthropod prey were visible for only 105 of these attacks, and the prey were classified as large (> 5 mm) for 37% (39/105) of these captures. Lepidoptera larvae were the most common large prey item (17/39), followed by adult Lepidoptera (9/39), Arachnids (4/39), Orthoptera (4/39) and unidentified items (5/39).

Table 4 Results of repeated measures mixed models for overall leaf damage at both sites and in both strata

Fixed effects	PNM						FTS					
	Canopy branches			Understory saplings			Canopy branches			Understory saplings		
	<i>df</i>	<i>F</i>	<i>P</i>	<i>df</i>	<i>F</i>	<i>P</i>	<i>df</i>	<i>F</i>	<i>P</i>	<i>df</i>	<i>F</i>	<i>P</i>
Bird enclosure treatment	1, 54	5.6	0.02	1, 31	0.1	0.77	1, 28	0.5	0.50	1, 48	0.5	0.50
Time	6, 174	20.5	< 0.001	5, 127	7.6	< 0.001	8, 124	2.9	< 0.001	7, 114	1.9	0.07
Tree species	2, 16	2.4	0.13	2, 25	10.5	< 0.001	2, 13	4.5	0.03	3, 45	3.9	0.02
Treatment \times time	6, 174	0.3	0.94	5, 124	0.4	0.87	8, 118	0.4	0.92	7, 101	1.0	0.44
Tree species \times treatment	2, 57	0.8	0.47	2, 31	0.4	0.70	2, 28	2.7	0.08	3, 43	0.4	0.76
Tree species \times time	12, 175	6.5	< 0.001	8, 124	5.6	< 0.001	15, 122	3.7	< 0.001	9, 97	0.8	0.62

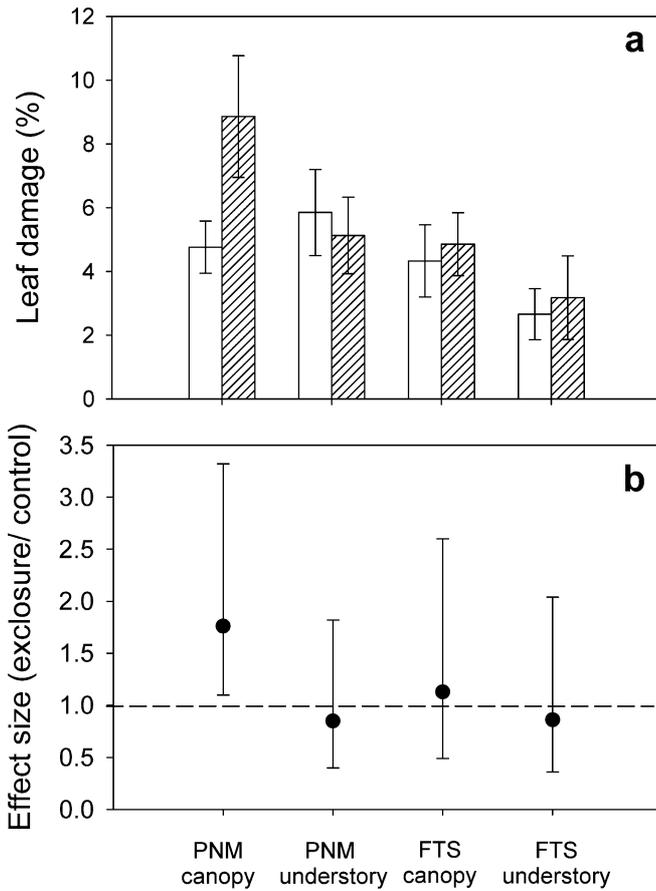


Fig. 3 [insert legend]

