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Impacts of major predators on tropical agroforest arthropods: comparisons within and across taxa

Received: 29 October 2003 / Accepted: 19 March 2004 / Published online: 17 April 2004
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Abstract In food web studies, taxonomically unrelated predators are often grouped into trophic levels regardless of their relative importance on prey assemblages, multiple predator effects, or interactions such as omnivory. Ants and birds are important predators likely to differentially shape arthropod assemblages, but no studies have compared their effects on a shared prey base. In two separate studies, we excluded birds and ants from branches of a canopy tree (*Inga micheliana*) in a coffee farm in Mexico for 2 months in the dry and wet seasons of 2002. We investigated changes in arthropod densities with and without predation pressure from (1) birds and (2) ant assemblages dominated by one of two ant species (*Azteca instabilis* and *Camponotus senex*). We first analyzed individual effects of each predator (birds, *Azteca instabilis*, and *C. senex*) then used a per day effect metric to compare differences in effects across (birds vs ants) and within predator taxa (the two ant species). Individually, birds reduced densities of total and large arthropods and some arthropod orders (e.g., spiders, beetles, roaches) in both seasons. *Azteca instabilis* did not significantly affect arthropods (total, small, large or specific orders). *Camponotus senex*, however, tended to remove arthropods (total, small), especially in the dry season, and affected arthropod

densities of some orders both positively and negatively. Predators greatly differed in their effects on *Inga* arthropods (for all, small, large, and individual orders of arthropods) both in sign (\pm) and magnitudes of effects. Birds had stronger negative effects on arthropods than ants and the two dominant ant species had stronger effects on arthropods in different seasons. Our results show that aggregating taxonomically related and unrelated predators into trophic levels without prior experimental data quantifying the sign and strengths of effects may lead to a misrepresentation of food web interactions.

Keywords Food webs · Birds · Dominant arboreal ants · Multi-trophic interactions · Coffee agroecosystems

Introduction

Identifying when predator taxa can be grouped into trophic levels is critical to community ecology. In attempts to understand food web complexity, many unrelated predator taxa are often grouped into trophic levels or trophospecies even when information regarding the relative importance of different predators is unknown (e.g., Hairston et al. 1960). Yet, species do not clearly separate into homogeneous trophic levels in part due to omnivory, intraguild predation, and ontogenetic or environmentally influenced diet shifts (Polis and Strong 1996). In nature, communities are often composed of complex webs, not of trophic chains (Pace et al. 1999; Polis et al. 2000). While inappropriate effects of aggregation are known for aquatic ecosystems (Hall and Raffaelli 1991; Martinez 1993; Abrams et al. 1996; Tavares-Cromar and Williams 1996; Sugihara et al. 1997; Yodzis and Winemiller 1999; Thompson and Townsend 2000; Abarca-Arenas and Ulanowicz 2002), less is known for terrestrial ecosystems (but see Martinez 1993; Sugihara et al. 1997). Studies on predators that share prey could potentially provide clues about the appropriateness of aggregating species into units such as trophic levels or trophospecies to describe food webs. To date, most such studies from terrestrial systems

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focus on predator species within a taxonomic group and less so on unrelated species (Simberloff and Dayan 1991; but see Davidson et al. 1980; Jaksic and Delibes 1987). Furthermore, many studies pool impacts of taxonomically similar species even though this can mask considerable variation in resource use (Davidson 1997; Murakami and Nakano 2000).

One focus of many current investigations is to examine the effects on food webs of multiple predators alone and in combination to determine a basis for grouping predators in food web models. Different predator species, even those from one taxa or guild, may greatly differ in their effects on prey communities (Harris 1995; Schmitz and Suttle 2001; Chalcraft and Resetarits 2003a, b) making aggregation of these species in food web models challenging, especially when individual predator species with putatively similar functions create nonlinear effects when they are combined (Sih et al. 1998; Eklöv and Werner 2000; Crumrine and Crowley 2003). Evidence has, however, shown that taxonomically related predators may be entirely substitutable in their effects on food webs and so aggregating them in a single functional unit is warranted (Schmitz and Sokol-Hessner 2002; Sokol-Hessner and Schmitz 2002). Whether or not this applies to distantly related taxa of predators remains open to question.

This study helps to resolve that question by examining how two unrelated predator taxa, ants and birds, affect a terrestrial arthropod assemblage. Ants and birds are taxonomically important predators of arthropods in natural and agricultural settings (Way and Khoo 1992; Marquis and Whelan 1994; Perfecto and Castiñeiras 1998; Greenberg et al. 2000; Schmitz et al. 2000; Sanz 2001; Mols and Visser 2002; Van Bael et al. 2003), and likely differentially affect prey based on differences in their mobility, size, and life history. Ants are numerous in tropical forests ($>10,000 \text{ ha}^{-1}$) (Schulz and Wagner 2002; Watt et al. 2002), patrol smaller areas than birds, cooperatively forage (using recruitment or tandem running) using chemical signals to alert other ants (Hölldobler and Wilson 1990), and generally cannot easily attack large or highly mobile prey (Koptur 1984). Relative to ants, birds are scarce ($10\text{--}50$ individuals ha^{-1} of forest or agroforest, R. Greenberg, personal observation). But, they are highly mobile, energy demanding, generalized, opportunistic, and vary in type and size of arthropod prey they select (Johnson 2000). We were interested in discerning how differences in size, abundance, and foraging strategies between these two predator taxa translated into effects on the arthropod assemblage.

