

# Cascading effects of insectivorous birds and bats in tropical coffee plantations

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**Abstract.** The loss of apex predators is known to have reverberating consequences for ecosystems, but how changes in broader predator assemblages affect vital ecosystem functions and services is largely unknown. Predators and their prey form complex interaction networks, in which predators consume not only herbivores but also other predators. Resolving these interactions will be essential for predicting changes in many important ecosystem functions, such as the control of damaging crop pests. Here, we examine how birds, bats, and arthropods interact to determine herbivorous arthropod abundance and leaf damage in Costa Rican coffee plantations. In an enclosure experiment, we found that birds and bats reduced non-flying arthropod abundance by ~35% and ~25%, respectively. In contrast, birds and bats increased the abundance of flying arthropods, probably by consuming spiders. The frequency of this intraguild predation differed between birds and bats, with cascading consequences for coffee shrubs. Excluding birds caused a greater increase in herbivorous arthropod abundance than excluding bats, leading to increased coffee leaf damage. Excluding bats caused an increase in spiders and other predatory arthropods, increasing the ratio of predators to herbivores in the arthropod community. Bats, therefore, did not provide benefits to coffee plants. Leaf damage on coffee was low, and probably did not affect coffee yields. Bird-mediated control of herbivores, however, may aid coffee shrubs in the long term by preventing pest outbreaks. Regardless, our results demonstrate how complex, cascading interactions between predators and herbivores may impact plants and people.

*Key words:* agriculture; bats; birds; coffee plantation; Costa Rica; ecosystem services; herbivorous arthropods; intraguild predation; pest control; predatory arthropods; species interactions.

## INTRODUCTION

Biodiversity is declining at an unprecedented rate (Barnosky et al. 2011), with societal implications that are difficult to project. The decline is often discussed in the context of species extinctions, but populations are declining even more rapidly, with severe consequences for Earth's life support systems (Hughes et al. 1997, Cardinale et al. 2012). Hairston et al. (1960) famously postulated that predator populations disproportionately affect the structure and functioning of ecosystems through their regulation of herbivores (Hairston et al. 1960). Now, as predators decline, we are witnessing fundamental state shifts in Earth's ecosystems; for example, eutriching lakes in the absence of bass, and restructured riparian areas in the absence of wolves (Estes et al. 2011). In agricultural landscapes, predators constitute a vital control of damaging crop pests. Arthropod pests destroy 8–15% of global wheat, rice, maize, potato, soybean, and cotton production; without natural biological control and pesticides, crop losses would be 9–37% (Oerke 2005). In the United States, arthropod pests consume ~13% of potential crop

production, worth ~US\$33 billion (Pimentel et al. 2005). Without native arthropod predators, the damage would be ~US\$4.5 billion higher (Losey and Vaughan 2006).

The impact of predator loss on herbivorous insect communities, however, remains unclear. When predators consume each other (intraguild predation), losing higher-order predators could actually reduce herbivore populations if intermediate predators are released from predation (Polis et al. 1989, Rosenheim 1998). Indeed, top-level predators tend to increase herbivore abundances, whereas intermediate-level predators reduce herbivore abundances (Vance-Chalcraft et al. 2007).

Intraguild predation may explain why the relationship between predator diversity and pest-control provision remains unclear. High-diversity communities may contain more intraguild predators and thus higher herbivore abundances (Finke and Denno 2005). Alternatively, high-diversity communities may contain more predator species that are complementary in their functional roles, feeding on different pest species or pest life stages, employing distinct hunting strategies, and/or differentially partitioning space or time (e.g., feeding at different strata or at different periods during pest population cycles) (Straub et al. 2008). A diversity of complementary predators may thus reduce pest abundances better than a few predators. In general, increasing predator

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biodiversity tends to reduce pest abundance, but insensitive or increasing pest abundances are also regularly observed (Finke and Denno 2005, Snyder et al. 2006, Vance-Chalcraft et al. 2007, Letourneau et al. 2009).

Identifying intraguild predation is therefore an important step to predicting the consequences of biodiversity decline for pest control (Polis et al. 1989, Rosenheim 1998). Investigations of intraguild predation in nature have centered on invertebrates (Vance-Chalcraft et al. 2007), despite great potential for vertebrates to serve as biological control agents (Mols and Visser 2002, Cleveland et al. 2006, Kellermann et al. 2008, Boyles et al. 2011). Because they feed as higher-order predators, intraguild predation would be expected to be common among insectivorous vertebrates. Intraguild predation has been documented among vertebrates (Spiller and Schoener 1990, Tscharnke 1992, Mooney and Linhart 2006); however, recent meta-analysis suggests that it is rare in nature (Mooney et al. 2010).