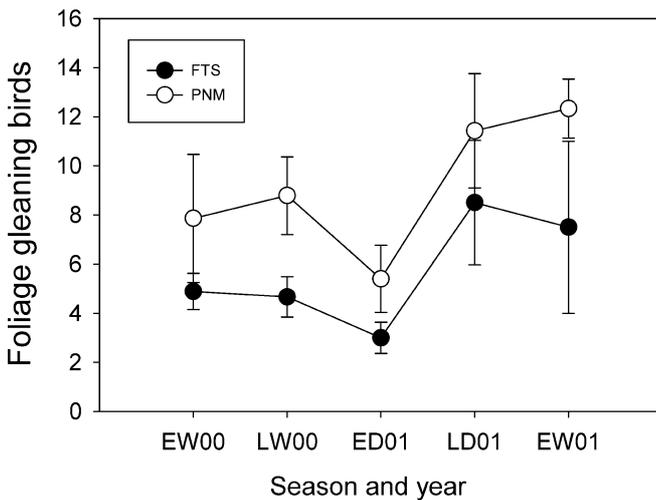


Fig. 4 [insert legend]

Discussion

Our results corroborate the predictions of basic food chain models that suggest predators will have higher abundances and limit herbivores when and where primary productivity is greater (Fretwell 1977; Oksanen

Table 5 Foraging rates for canopy bird species

Genus and species	No. sequences (total seconds)	No. attacks	Average rate (No./min)		
			Move ^a	Attack	Capture
PNM					
<i>D. cayana</i>	14 (795)	30	12.2	2.3	0.75
<i>H. decurtatus</i>	15 (779)	37	18.2	3.0	0.87
<i>P. plumbea</i>	12 (861)	35	27.2	2.7	0.48
FTS					
<i>D. cayana</i>	6 (538)	17	13.7	2.4	0.45
<i>H. decurtatus</i>	12 (1009)	46	25.1	2.5	0.47
<i>P. plumbea</i>	8 (525)	13	36.8	1.7	0.23

^a The average number of times the bird species moved from one perch to another by hopping or flying

et al. 1981). Although these models were developed to compare different systems along an evapotranspiration gradient, they were also used to describe potential variation within sites (Fretwell 1977). For example, Fretwell (1977) predicted a change in predator limitation along a gradient of plant productivity from the low light understory to the high light canopy of tropical forests; essentially predicting one of the results we observed here. We observed direct and indirect effects of predation when and where we observed high leaf production and short leaf life-spans, suggesting that these tree species were investing in rapid leaf production with lower levels of anti-herbivore defense. This pattern was evident for the site comparison, the canopy/understory comparison, and the wet/dry season comparison.

Site comparison

We observed that leaf productivity and turnover were greater in the drier, more seasonal site, providing a greater abundance of new leaf material for chewing arthropods. Santiago et al. (2004) also reported greater leaf turnover and shorter leaf-life spans at PNM relative to FTS, and suggested that the nutritional quality of leaves for insects (as measured by fiber: N ratio) was greater at PNM relative to FTS. In the current study, arthropod densities were similar at both sites in the presence of bird predation, but when birds were excluded, arthropod densities were seasonally greater at the drier site. Moreover, bird densities were higher at the drier site, throughout the year. Although the density differences were only recorded for canopy birds, counts in the understory revealed similar patterns of higher bird density at PNM relative to FTS (J.D. Brawn, unpublished data). Interestingly, bird abundances were high at both sites in the late dry season (Fig. 4), despite the fact that arthropod abundances were relatively low throughout the dry season (Figs. 1, 2). The late dry season is when many of the trees produce fruit (personal observation), and nearly all birds in our study were omnivorous (S1). Other studies have noted that tropical canopy birds, especially passage migrants, switch between fruit and arthropods with respect to their

availability (Greenberg 1981; Loiselle 1988; Greenberg et al. 1993).

Attack and capture rates of birds are expected to be indicative of prey availability within a habitat (Thiollay 1988). We observed a greater rate of successful arthropod captures at PNM relative to FTS, even though movement rates were greater at FTS. The lower rate of return per movement at FTS suggests that there were fewer suitable food items available at FTS than at PNM. This trend would also explain the lower densities of birds at FTS relative to PNM, especially since densities of their favored food item, caterpillars, were low at FTS relative to PNM.