Here, we investigate the importance of birds and two ant species as predators in a coffee agroecosystem. Birds and ants are abundant in traditional farms where coffee grows under a diverse shade canopy (Perfecto and Snelling 1995; Greenberg et al. 1997; Moguel and Toledo 1999). Traditional farms resemble natural forests, but relatively low diversity therein makes them useful for exploring functional relationships difficult to explore in more diverse, natural systems. We experimentally removed

birds or ants from individual branches of *I. micheliana* trees from the canopy of a coffee agroforest and measured changes in arthropod assemblages. To investigate the effects of each predator and to compare effects of unrelated taxa (birds and ants) and taxonomically related taxa (two dominant ants), we addressed the following questions: (1) Do birds and/or ants affect arthropod assemblages in canopy trees? (2) Do birds and ants differ in their effects on arthropods? (3) Do dominant ant species differ in their effects on arthropods?

Materials and methods

We conducted all studies at Finca Irlanda ($15^{\circ}11'N$, $92^{\circ}20'W$; 900 m elevation; 4,500 mm rain/year), a shaded coffee farm in the Soconusco region of SW Chiapas, Mexico, during the dry and wet seasons of 2002. The shade canopy at Finca Irlanda is diverse (>60 species), but is largely dominated by *Inga* spp. (Perfecto and Vandermeer 2002). Although abundance of birds and ants likely differ in this site, species richness of birds and ants, especially those foraging on *Inga* spp. trees, is generally comparable. Based on 6 years of intensive work, we have found 59 bird species and ~ 60 ant species that forage on *Inga* spp. shade trees at this site (Dietsch 2003; S. Philpott, unpublished data).

We focused our work on dominant arboreal ants, defined as numerically abundant and competitively superior to other ants. Such ants are predaceous, polydomous, and tend homopterans (Leston 1973). In tropical forests and agroforests, dominant ants are spatially arranged in mosaic patterns whereby different species form mutually exclusive patches (Leston 1973; Room 1975; Majer 1978; Majer and Queiroz 1993). This spatial mosaic has allowed researchers to determine if dominant ants are associated with different homopterans within ant patches (Leston 1973; Majer 1978). Feeding habits of dominant species may be more similar to each other than to other ant guilds (Davidson 1997). Yet with substantial heterogeneity in resource use among dominant ants, arthropod assemblages within ant mosaic patches may differ as well.

Many dominant ants associate with plants (including *Inga* spp.) with extrafloral nectaries often resulting in lower herbivory (Bentley 1977; Horvitz and Schemske 1984; Koptur 1984; Fiala et al. 1994; Del-Claro et al. 1996) and increased growth and reproductive output (Janzen 1966; Fonseca 1994; Letourneau 1998; de la Fuente and Marquis 1999). But results of ant-plant studies are not conclusive because plant-ants may remove all herbivores presented to them, limit some herbivores, and not others, or may not limit herbivores at all (Schemske 1980; Koptur 1984; Barton 1986; Kelly 1986; Koptur and Lawton 1988; Whalen and MacKey 1988; Rashbrook et al. 1992; Fiala et al. 1994; Del-Claro et al. 1996; Oliveira 1997; de la Fuente and Marquis 1999). Thus although ants may protect *Inga* spp. from herbivores, effects on ant-plant arthropod assemblages are largely unknown (see Risch and Carroll 1982; James et al. 1999; Gibb 2003).

We established and maintained ant exclosures on *I. micheliana* trees during the dry (2 February–30 April) and wet seasons (10 May–26 July) of 2002. We located 20 trees each dominated by either *A. instabilis* or *C. senex* ants. On each tree, we selected two branches (4–8 leaves, 3–4 m above ground) and randomly assigned each to a control or exclosure treatment. To exclude ants (initially and every 2 weeks thereafter), we placed Tanglefoot (The Tanglefoot Company, 314 Straight Avenue, S.W., Grand Rapids, Mich., USA) around the base of branches (over wrapped flagging tape), clipped arboreal connections, and manually picked off ants. We also clipped arboreal connections and wrapped flagging around control branches. On some trees, ants crossed Tanglefoot barriers, and we eliminated all trees with >20 ants on exclosure branches at the time of arthropod collection. Furthermore, farm workers pruned some shade trees accidentally cutting some experimental branches. Final

sample sizes were thus 6 and 14 trees for *A. instabilis* in the dry and wet seasons respectively and 16 trees for *C. senex* in each season.

We also established bird exclosures in *I. micheliana* trees in the dry (12 December 2001–12 February) and wet seasons (2 May–15 July) of 2002. Within the range of locations of ant exclosures, we selected two areas (>800 m apart) with similar vegetation characteristics. Within each area, we selected ten trees (30–80 m between each), on each tree picked two branches (4–8 leaves, 3–4 m above ground), and randomly assigned each to a control or exclosure treatment. We eliminated birds by placing monofilament

nylon fishing nets (35×35 mm mesh) over entire branches and tying nets to form a bag. Choice of mesh size is a trade-off between allowing movement of large arthropods (e.g., lepidopterans) and preventing access to small birds. Our mesh size nonetheless is comparable to other bird-exclosure studies [e.g., Greenberg et al. 2000 (29×29 mm); Mols and Visser 2002 (25×25 mm); Van Bael et al. 2003 (20×20 mm)]. We did not see spiders using the mesh as a web substrate. Data analyses include 18 trees in the dry season (2 trees were lost) and 20 trees in the wet season.