The meta-analysis of Mooney et al. (2010) focused on three vertebrate taxa: bats, birds, and lizards. Because birds and bats are warm blooded and must regularly consume a higher proportion of their body mass, per capita effects of birds and bats on insects may be stronger than per capita effects of lizards or frogs. Accordingly, Mooney et al.'s (2010) meta-analysis focuses primarily on endotherms, with birds significantly over-represented: 104 of 113 experiments focused on birds, 7 of 113 on lizards, and 2 of 113 on bats. In fact, these numbers are misleading because the vast majority of studies confound bird-mediated and bat-mediated predation. Bird predation rates are quantified by excluding birds from plants with mesh-net cages and measuring resulting changes in arthropod communities. These cages also exclude insectivorous bats. Therefore, although birds are believed to consume herbivores and yield net positive effects on plants, the relative contribution of birds and bats is largely unknown (Van Bael et al. 2008, Mäntylä et al. 2010). To date, only three studies have differentiated bird and bat predation, with different conclusions concerning their effects on plants (Kalka et al. 2008, Williams-Guillén et al. 2008, Morrison and Lindell 2012).

A majority of the studies that pioneered research on vertebrate predation in agroecosystems, including the seminal work that first differentiated bird and bat predation, focused on coffee plantations (Greenberg et al. 2000, Perfecto et al. 2004, Williams-Guillén et al. 2008). Coffee is arguably the world's most economically important crop, supporting 20 million households worldwide and garnering a total retail value of ~\$US90 billion (Vega et al. 2003, Jaramillo et al. 2011). Approximately 10 million hectares in more than 50 countries are dedicated to coffee production, making it a dominant land use throughout the tropics.

Coffee was originally cultivated under a canopy of trees; however, desire to increase yields has resulted in

shade-tree removal and fine-scale deforestation surrounding farms (Perfecto et al. 2009). This has caused declines in the substantial biodiversity that persists in coffee plantations (Philpott et al. 2008). In particular, changes in insectivorous bird and bat communities may result in lower predation rates on insect pests, reducing farm yields and incomes (Kellermann et al. 2008, Johnson et al. 2009, 2010, Williams-Guillén and Perfecto 2010, Karp et al. 2011, Mendenhall et al. 2011). Although increased leaf damage has been documented when birds and bats are excluded simultaneously (Greenberg et al. 2000), the one study differentiating bird and bat predation found no effect on leaf damage of either group (Williams-Guillén et al. 2008).

Here, we compare bird- and bat-mediated control of arthropod communities in a well-studied coffee agroecosystem in southern Costa Rica (Mendenhall et al. 2013). We provide the first direct comparison of intraguild predation by bats and birds, and use these findings to compare the relative roles of birds and bats in providing pest-control services to coffee farmers.

## METHODS

### *Study site*

We studied bird- and bat-mediated control of arthropod communities in southern Costa Rica near the Las Cruces Biological Station of the Organization for Tropical Studies (OET/OTS). Our study sites were two coffee plantations, situated at 1100 m above sea level in the Coto Brus Valley. Annual precipitation and temperature, respectively, average 3600 mm and 17–24°C. The landscape was previously premontane tropical wet forest, but was deforested in the 1950s and 1960s (Sansonetti 1995). Now the landscape is a mosaic of forest patches, pasture, sun coffee plantations, and small mixed gardens (Mendenhall et al. 2011).

Our two study plantations, “Finca San Antonio” and “Hacienda Rio Negro,” cultivate *Coffea arabica*. Finca San Antonio is a small family-owned plantation, comprising ~30 ha of coffee and a ~2-ha riparian forest remnant. The majority is the “Costa Rica 1995” cultivar, seeded in the early 2000s. The plantation employs full sun, with occasional nitrogen-fixing Poró trees (*Eythrina* spp., Fabaceae) and bananas and plantain plants. In contrast, Hacienda Rio Negro is a large commercial operation, comprising ~250 ha of coffee. Two large (~80-ha) forest fragments and La Amistad National Park abut the plantation. Although considered sun coffee, a diverse set of fruit trees and pioneer tree species (e.g., *Cecropia* spp.) are interspersed throughout the plantation. Coffee ages and cultivars vary; however, age (13–18 years) and variety (Catuii) were standardized in our experiments. Both plantations apply fertilizers, herbicides, and fungicides throughout the year. Pesticides are not used on Finca San Antonio, while Hacienda Rio Negro applies low doses of Endosulfan (0.35 L/ha in 2010; 0.5 L/ha in 2011).

### *Experimental design*

We built bamboo-frame mesh cages around coffee plants to exclude birds and bats. The mesh size was small enough to exclude birds and bats, but large enough to allow insects and other small animals to enter (1.5 square inch [3.8 cm] nylon gill net N163A; Nylon Net Company, Memphis, Tennessee, USA) (Greenberg et al. 2000, Kellermann et al. 2008, Johnson et al. 2010). Lizards, frogs, and large insects were encountered within cages during the experiment.