The main focus of this study was to examine the effects of bird predation on herbivores and their damage. However, intraguild predation (e.g. Polis et al. 1989) may have occurred in this experiment, because both birds and spiders consume herbivorous arthropods. In the PNM canopy, removing bird predation had large effects on spider densities. We observed a doubling of spider densities on inaccessible branches (Fig. 1), but spider predation on caterpillars did not compensate enough to counteract the overall indirect effects of bird predation. At FTS, there was no evidence of an increase in spiders when birds were excluded (i.e., intraguild predation and compensation, Fig. 2), but spider densities were generally higher at FTS and PNM throughout the year. Thus, despite some changes in taxonomic composition of a trophically complex arthropod community, the effects of removing bird predation still behaved as expected from simple food chain models. A recent study comparing the predation pressure of birds and ants on herbivores revealed similar patterns of consistently stronger effects of vertebrate predators relative to invertebrate predators on herbivore densities (Philpott et al. 2004).

The comparison between two sites was confounded by the necessary use of different tree species at the two sites. Several observations, however, suggest the patterns we observed are due to site differences. First, we chose the most common canopy tree species at the two sites, so they are representative of the community. Second, none of our models yielded significant tree species by treatment interactions. Thus, within each of the sites, the tree species responded or did not respond to the treatment uniformly. Finally, the contrasting bird densities at the two sites are likely indicative of habitat quality as a whole rather than just the focal tree species of the experiment.

Canopy/understory comparison

The results from the within-site comparison supported the basic proposition that high plant productivity makes it possible for top-down influences to be important in the canopy. In the understory, however, low light availability reduced the level of leaf production, and fewer young leaves were available for herbivores.

The *Cecropia* spp. in this study have an obligate mutualism with *Azteca* ant colonies (e.g. Janzen 1969, 1973a). Using canopy access, we observed that ant colonies were always present in canopy trees, but saplings would cycle through periods of high and low ant activity. Furthermore, the canopy *Azteca* ants appeared to tolerate herbivores in more mature trees. In sum, our results and observations suggest that ants, when they were present, were a more effective anti-herbivore defense when they were on saplings relative to when they were on canopy trees. For *Cecropia* spp. established in the canopy, anti-herbivore defense via bird predation may continue or bolster the defense that ants provide in the understory.

Seasonal patterns

Temporal heterogeneity in leaf productivity played a large role in determining when bird predation was effective at limiting herbivore prey. One consequence of more temporally diffuse leaf production at FTS was that chewing arthropod densities did not reach a peak in the wet season, as they did in the PNM canopy. Similarly, studies in Costa Rica and Panama demonstrated that as rainfall seasonality becomes less extreme (i.e. a milder dry season), arthropod numbers fluctuate less (Janzen and Schoener 1968; Janzen 1973b). Thus, arthropods are expected to have a more constant, year-round selective pressure on their host tree species in wetter habitats.

Implications and conclusions

In temperate and tropical forests, many forest bird populations are declining due to habitat loss and fragmentation (Stotz 1996; Robinson 2001). Several community-wide consequences for such declines have been suggested. Important ecological services provided by birds, for example, include seed dispersal and pollination (Silva et al. 1996; Levey et al. 2001). Some recent trophic cascade studies have suggested that predator declines may have important implications for forest productivity (Marquis and Whelan 1994; Terborgh et al. 2001). The results from the present experiment, however, imply that decreasing bird numbers may affect some, but not all, plant communities.

Differences in resource availability, specifically the seasonal presence of young leaves, appeared to play a major role in determining when and where bird predation was important for limiting herbivore densities and damage. This implies that simply describing the limitation of herbivore communities as either a top-down or bottom-up process is an oversimplification. Rather, predator effects on their prey are differentially distributed in space and time, and depend on the prey's resource quality and availability. Our study suggests that species interactions should not be viewed as static processes from one forest to another; further studies will

likely uncover more patterns and sources of variation in the outcome of multitrophic interactions.

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