Table 1 Mean (\pm SE) number of arthropods dg^{-1} collected from *Inga* tree branches with (C) or without (E) bird or ant predation during dry and wet seasons of 2002. The two ants (*Azteca instabilis*

and *Camponotus senex*) were eliminated on separate trees and data was combined for the “Ants” category

	Birds		Ants		<i>A. instabilis</i>		<i>C. senex</i>	
	C	E	C	E	C	E	C	E
Dry season								
Acarida	4.2 \pm 1.2	5.7 \pm 1.9	12.4 \pm 3.5	17.4 \pm 6.3	12.0 \pm 5.0	15.4 \pm 8.0	12.5 \pm 4.5	18.2 \pm 8.3
Araneae	8.2 \pm 1.3	24.6 \pm 4.4	12.4 \pm 3.6	14.6 \pm 3.3	27.9 \pm 10.6	11.1 \pm 2.4	6.6 \pm 1.5	15.9 \pm 4.5
Blattodea	0.4 \pm 0.2	13.2 \pm 2.8	3.7 \pm 0.9	1.3 \pm 0.4	7.8 \pm 2.6	2.8 \pm 1.0	2.2 \pm 0.5	0.7 \pm 0.3
Coleoptera	6.2 \pm 2.6	11.8 \pm 3.7	7.9 \pm 1.4	15.6 \pm 2.6	9.8 \pm 2.6	14.3 \pm 2.7	7.1 \pm 1.7	16.1 \pm 3.5
Collembola	0 \pm 0	0.8 \pm 0.3	0.5 \pm 0.3	0.3 \pm 0.2	0.3 \pm 0.3	0.3 \pm 0.3	0.6 \pm 0.3	0.4 \pm 0.2
Diptera	1.6 \pm 0.4	1.1 \pm 0.3	1.6 \pm 0.4	3.2 \pm 1.1	1.9 \pm 0.7	2.1 \pm 1.0	1.5 \pm 0.5	3.6 \pm 1.5
Hemiptera	7.1 \pm 2.3	4.3 \pm 0.8	3.4 \pm 0.8	3.6 \pm 0.9	5.3 \pm 2.1	4.1 \pm 2.0	2.8 \pm 0.7	3.4 \pm 1.0
Homoptera (non-scales)	11.8 \pm 3.4	8.5 \pm 1.5	3.9 \pm 1.0	4.7 \pm 1.3	5.7 \pm 2.5	4.3 \pm 1.7	3.2 \pm 1.1	4.8 \pm 1.8
Scales	0 \pm 0	0 \pm 0	36.1 \pm 26.5	0.2 \pm 0.1	131.6 \pm 91.1	0.4 \pm 0.3	0.2 \pm 0.2	0.1 \pm 0.1
Hymenoptera (non-ants)	6.0 \pm 3.3	6.2 \pm 2.8	4.1 \pm 1.0	4.2 \pm 0.8	2.6 \pm 1.0	4.0 \pm 1.5	4.6 \pm 1.4	4.3 \pm 0.9
Formicidae	12.3 \pm 5.5	46.0 \pm 29.6	34.0 \pm 12.6	2.6 \pm 0.9	86.2 \pm 37.3	2.0 \pm 0.8	14.5 \pm 6.3	2.8 \pm 1.2
Lepidoptera	1.8 \pm 0.6	3.3 \pm 1.1	1.6 \pm 0.5	1.3 \pm 0.4	3.6 \pm 1.7	1.1 \pm 0.8	0.9 \pm 0.3	1.4 \pm 0.5
Neuroptera	0.2 \pm 0.1	0.7 \pm 0.2	0.2 \pm 0.1	0.3 \pm 0.1	0 \pm 0	0.3 \pm 0.2	0.2 \pm 0.1	0.3 \pm 0.2
Orthoptera	0.4 \pm 0.2	0.9 \pm 0.2	0.3 \pm 0.2	0 \pm 0	0.2 \pm 0.2	0 \pm 0	0.4 \pm 0.1	0 \pm 0
Psocoptera	0 \pm 0	0 \pm 0	3.5 \pm 1.0	4.4 \pm 1.2	4.9 \pm 2.4	5.0 \pm 2.2	3.0 \pm 1.0	4.2 \pm 1.4
Thysanoptera	5.6 \pm 0.1	3.8 \pm 1.1	5.4 \pm 0.9	3.4 \pm 0.8	2.3 \pm 1.6	4.0 \pm 2.2	6.5 \pm 1.0	3.2 \pm 0.8
Total arthropods	54.1 \pm 9.6	86.3 \pm 40.6	60.9 \pm 7.7	74.5 \pm 9.2	84.2 \pm 16.2	69.0 \pm 12.8	55.2 \pm 8	76.5 \pm 11.9
Arthropods <3 mm	34.2 \pm 8.6	40.8 \pm 7.9	47.4 \pm 7.3	61.5 \pm 2	70.9 \pm 15.1	55.4 \pm 13	38.6 \pm 7.4	63.9 \pm 11.9
Arthropods >5 mm	4.1 \pm 0.6	19.2 \pm 2.5	8.0 \pm 1.0	6.9 \pm 0.9	10.0 \pm 2.1	7.4 \pm 1.2	7.3 \pm 1.1	6.7 \pm 1.2
Wet season								
Acarida	0.6 \pm 0.2	4.1 \pm 1.4	13.0 \pm 5.2	8.2 \pm 3.6	8.1 \pm 4.1	13.7 \pm 7.5	17.4 \pm 9.1	3.3 \pm 1.2
Araneae	11.4 \pm 4.4	20.5 \pm 4.0	5.1 \pm 1.0	13.6 \pm 3.5	4.3 \pm 1.7	16.5 \pm 5.9	5.8 \pm 1.2	11.0 \pm 4.1
Blattodea	3.0 \pm 1.0	34.1 \pm 11.7	4.6 \pm 1.3	3.3 \pm 1.0	5.5 \pm 2.5	4.4 \pm 2.1	3.8 \pm 1.0	2.3 \pm 0.5
Coleoptera	14.4 \pm 3.3	39.6 \pm 10.0	10.8 \pm 2.2	20.4 \pm 4.2	11.0 \pm 4.3	28.8 \pm 7.3	10.6 \pm 2.0	13.1 \pm 4.0
Collembola	0.6 \pm 0.4	0.6 \pm 0.3	0.4 \pm 0.3	0.2 \pm 0.1	0.8 \pm 0.6	1.1 \pm 0.1	0.1 \pm 0.1	0.3 \pm 0.2
Diptera	2.0 \pm 0.5	1.6 \pm 0.5	2.7 \pm 0.6	3.0 \pm 0.7	2.0 \pm 0.7	3.3 \pm 1.3	3.3 \pm 0.9	2.7 \pm 0.8
Hemiptera	2.3 \pm 0.5	3.3 \pm 0.7	1.9 \pm 0.3	2.2 \pm 0.4	2.4 \pm 0.8	2.8 \pm 0.7	1.5 \pm 0.5	1.6 \pm 0.5
Homoptera (non-scales)	4.3 \pm 0.7	7.1 \pm 5.0	5.4 \pm 1.4	5.5 \pm 0.8	7.9 \pm 2.7	6.1 \pm 1.1	3.2 \pm 0.6	5.0 \pm 1.2
Scales	0 \pm 0	0 \pm 0	94.4 \pm 64.6	0.5 \pm 0.2	202.2 \pm 135.1	0.7 \pm 0.3	0 \pm 0	0.4 \pm 0.2
Hymenoptera (non-ants)	2.3 \pm 0.5	3.3 \pm 0.8	4.7 \pm 2.0	3.3 \pm 0.7	7.4 \pm 4.3	4.3 \pm 1.2	2.3 \pm 0.6	2.3 \pm 0.6
Formicidae	7.9 \pm 2.3	17.8 \pm 4.8	55.1 \pm 22.2	4.0 \pm 1.2	88.9 \pm 45.3	3.4 \pm 1.2	24.6 \pm 9.9	4.5 \pm 2.0
Lepidoptera	6.5 \pm 1.4	6.6 \pm 1.7	12.0 \pm 2.2	17.7 \pm 4.9	10.4 \pm 2.7	21.1 \pm 10.2	15.1 \pm 3.4	14.7 \pm 2.9
Neuroptera	0.6 \pm 0.3	0.3 \pm 0.2	0.2 \pm 0.1	0.3 \pm 0.1	0.1 \pm 0.1	0.1 \pm 0.1	0.2 \pm 0.1	0.4 \pm 0.3
Orthoptera	0.4 \pm 0.1	1.1 \pm 0.4	0.4 \pm 0.2	0.1 \pm 0.1	0.4 \pm 0.3	3.3 \pm 0.2	0.4 \pm 0.3	0 \pm 0
Psocoptera	0 \pm 0	0 \pm 0	0.8 \pm 0.2	2.0 \pm 0.5	1.1 \pm 0.5	2.5 \pm 0.8	0.5 \pm 0.2	1.6 \pm 0.5
Thysanoptera	4.1 \pm 0.9	5.4 \pm 1.4	4.0 \pm 0.9	5.6 \pm 1.0	2.0 \pm 1.1	5.1 \pm 1.4	5.7 \pm 1.2	6.1 \pm 1.5
Total arthropods	52.6 \pm 8.0	128.2 \pm 19.8	69.2 \pm 8.1	85.7 \pm 11.2	68.3 \pm 12.2	109.6 \pm 18.0	70.0 \pm 11.2	64.7 \pm 12.3
Arthropods <3 mm	29.0 \pm 6.1	59.7 \pm 15.3	40.7 \pm 6.6	53.1 \pm 9.2	41.8 \pm 9.2	72.2 \pm 15.5	39.8 \pm 9.8	36.5 \pm 9.4
Arthropods >5 mm	9.6 \pm 1.1	28.0 \pm 5.3	18.1 \pm 2.6	23.5 \pm 5.2	15.3 \pm 2.7	28.8 \pm 10.6	20.5 \pm 4.2	18.8 \pm 3.0