We built 36 cages ( $\sim 2 \times \sim 3 \times \sim 2$  m) at the small plantation, each surrounding four coffee plants ( $n = 144$  plants). Cages were assigned to one of four treatments: permanently closed (excluding birds and bats), closed from sunrise to sunset but open at night (excluding birds), closed from sunset to sunrise but open during the day (excluding bats), or permanently open (excluding neither). Open cages consisted of an open bamboo frame cage. Each block was separated by at least 50 m. We constructed 60 cages ( $\sim 1 \times \sim 1 \times \sim 2$  m) at the large plantation, each surrounding a single coffee plant. Plants either received a permanent mesh net cage or an open bamboo frame. Logistical and financial constraints precluded the possibility of assessing differences between bird and bat effects at the large plantation; we included this work to verify general trends at the small plantation. The site was still visited, however, 1–2 times per week to ensure that cages remained in good shape. At both plantations, cages were placed along distance gradients from forest patches: one-third of the cages were placed near forest ( $< 50$  m), one-third at intermediate distance ( $> 50$  m,  $< 350$  m), and one-third far from forest ( $> 350$  m).

The enclosure experiment occurred in the wet season of 2010 and the dry season of 2011. The wet-season experiment began when coffee berries were growing (15 July 2010) and ended at the height of harvest (15 October 2010). The dry-season experiment began during coffee flowering (15 February 2011) and ended during berry growth (5 June 2011).

### *Arthropod and herbivory surveys*

We used sweep nets to sample non-flying arthropods and sticky traps to sample flying arthropods. To verify that there were no initial differences between treatments, we acquired sweep samples prior to the experiment. Then, at the end of the wet and dry seasons, we resampled arthropod communities, with two sweep samples per plant (from two visits spaced one week apart). Sweep samples were acquired with a 15-inch (38 cm) diameter, sturdy cotton cloth sweep net. In one continuous motion, we swept each shrub in the top, middle, and bottom layers of the shrub, as well as one vertical sweep. All contents were immediately emptied from the net into a large plastic bag, with cotton soaked in acetone as the killing device. Each arthropod was sorted minimally to order and measured in length with digital calipers.

At the same time points, we placed one sticky trap oriented North at chest height on each coffee shrub. Sticky traps were yellow ribbons (Arbico Organics, Oro Valley, Arizona, USA) coated with Tanglefoot (Contech Enterprises, Victoria, British Columbia, Canada) and affixed to a  $15 \times 23$  cm manila envelope. At the end of the dry season, we applied Tanglefoot directly to the manila envelope, avoiding the yellow ribbon that may have served as an arthropod attractant. Sticky traps were deployed for two consecutive days. Upon collection, we covered each trap in plastic wrap for storage, later identifying each trapped arthropod minimally to order. Although coffee's primary pest, the coffee berry borer beetle (*Hypothenemus hampei*), was present at both plantations, we do not report borer-specific surveys here, as these were the subject of other work (Karp et al. 2013).

We assessed arthropod-induced plant damage on each coffee shrub with two methods. First, we visually inspected 20 leaves per shrub, selecting 10 leaves on the seventh branch from the top of the bush and 10 leaves on the fourth branch from the bottom. Each leaf was scored according to the percentage of area eaten (0, not consumed; 1, 1–6% damage; 2, 7–12%; 3, 13–25%; 4, 26–50%; 5, 51–100%). Visual surveys were performed at the same time points as arthropod surveys. Second, at the beginning of each experiment, we marked 10 undamaged leaves on each bush at the third or fourth phyllotaxic position with fine, colored wire. At the end of the experiments, we recovered as many marked leaves as possible, scanned leaves with an Epson Perfection 3490 photo-quality scanner, and computed the change in percentage area consumed using Photoshop.

### *Statistical analysis*

We examined the consequences of bird and bat exclusion on arthropod abundance, predator to herbivore ratios, and herbivory, using generalized linear mixed models (GLMMs). An advantage of GLMMs is their simultaneous accommodation of non-normal data (counts and proportions) and spatial autocorrelation (Zuur et al. 2009). We modeled count data with Poisson distributions and log links (arthropod abundances), proportion data with binomial distributions and logit links (herbivory incidence), and continuous data with Gaussian distributions and identity links (predator to prey ratios).

At the small plantation, cages were constructed in experimental blocks, and each cage surrounded four coffee plants. Therefore, plants within the same cage, and cages in the same experimental block could not be considered spatially independent. In most analyses, we accounted for nonindependence by modeling experimental blocks and cages as nested random effects. For analyses of predator to herbivore ratios, we used only experimental blocks (not cages) as random effects because arthropod abundances were summed across cages to avoid dividing by 0. Similarly, we included only

