Bats Limit Insects in a Neotropical Agroforestry System

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Top-down limitation of herbivores is an important ecosystem service that facilitates agricultural production (*1*). Several experiments in natural and managed ecosystems demonstrate the importance of avian predators in arthropod control (*2*). Although insectivorous bats are expected to have major impacts on arthropods (*3*), few studies have quantified the effects of bats on standing crops of arthropods. Because all previous exclosure-based studies of avian insectivory have left exclosures up during the night, it is possible that a proportion of predation attributed to birds may represent predation by foliage-gleaning bats. Here, we report an exclosure experiment conducted in a Mexican coffee agroforest, in which we directly measured the impact of predation by foliage-gleaning birds and bats on arthropods found on coffee plants.

We used exclosures made of agricultural netting erected around individual coffee plants in Finca Irlanda, an organic shade coffee plantation harboring abundant populations of ≥120 bird species and ≥45 bat species. We established 22 blocks of four treatments: birds-only excluded (exclosure netting in place only during the day), bats-only excluded (netting in place only during the night), both excluded (netting in place day and night), and control (no netting). We visually censused noncolonial arthropods (primarily insects, but also spiders, harvestmen, and mites) on all plants at the beginning of the experiments, every 2 weeks thereafter, and at the end of the experiment. We conducted the experiment for a 7-week period beginning January 2007 (dry season) and for an 8-week period beginning June 2007 (wet season).

Exclusion of birds and bats resulted in significant increases in total arthropods on experimental plants, although a significant amount of variation was also explained by foliage biomass and initial arthropod density (table S1). On average, total arthropod densities on plants from which both predators were excluded were 46% higher than those observed on control plants. There was a clear seasonal effect with regard to bats: Although bats did not have significant effects on arthropod densities in the dry season, their impacts were highly significant in the wet season, with an 84% increase in arthropod density in bat-only exclosures, exceeding the effects of birds (Fig. 1). In neither season was there a significant interaction between bats and birds, indicating an additive effect. Regardless of season, arthropod densities increased the most on plants from which both birds and bats were excluded (Fig. 1). These seasonal and additive patterns held for various arthropod taxa (table S2), although only birds significantly reduced spiders. Although predator exclusions resulted in increased arthropod density, no significant differences were seen between treatments in the prevalence or the intensity of leaf damage.

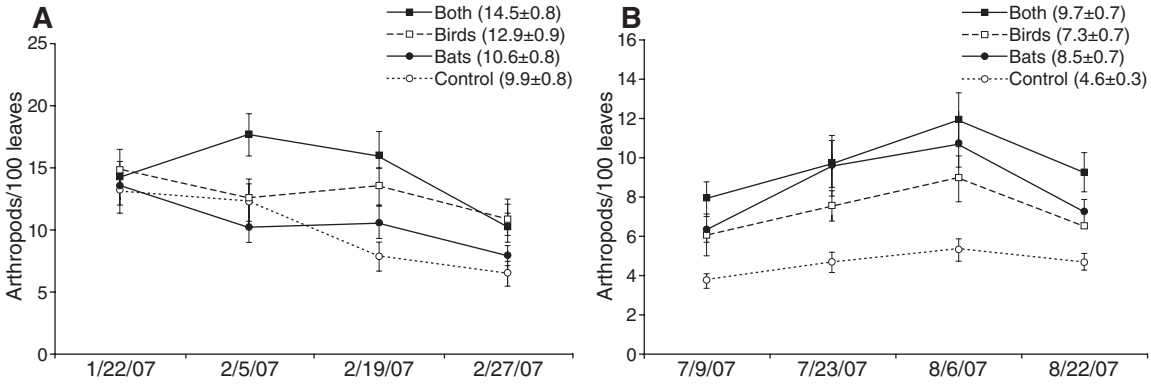

Fig. 1. Mean number of arthropods ± SEM per 100 coffee leaves in four exclosure treatments in (**A**) dry season and (**B**) wet season. "Both" indicates birds and bats excluded (■); "Birds," only birds excluded (□); "Bats," only bats excluded (●); and "Control," no predators excluded (○). Numbers after treatment name in legends indicate mean number of arthropods ± SEM per 100 leaves across all counts. $N = 88$ for each season.

At our site, bats were as important as birds in regulating insect populations across the course of the year. We suspect that increased impacts of birds in the dry season may result from an influx of insectivorous overwintering migrants from North America (*4*). We have no data on the absolute density of bats versus birds; however, at our site the capture rates (and presumably abundance) and reproductive activity of bats increased during the wet season. Bats' relatively higher surface area may result in greater heat loss and concomitantly higher energy requirements (*5*), and reproduction increases females' energetic needs; thus, increased bat abundance and reproduction in the wet season may result in an increased impact of bat predation on understory arthropods.

Our results are consistent with arguments that functional diversity is central to the maintenance of ecosystem services (*6*). In this case, the presence of these two vertebrate taxa maintains a functional difference that enhances the efficacy of arthropod reduction. Previous exclosure studies have not differentiated between diurnal and nocturnal predators, attributing observed changes to birds. We suggest that these studies of the impacts of "bird" predation may have underestimated the importance of bats in limiting insects. Bat populations are declining worldwide (*7*), but monitoring programs and conservation plans for bats lag far behind those for birds. Declining bat populations may compromise critical ecosystem services, making an improved understanding of their conservation status vital.

References and Notes

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Supporting Online Material

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Tables S1 and S2

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