Arthropod sampling for both ant and bird enclosures followed the same protocol. To collect arthropods from *Inga* trees, entire enclosure or control branches were covered with 60×90 mm plastic bags and cut. We killed arthropods inside bags with ethyl acetate and collected all arthropods found on leaves, branches, plastic bags, and bird-enclosure nets. We identified all arthropods to order (and some to family) and measured the length (mm) of each individual. We dried and weighed all foliage collected with samples and standardized all arthropod data as the number of individuals per gram dry foliage (only leaves).

We first examined individual effects of each predator (birds, *A. instabilis*, *C. senex*) on densities of total arthropods, different sized arthropods [small (<3 mm) and large (>5 mm)], and individual orders. We analyzed effects on total, small, and large arthropods using separate ANOVAs with treatment (each predator alone versus enclosure) and season as fixed factors. We examined effects on individual arthropod orders using MANOVA with each order (>25 individuals) as dependent variables and treatment (as above) and season as fixed factors. We followed significant MANOVAs with ANOVAs to test for effects on particular orders. We did not include scales or ants in arthropod totals or as dependent variables in MANOVA (ants were included in bird MANOVA) because (1) ants were intentionally excluded on some trees and (2) ants tend scales (Way 1963) and we expected elevated scale densities on control branches. We instead used separate ANOVA for scales and ants as above. For all tests, we used square-root-transformed data to conform to assumptions of normality.