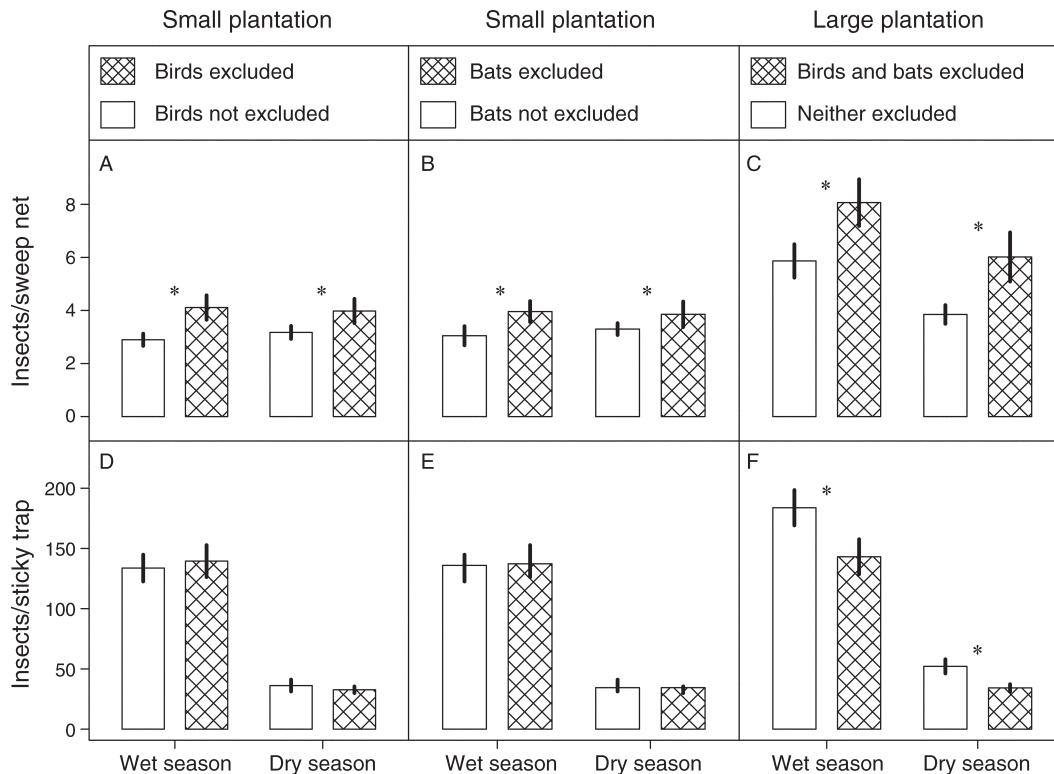


FIG. 1. Birds and bats limited non-flying arthropod abundances in tropical coffee plantations. In both wet and dry seasons, (A) excluding birds and (B) excluding bats caused the total number of arthropods sampled in sweep nets to increase. The same trend was observed (C) when both birds and bats were excluded simultaneously at the large plantation. No differences were recorded at the small plantation in sticky trap samples for (D) birds or (E) bats. (F) At the large plantation, arthropod abundance in sticky traps significantly decreased with bird and bat exclusion. Asterisks denote significance ( $P < 0.05$ ) under log-likelihood tests, comparing nested generalized linear mixed models (see *Methods*). Values are means  $\pm$  SE.

experimental blocks as random effects at the large plantation, because cages were constructed around individual plants.

Bird presence and bat presence were included as explanatory variables in each model. We do not report the interaction of bird and bat presence, as this did not yield explanatory power. We also tested whether effects varied by season (wet season or dry season) by including interactions with season as additional explanatory variables. In all cases, variable significance was tested using backwards model selection. Explanatory variables and interactions were removed from models iteratively, and nested models were compared with Akaike Information Criteria and log-likelihood tests (Zuur et al. 2009).

We used these procedures to assess the effect of bird and bat predation on (1) total arthropod abundance, (2) abundance of individual orders with  $>50$  samples, (3) herbivorous arthropod abundance, (4) predatory arthropod abundance, and (5) predator to herbivore ratios, utilizing both sweep net and sticky trap samples. We also divided arthropods into small and large size classes, and repeated analyses of bird and bat predation for each group. "Small arthropods" were  $\leq 3$  mm in body length, which equated to half of the total insects

surveyed in sweep nets. Finally, we tested whether birds and bats affected the incidence of herbivory (percentage of leaves attacked) in visual herbivory surveys and analyses of marked leaves. All analyses were conducted in R using the lme4 package (R Development Core Team 2008).

## RESULTS

With sweep nets, we collected and identified 4981 arthropods to order, and found that excluding birds and bats increased total arthropod abundance in both seasons and on both plantations (Fig. 1; Appendix: Table A1). Prior to the experiment, we observed no differences between enclosures and open controls in the number of arthropods captured in sweep samples (Appendix: Fig. A1, Table A1). After both seasons of the experiment, however, excluding birds caused an increase in arthropod abundance (see Plate 1). Specifically, arthropod abundances were 42% and 25% lower on plants exposed to bird predation than on plants not exposed to predation in the wet and dry seasons, respectively. The effect of excluding bats was smaller: 30% in the wet season and 17% in the dry season. Excluding birds caused increases in arthropods of all sizes (for large arthropods,  $\Delta\text{AIC} = 10.8$ ,  $\chi^2 = 12.8$ ,  $P <$