Because our study included two separate experiments (one for birds and one for ants) we used a metric to compare effects across and within predator taxa (Osenberg et al. 1997; Laska and Wootton 1998; Chalcraft and Reserairts 2003b). We chose the per day effect of predators on arthropod density such that:

$$\Delta r = \ln[(D_C + 1)/(D_E + 1)]t \quad (1)$$

where D_C is the total arthropod density on control branches at the end of the trial period, D_E is the arthropod density on enclosure branches at the end of the trial period, and t is the number of days enclosures were maintained (Osenberg et al. 1997). The metric was calculated on a per tree basis highlighting our paired experimental design. We compared per day effects (Δr) of birds, *A. instabilis*, and *C. senex* on total, small, and large arthropods using ANOVAs and compared effects on the ten most common orders using MANOVA followed by individual ANOVAs. For each test, treatment (with levels of birds, *A. instabilis*, and *C. senex*) was crossed with season. Where there was a significant treatment by season interaction, we

followed with separate ANOVAs and MANOVAs for each season. We used planned contrasts within ANOVA and MANOVA to statistically compare effects of birds and ants (*A. instabilis* + *C. senex*), and then to compare effects of the two ant species. We further differentiated predator effects qualitatively by comparing sign (positive or negative) of effects on arthropods. Because our data included many zeros, we added one to all densities before calculating per tree metric values. We carried out all statistical analyses using Statistica v 6.1 for Windows.

Results

Effects of birds on arthropods

Total arthropod densities were 51% lower on control than on enclosure branches across seasons. These reductions were significant in the dry (by 37%; $F_{1,34}=6.46$, $P=0.016$) and wet seasons (59%; $F_{1,38}=17.45$, $P<0.001$) (Table 1). Birds reduced small (38%) and large arthropods (71%) (Table 2), but effects on large arthropods varied with season. Even so, birds significantly reduced large arthropods in both the dry (79%; $F_{1,34}=50.45$, $P<0.001$) and wet seasons (66%; $F_{1,38}=14.18$, $P=0.001$) (Table 1). Birds also reduced densities of several arthropod orders (Table 3). Although bird effects on particular orders differed with season, there was no significant treatment by season interaction. Birds significantly reduced roaches (by 93%), beetles (62%), orthopterans (62%), spiders (56%), and mites (53%), and tended to reduce ants (68%) and collembolans (57%).

Effects of ants on arthropods

On ant enclosure trees, ant densities were greatly reduced (by 93%) on enclosure branches ($F_{1,98}=24.51$, $P<0.000001$) demonstrating effectiveness of Tanglefoot treatments (Table 1). On *A. instabilis* trees, 97% of ants

Table 2 Effects of predators (birds and two ant species (*A. instabilis*, *C. senex*)) on *Inga* arthropods across the wet and dry seasons of 2002. Statistical results show individual effects of birds and ants on arthropod densities compared with no-predator treatments, and comparison between mean per day effects of predators on arthropods. See text for explanation of statistics used. **Bold numbers** are for significant effects, *italics* show trends

	Arthropods (total)			Arthropods (<3 mm)			Arthropods (>5 mm)		
	<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>
Individuals foliage g ⁻¹									
Birds	1, 72	22.77	<0.001	1, 72	5.09	0.027	1, 72	47.61	<0.001
Season	1, 72	2.08	0.154	1, 72	0.42	0.521	1, 72	8.27	0.005
Birds × season	1, 72	2.23	0.140	1, 72	1.66	0.202	1, 72	0.59	0.446
Ants	2, 98	1.46	0.238	2, 98	1.97	0.146	2, 98	0.06	0.941
<i>A. instabilis</i>	1, 98	0.03	0.869	1, 98	0.00	0.973	1, 98	0.11	0.737
<i>C. senex</i>	1, 98	2.78	0.099	1, 98	3.51	0.064	1, 98	0.03	0.852
Season	1, 98	0.04	0.852	1, 98	2.96	0.088	1, 98	16.54	<0.001
Ants × season	2, 98	0.94	0.393	2, 98	0.97	0.383	2, 98	1.40	0.251
Mean per day effect (Δr)									
Predator	2, 84	8.036	<0.001	2, 84	0.803	0.451	2, 84	10.902	<0.001
Birds vs. ants	1, 84	14.753	<0.001	1, 84	1.579	0.212	1, 84	18.440	<0.001
<i>A. instabilis</i> vs. <i>C. senex</i>	1, 84	0.096	0.758	1, 84	0.011	0.916	1, 84	0.780	0.380
Season	1, 84	1.659	0.201	1, 84	1.432	0.235	1, 84	0.671	0.415
Predator × Season	2, 84	3.672	0.030	2, 84	4.054	0.021	2, 84	1.002	0.372

Table 3 Individual effects of each predator on density of particular arthropod orders compared to no-predator controls across dry and wet seasons of 2002. *Bold* shows significant effects and *italics* show trends