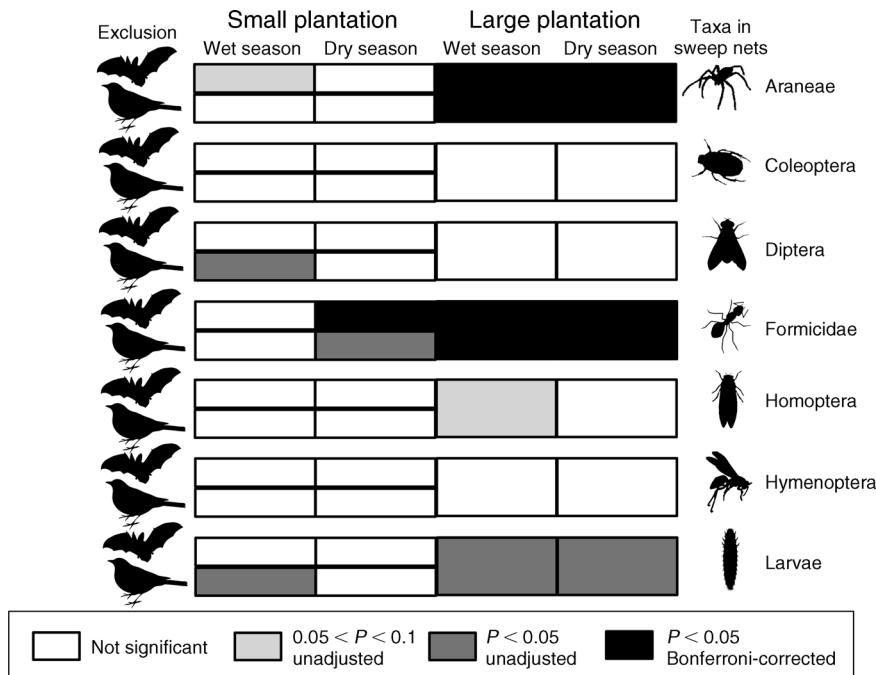


FIG. 2. Analyses of bird and bat predation by arthropod taxa in sweep net samples. Excluding birds caused an increase in flies, ants, and arthropod larvae at the small plantation. Excluding bats caused an increase in ants and spiders at the small plantation. At the large plantation, simultaneously excluding birds and bats increased abundances of spiders, ants, larvae, and Homoptera. Black boxes indicate significance under log-likelihood tests ( $P < 0.05$ ), comparing nested generalized linear mixed models after Bonferroni correction. Dark gray boxes indicate results that were no longer significant after Bonferroni correction, and light gray boxes indicate marginal trends ( $0.05 < P < 0.10$ ).

0.01; for small arthropods,  $\Delta AIC = 7.12$ ,  $\chi^2 = 5.12$ ,  $P < 0.01$ ). Excluding bats, however, caused increases in small, but not large, arthropods (for large arthropods,  $\Delta AIC = 1.94$ ,  $\chi^2 = 0.06$ ,  $P = 0.81$ ; for small,  $\Delta AIC = 7.84$ ,  $\chi^2 = 9.84$ ,  $P < 0.01$ ). No differences were observed in arthropod sizes between treatments prior to the beginning of the experiment ( $P > 0.05$ ).

In contrast, we identified 66 478 arthropods captured in sticky traps to order, and found that excluding birds and bats did not affect their total numbers (Fig. 1; Appendix: Table A1). However, at the large plantation, the number of arthropods captured in sticky traps decreased with bird and bat exclusion. A key difference between sticky traps and sweep nets was that sticky traps sampled many more flying arthropods. In sticky traps, 64% of 66 478 arthropods were Diptera and 8.5% were Hymenoptera, whereas sweep nets yielded 16% Diptera and 4.5% Hymenoptera.

We assessed bird and bat predation on individual arthropod taxa for all taxa with more than 50 individuals captured. At the small plantation, we found that excluding bats significantly increased ant abundance and marginally increased spider abundance in sweep nets. Sticky traps also showed that excluding bats significantly increased spider abundance. Excluding birds caused moderate increases in flies, ants, and larvae in sweep samples, but decreased ant abundance in sticky samples (Fig. 2; Appendix: Fig. A2). At the large

plantation, abundances of spiders, ants, and larvae increased with bird and bat exclusion in sweep nets. In contrast, Diptera and Hymenoptera decreased in sticky traps (Appendix: Fig. A2).

We grouped herbivorous taxa (arthropod larvae, Homoptera, land snails, and Phasmatodea) and predatory taxa (Araneae, Neuroptera, Hemiptera: Reduviidae), and found that excluding birds tended to increase herbivores, whereas excluding bats tended to increase predators. Specifically, excluding birds significantly increased herbivores in the dry season, whereas excluding bats only marginally increased herbivores (Fig. 3; Appendix: Table A2). In contrast, excluding bats (but not birds) significantly increased predatory arthropods in the wet season in both sweep net and sticky trap samples (Fig. 3; Appendix: Table A2). This was driven by predation on spiders: spiders made up 70% of the predatory taxa in sticky traps and 93% of the predators in sweep nets. By consuming predatory arthropods, bats decreased the ratio of predatory arthropods to herbivorous arthropods in the wet season (Fig. 4; Appendix: Table A3). Birds, in contrast, increased the ratio of predators to herbivores in the dry-season sticky traps (Fig. 4; Appendix: Table A3).

We found evidence that birds prevented coffee leaf damage (Fig. 5; Appendix: Table A4). In general, coffee damage was very low. For all marked leaves, we found that attacked leaves lost only ~1% of their leaf area, on

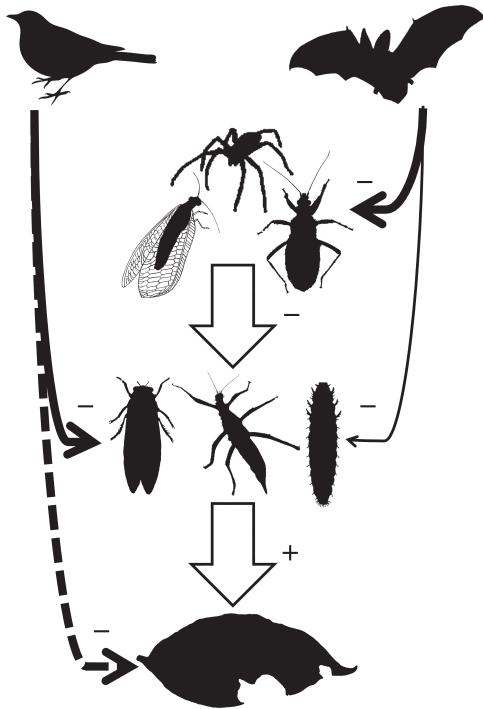


FIG. 3. Schematic indicating cascading effects of birds and bats on arthropods and coffee leaf damage. Birds significantly reduced herbivorous arthropods but not predatory arthropods. Bats mainly consumed predatory arthropods. Probably because they preferentially fed on herbivores, only birds prevented leaf damage. Thick arrows represent significant relationships ( $P < 0.05$ ), thin arrows represent marginal trends ( $0.05 < P < 0.10$ ), and block arrows (the large, open arrows) represent untested relationships. Dashed arrows indicate indirect effects.

average. Therefore, in all herbivory analyses, we report the percentage of leaves with arthropod herbivory rather than a leaf area index. At the small plantation, excluding birds caused a significant increase in herbivory in the dry season in herbivory surveys and in the wet season for analyses of marked leaves. Excluding bats had no effect on herbivory for either plantation or season. At the large plantation, simultaneously excluding birds and bats caused a marginally significant increase in herbivory in both seasons, for both herbivory surveys and marked leaves. For herbivory surveys, these relationships became significant after accounting for preexisting differences in herbivory rates among treatments (Appendix: Figs. A1 and A3).

#### DISCUSSION

We found that excluding birds and bats caused higher arthropod abundances in sweep nets at the two Costa Rican coffee plantations. Specifically, we measured significant increases in ants, spiders, and arthropod larvae with predator exclusion, paralleling results from similar bird and bat exclusion experiments (Mooney et al. 2010). Sticky trap samples, however, yielded no differences between treatments at the small plantation,



PLATE 1. The Yellow Warbler (*Setophaga petechia*), a common resident of tropical coffee plantations, consumes insects and may help limit coffee leaf damage. Photo credit: D. S. Karp.

and lower arthropod abundances with bird and bat exclusion at the large plantation. A key difference between sampling methods is that sticky traps captured more flying arthropods than sweep nets. These flying arthropods declined when birds and bats were excluded, driving different trends between sweep nets and sticky traps.

Decreased abundance of flying arthropods with bird and bat exclusion may have been caused by intraguild predation on intermediate predators. Previous work in the Caribbean showed that lizards increase Dipteran abundances by consuming web-building spiders (Pacala and Roughgarden 1984, Spiller and Schoener 1990). Correspondingly, we found that excluding birds and bats at the large plantation increased spider abundances but decreased Dipteran and Hymenopteran abundances.

Our results also indicate that the frequency of intraguild predation among bats and birds may differ. We found that excluding birds had a greater effect on herbivorous arthropods, whereas excluding bats had a greater effect on predatory arthropods. Bats seemed to target spiders in particular, a finding replicated in some but not all studies differentiating bird and bat predation (Kalka et al. 2008, Williams-Guillén et al. 2008). Because most spiders are nocturnal, predation on spiders by bats was expected. These results therefore both parallel and contradict aspects of the review by Mooney et al. (2010) of vertebrate intraguild predation. That birds did not seem to feed as intraguild predators affirms Mooney et al. (2010)'s findings; however, by partitioning bird- and bat-mediated predation, we also show that intraguild predation can occur within some vertebrate groups.