	Birds			<i>A. instabilis</i>			<i>C. senex</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>
MANOVA									
Treatment	14, 59	5.84	< 0.001	11, 26	0.99	0.480	11, 50	2.500	0.014
Season	14, 59	7.03	< 0.001	11, 26	2.69	0.019	11, 50	13.210	< 0.001
Treatment × season	14, 59	1.46	0.155	11, 26	0.99	0.477	11, 50	1.040	0.430
Individual ANOVA									
Treatment									
Acarida	1, 72	4.95	0.029	NA	NA	NA	1, 60	1.368	0.247
Araneae	1, 72	21.29	< 0.001	NA	NA	NA	1, 60	5.844	0.019
Blattodea	1, 72	56.22	< 0.001	NA	NA	NA	1, 60	6.023	0.017
Coleoptera	1, 72	14.47	< 0.001	NA	NA	NA	1, 60	4.182	0.045
Collembola	1, 72	3.58	0.062	NA	NA	NA	NA	NA	NA
Diptera	1, 72	2.11	0.150	NA	NA	NA	1, 60	0.587	0.446
Hemiptera	1, 72	0.01	0.920	NA	NA	NA	1, 60	0.573	0.452
Homoptera (non-scales)	1, 72	0.61	0.437	NA	NA	NA	1, 60	0.739	0.393
Hymenoptera (non-ants)	1, 72	0.76	0.388	NA	NA	NA	1, 60	0.062	0.805
Formicidae	1, 72	3.44	0.068	NA	NA	NA	NA	NA	NA
Lepidoptera	1, 72	0.28	0.601	NA	NA	NA	1, 60	0.089	0.766
Neuroptera	1, 72	1.07	0.305	NA	NA	NA	NA	NA	NA
Orthoptera	1, 72	5.61	0.021	NA	NA	NA	NA	NA	NA
Psocoptera	NA	NA	NA	NA	NA	NA	1, 60	2.763	0.102
Thysanoptera	1, 72	0.52	0.475	NA	NA	NA	1, 60	2.918	0.093
Season									
Acarida	1, 72	6.43	0.013	1, 36	1.16	0.288	1, 60	1.41	0.240
Araneae	1, 72	0.42	0.522	1, 36	5.46	0.025	1, 60	1.47	0.230
Blattodea	1, 72	9.63	0.003	1, 36	0.44	0.509	1, 60	7.76	0.007
Coleoptera	1, 72	23.98	< 0.001	1, 36	0.77	0.385	1, 60	0.01	0.941
Collembola	1, 72	0.47	0.496	NA	NA	NA	NA	NA	NA
Diptera	1, 72	0.86	0.358	1, 36	0.02	0.892	1, 60	1.36	0.248
Hemiptera	1, 72	6.01	0.017	1, 36	2.31	0.138	1, 60	7.48	0.008
Homoptera (non-scales)	1, 72	9.77	0.003	1, 36	0.73	0.399	1, 60	0.16	0.688
Hymenoptera (non-ants)	1, 72	1.60	0.211	1, 36	0.00	0.964	1, 60	4.73	0.034
Formicidae	1, 72	0.14	0.707	NA	NA	NA	NA	NA	NA
Lepidoptera	1, 72	13.29	0.001	1, 36	7.10	0.011	1, 60	82.06	< 0.001
Neuroptera	1, 72	0.15	0.700	NA	NA	NA	NA	NA	NA
Orthoptera	1, 72	0.02	0.899	NA	NA	NA	NA	NA	NA
Psocoptera	NA	NA	NA	1, 36	9.58	0.004	1, 60	12.51	0.001
Thysanoptera	1, 72	0.04	0.848	1, 36	0.01	0.924	1, 60	0.24	0.626
ANOVA (scales)									
Treatment	1, 72	2.31	0.133	1, 36	5.52	0.024	1, 60	1.429	0.237
Season	1, 72	4.985	0.029	1, 36	0.12	0.736	1, 60	0.168	0.683
Treatment × season	1, 72	2.31	0.133	1, 36	0.13	0.716	1, 60	3.930	0.052

were removed from no-ant branches ($F_{1,98}=48.39$, $P<0.000001$) (Table 1). On *C. senex* trees, fewer (81%), but a still significant number of ants were eliminated ($F_{1,98}=8.47$, $P=0.004$) (Table 1).

Individually, *A. instabilis* did not reduce total, small, or large arthropod densities (Table 2) or densities of arthropod orders with the exception of scales (Table 3). Across both seasons, scale densities increased (by 99%) on branches with *A. instabilis* (Table 3). Effects of *A. instabilis* on other orders differed with season, but there

was not a significant treatment by season interaction (Table 3).

Camponotus senex tended to reduce total and small arthropods, and these trends were slightly stronger in the dry season (Tables 1, 2). Across both seasons, *C. senex* reduced total (14%) and small (22%) arthropods and in the dry season limited total (34%; $F_{1,41}=3.40$, $P=0.072$) and small (40%; $F_{1,57}=3.99$, $P=0.052$) arthropods (Tables 1, 2). *C. senex* significantly affected specific arthropod orders (Table 3). Densities of spiders (54%) and beetles (39%)

were twice as strong as those of ants, and negative bird effects on roaches significantly differed from ants both in magnitude (Δr) and in sign of effect. Ants had significantly greater positive effects on scales than did birds across both seasons.

The two ant species (*A. instabilis* and *C. senex*) also differed somewhat in their overall effects on arthropods. Ant species did not differ in the magnitude of their effects on total, small, or large arthropods for both seasons (Table 2) but effect sign of ant species on large arthropods differed. Yet, for total and small arthropods, there was a significant predator by season interaction. During the wet season, *A. instabilis* tended to have a stronger negative effect on total arthropods than *C. senex*. *C. senex* tended to have stronger effects on small arthropods in the dry season, and *A. instabilis* tended to have greater negative effects on small arthropods in the wet season. Furthermore, in the dry season, ant species tended to differ in effects on individual arthropod orders, where *C. senex* tended to have stronger negative effects on spiders (Table 4). Effects of ant species differed in sign for spiders and lepidopterans across both seasons, for spiders and beetles in the dry season, and for beetles and lepidopterans in the wet season. *A. instabilis* had significantly greater positive effects on scales than *C. senex* in both seasons.