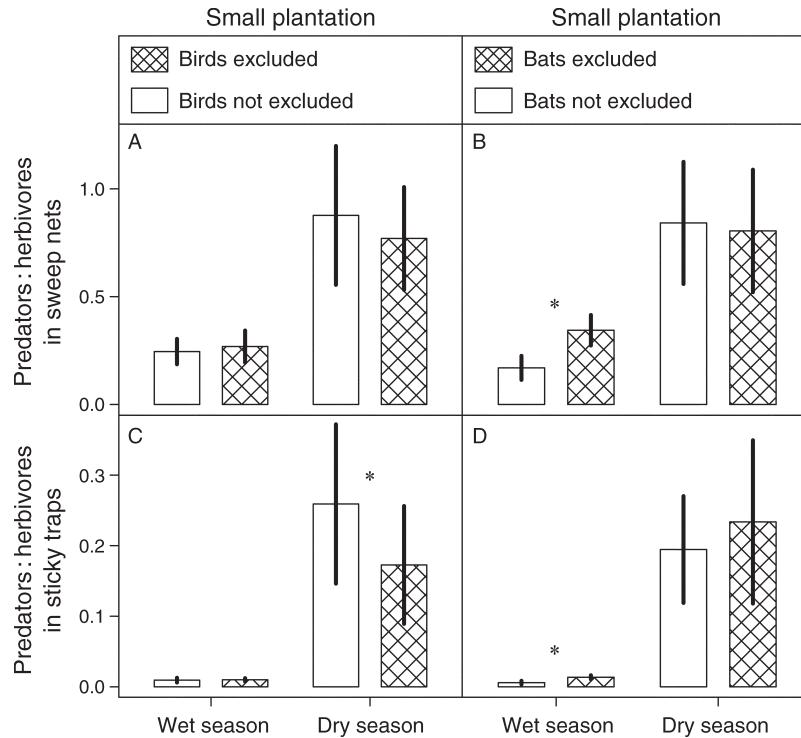


FIG. 4. Bats, but not birds, fed as intraguild predators. (A) Birds did not change the ratio of predators to herbivores in sweep net samples, but (C) increased the proportion of herbivores to predators in sticky trap samples in the dry season. In contrast, excluding bats caused predator to herbivore ratios to increase in the dry season for (B) sweep net and (D) sticky trap samples. Asterisks denote significance under log-likelihood tests of nested generalized linear mixed models ( $P < 0.05$ ). Values are means  $\pm$  SE.

Differences in intraguild predation between birds and bats may have driven differences in their effects on coffee plants. Insectivorous birds are widely believed to prevent leaf damage; however, previous studies have confounded bird predation by simultaneously excluding bats (Van Bael et al. 2008, Mäntylä et al. 2010). Our results support attributing the prevention of coffee leaf damage to birds. Excluding birds increased herbivorous insect abundance, including arthropod larvae. We found no evidence, however, that bats fed on arthropod larvae, which may explain why bat effects were stronger on small arthropods: arthropod larvae were generally larger than adults (mean larval length 3.9 mm; mean adult length 3.3 mm).

Excluding birds caused increases in large and small arthropods. Assuming that predatory arthropods consume small prey items, birds may thus reduce herbivore abundances by feeding synergistically with other predators (Johnson et al. 2009, Mooney et al. 2010). Bats, in contrast, may both limit predatory arthropod abundance directly and compete with predatory arthropods over shared herbivorous prey. A caveat is that our study provides no direct evidence that predatory arthropods limited herbivore abundances. Future work that factorially manipulates vertebrate and arthropod predators is needed to resolve hypothesized mechanisms fully.

Regardless, that excluding birds increased leaf damage and excluding bats had no effect on leaf damage supports the idea that bat predation on predatory arthropods may mitigate benefits to plants.

Three other studies have isolated cascading effects of birds and bats on plants, two of which found that both taxa reduced leaf damage (Kalka et al. 2008, Morrison and Lindell 2012). The other study reported no effect of birds or bats on coffee leaf damage (Williams-Guillén et al. 2008), despite contrasting findings from other investigations (Greenberg et al. 2000, Johnson et al. 2009). This inconsistency may arise from low herbivory rates on coffee. Few arthropods are able to consume large quantities of caffeine (Filho and Mazzafera 2000, Nathanson 2009), and top-down control by predators is expected to attenuate when plants boast strong anti-herbivore defenses (Schmitz et al. 2000).

Future work should focus on extending our analyses to other study systems, especially to plants that are more sensitive to herbivory. Our finding that bats, more than birds, feed as intraguild predators is probably not universal. Bats consume herbivorous arthropods at other sites (Cleveland et al. 2006, Kalka and Kalko 2006, Boyles et al. 2011). Insectivorous bats on Barro Colorado Island feed extensively on herbivores such as Lepidoptera, Orthoptera, and Anisoptera, all of which