Discussion

Birds and ants differed in their effects on total and large arthropods indicating that these different taxa could not be treated as an aggregate entity. Birds reduced total, small, and large arthropod densities and reduced densities of several arthropod orders in both dry and wet seasons. *A. instabilis* ants alone did not affect arthropod densities for any size or specific orders. In the dry season, *C. senex* ants tended to reduce small arthropods, significantly reduced spider and beetle densities, and increased roach and

thysanopteran densities. Predators (both across and within taxa) significantly differed in both signs and magnitudes of their effects on arthropods (total and of several orders). The qualitative effects of ant species on small arthropods appeared to be generally substitutable between seasons (Fig. 1). However, this substitutability did not apply to large arthropods.

Ants are regarded as useful biological control agents in agricultural systems (Way and Khoo 1992; Perfecto and Castiñeiras 1998), yet most studies examine ant effects on particular pest species. Examinations of ant effects on arthropod assemblages give highly variable insight into their effects, especially as regards to limitation of large arthropods. Risch and Carroll (1982) excluded *Solenopsis geminata* from maize plants and found overall increases in herbivore and predator abundance, but many arthropod groups were not affected by ant removal and some ant-tended homopterans were more abundant with ants. Similarly, James et al. (1999) removed two species of the *Iridomyrmex rufoniger* group from citrus trees and found overall increases in beneficial and incidental arthropods after 2 years. However, for most intermediate sampling periods, ants did not affect total arthropods, but did influence particular orders. Gibb (2003) removed *Iridomyrmex purpureus* and found no effects on ground-foraging arthropod assemblages. Furthermore, Koptur (1984) found that different ants varied in their abilities to remove caterpillars from *Inga* trees. The particular ants chosen for our study have different foraging strategies (Hölldobler and Wilson 1990; S. Philpott, unpublished data) and may have different diets including much honeydew and nectar (Davidson et al. 2003). Our results thus reinforce ideas that ant species differentially influence particular arthropods within arthropod assemblages and thus tend not to have substitutable effects.

Although one goal of this study was to determine how species of one predator taxa (ants) differ, we did not address how bird species may differ. Bird species may strongly differ in their effects on herbivores and leaf

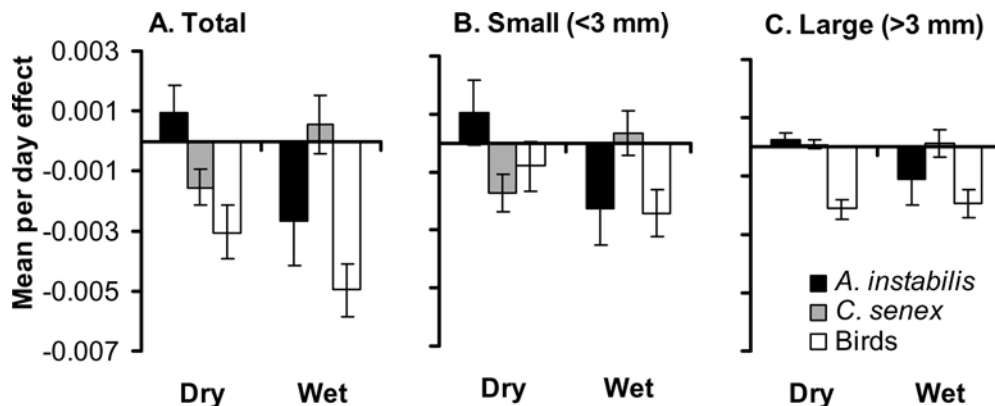


Fig. 1 Mean per day effects (± 1 SE) of ant (*A. instabilis* and *C. senex*) and bird predators on *Inga* arthropods. Graphs show comparisons for all (total), small (<3 mm), and large arthropods (>5 mm) for both the dry and wet seasons of 2002. Positive numbers show net positive effects on arthropods, negative numbers show net negative effects. Mean per day effects on arthropods were calculated

by averaging a metric $\{\ln [(D_C + 1)/(D_E + 1)]/t\}$ calculated on a per tree basis where D_C is the total arthropod density [number/dry foliage (g)] on control branches at the end of the trial period, D_E is the arthropod density on enclosure (no-predator) branches at the end of the trial period, and t is the number of days enclosures were maintained

damage (Murakami and Nakano 2000). Thus the >100 bird species at our study site (R. Greenberg, unpublished data) may differ in effects on arthropods, and indeed many birds at the study site have very different foraging strategies and likely differentially affect prey (Dietsch 2003). But because birds tend not to defend strict foraging territories (R. Greenberg, personal observation), and form mixed-species flocks with constantly changing composition over time (R. Greenberg, personal observation), differential effects of bird species will be negated because birds mix (rather than separate) in space. It is thus impractical to look at individual bird species in this setting.