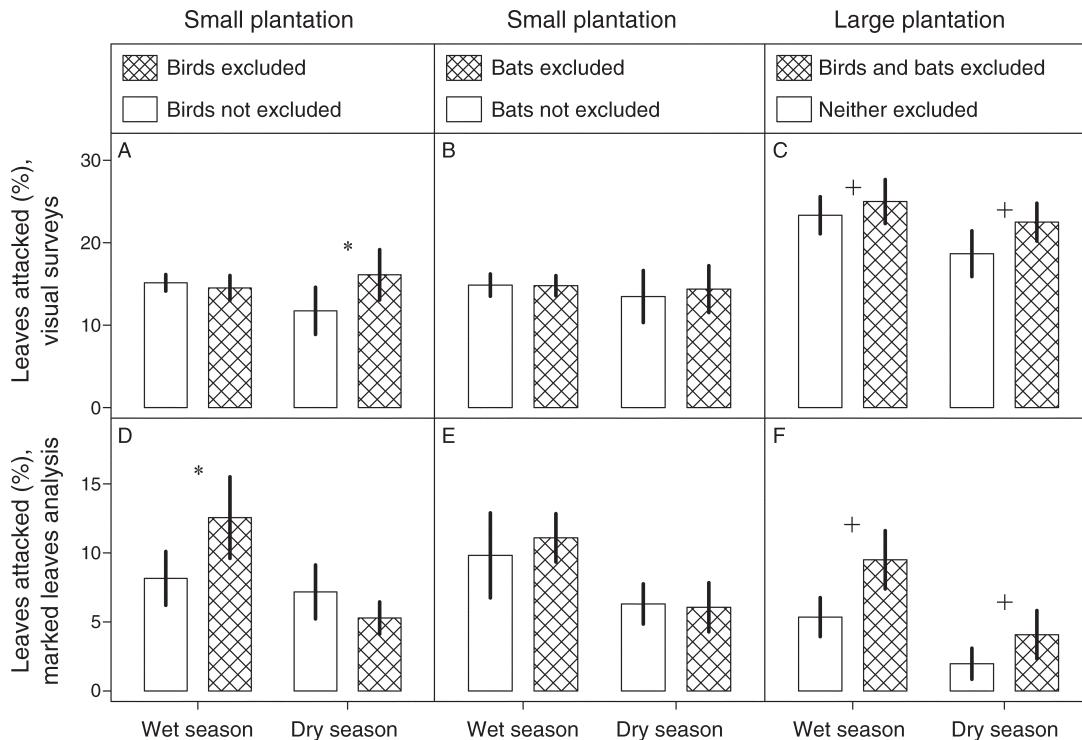


FIG. 5. Birds, but not bats, reduced coffee leaf damage. Excluding birds caused the percentage of coffee leaves with arthropod-induced damage (A) to increase in the dry season for visual leaf surveys and (D) to increase in the wet season for analyses of marked leaves. (B, E) Excluding bats caused no change in leaf damage. Excluding both birds and bats simultaneously at the large plantation caused marginal increases in leaf damage in both seasons for (C) leaf surveys and (F) analyses of marked leaves. Asterisks denote significance ( $P < 0.05$ ) under log-likelihood tests, comparing nested generalized linear mixed models. Plus signs denote marginal trends ( $0.05 < P < 0.10$ ). Values are means  $\pm$  SE.

were rare in our coffee plantations (2.5% of sweep net samples, 0.1% of sticky trap samples). Bats, therefore, may provide net benefits to plants in other systems. On the other hand, birds may not always provide net benefits to plants. As opportunistic feeders, birds consume spiders and other predatory arthropods (Mooney and Linhart 2006), even in coffee plantations (Williams-Guillén et al. 2008). Birds can have mixed effects in the same study system. For example, birds increased pine tree biomass by eating leaf-tending ants, but had no effect on pine leaf damage as a result of their consumption of arthropod predators (Mooney and Linhart 2006).

Future experiments should also be repeated over multiple seasons. Only one of the three previous studies to isolate the effects of birds and bats on arthropods repeated their experiment in multiple seasons (Williams-Guillén et al. 2008). Given temporal fluctuations in arthropod abundances (Janzen 1973), it is unsurprising that this study reported different predation dynamics in the wet and dry seasons (Williams-Guillén et al. 2008). We also found temporal variation here, with greater bird-mediated predation on herbivores in the dry season and greater bat-mediated predation on predators in the wet season. One explanation is that many insectivorous migratory birds occupy our sites in the dry season,

which could increase aggregate predation pressure on herbivorous arthropods.

#### CONCLUSION

Our study is one of the first to isolate and track the cascading effects of insectivorous birds and bats to consequences for plants. We suggest that differences in intraguild predation frequency between the two taxa mediated their distinct roles in preventing coffee leaf damage. Because herbivory was low, it is unlikely that arthropod-induced leaf damage currently affects coffee yields in our study system. It is possible, however, that natural biological control could help to prevent future pest outbreaks (Perfecto et al. 2004). Also, birds are known to control other pests that attack coffee berries directly, contributing economic benefits to plantation owners (Kellermann et al. 2008, Johnson et al. 2010, Karp et al. 2013). Therefore, tailoring agricultural production practices to support vertebrate insectivores and increase pest control shows great promise for aligning conservation activities with food production and rural livelihoods. Before this is possible, however, more study is needed to elucidate further the complex dynamics between vertebrate insectivores, arthropod predators, and damaging pests that ultimately determine outcomes for farm yields and profits.

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#### SUPPLEMENTAL MATERIAL

##### Appendix

Statistical tables of predation on insects and effects on herbivory and figures that show insect abundances and herbivory prior to the experiment, sticky trap samples by order, and changes in leaf damage ([Ecological Archives E095-090-A1](#)).