The effects of birds and ants on arthropod assemblages also differed from one another over time. Effects of birds on arthropod assemblages were consistent over seasons, whereas the sign and strength of ant species effects differed between the dry and wet seasons. Bird effects on total and small (but not large) arthropods were slightly greater in the wet season—an unexpected result considering that bird abundance in the study site is higher in the dry season (when migrants are present) (R. Greenberg, unpublished data). Larger bird effects in the wet season may be explained by added resource requirements (or possible diet shifts to insectivory) for breeding tropical resident birds (Polis 1991; Levey and Stiles 1992). In contrast, overall ant abundance is consistent but abundances of *A. instabilis* and *C. senex* may fluctuate seasonally. In 2002, *A. instabilis* was more abundant in the wet season, and *C. senex* was more abundant in the dry season (S. Philpott, unpublished data) possibly explaining changes in their relative effects. Furthermore resource use by ants may change with ontogeny or colony reproduction (Hölldobler and Wilson 1990). Thus seasonal differences in ant effects may be expected.

The effects of birds and ants on arthropods differed both by arthropod order and size. Birds affected large arthropods and ants tended to reduce small arthropods; expected given the size of each predator. No predator affected densities of dipterans, hemipterans, non-scale homopterans, or non-ant hymenopterans—all highly mobile prey. Mobility may make capture more difficult, or may reduce effects of exclosures if prey constantly recolonized branches. No predator reduced lepidopterans (94% captured were caterpillars) but *C. senex* and birds reduced spider and beetle densities. Spiders are important predators in coffee systems (Ibarra-Núñez et al. 2001), and many predaceous beetles (e.g., coccinellids) were captured. Omnivory by birds and ants thus may have indirectly limited effects on lepidopterans or total arthropods (in the case of ants), especially if other predators compensated for the removal of birds or ants.

Birds and ants may compete for prey or interact via intraguild predation potentially masking ant effects on arthropod assemblages. Many studies have demonstrated risk reduction for prey in the presence of multiple predators because either top predators have alternative prey (the other predator) or because of behavioral inhibition of one or the other predator (e.g., Sih et al.

1998). Birds sometimes eat ants (Poulon and Lefebvre 1996; Strong and Sherry 2000) and in this study, birds tended to reduce ant densities. Ants were unavailable to birds on no-ant branches, and if ants, in coffee systems, constitute a large part of bird diets, bird predation on other arthropods may have significantly increased where ants were excluded masking isolated effects of ants on arthropods. Alternatively, aggressive ants may deter bird feeding (Aho et al. 1999; Haemig 1992, 1996). In this case, if ants significantly limit bird feeding when both predators are present, bird predation also would have increased and may have compensated for effects of ant removal, masking large effects of one or both ant species. At least in one case, however, combined effects of bird and ant predators on prey were additive (Floyd 1996).

There are additional factors that may have confounded our experimental results. First, bird and ant exclosures were established during different times in the dry season, perhaps resulting in some differences not attributable to predator effects. Second, Tanglefoot may have limited colonization by non-flying arthropods (i.e., lepidopteran larvae, spiders, mites, or scales). Total arthropod densities on no-bird branches were significantly higher than no-ant branches ($F_{1,48}=4.69$, $P=0.035$) (Table 1). In fact, lepidopteran larvae were more abundant on no-ant ($F_{1,48}=5.55$, $P=0.022$) branches and mite density did not differ ($F_{1,48}=0.09$, $P=0.759$), but spiders tended to be more abundant on no-bird branches ($F_{1,48}=3.67$, $P=0.061$). Although scales were not included in total arthropod calculations, scale densities were higher on *C. senex*-excluded branches in the wet season (even though this ant tends scales) perhaps because Tanglefoot prevented emigration from treated branches. Alternatively, increased scale density on no-ant branches may be because ants periodically harvest homopterans especially when extrafloral nectar resources are available (as in *Inga* spp.) (Ricogray 1993; Offenberg 2001). Thus, in general, differences in arthropod densities do not seem to be due to experimental treatment. Third, although total richness of birds and ants likely to forage on *Inga* spp. trees in our study site is comparable (~60 species), we may have removed a higher diversity of birds than ants from individual trees. Ant exclosure treatments were established on trees where *A. instabilis* or *C. senex* were visibly abundant on quick inspection but treatments effectively prevented all ant species from visiting branches. At the time control branches were harvested, we found 2–3 ant species per branch, on average, of which *A. instabilis* or *C. senex* represented the majority of individuals. For birds, 2–4 species may visit individual *Inga* trees over a 2 h period (R. Greenberg et al, unpublished data). Based on differences in mobility between these two taxa, however, temporal turnover in bird species visiting individual trees may be greater than for ants. Thus, although richness of the two taxa on *Inga* spp. trees is very similar, differences in predator richness per tree may have confounded effects of predator identity.

In conclusion, our study showed that each predator varied in effects on arthropods. The effects of birds versus

ants on arthropod assemblages differed both qualitatively and quantitatively. This also held for comparisons between ant species. Thus, aggregating bird and ant species into one trophospecies would not represent the effects of each species accurately even though they overlap considerably in arthropod prey species used. Our results thus show the necessity of examining differential effects of predators experimentally on the basis of effect magnitudes, rather than on the basis of diets (e.g., Yodzis and Winemiller 1999) before aggregating either related or unrelated taxa into trophic levels in food web models. Our study also reiterates the general importance of ants and birds as predators in coffee agroecosystems, even though ant effects differed seasonally.

Acknowledgements For field help we thank J. A. García Ballinas, G. López Bautista, J. Maldonado, J. Cabrera Santos, F. Camposeco Silvestre, B. E. Chilil, A. González, F. Hernández Gómez, and L. Morales. R. Burnham, E. DeMattia, T. Dietsch, P. Foster, J. Jedlicka, M. Reiskind, O. J. Schmitz, S. Van Bael, J. Vandermeer, J. Wyatt, and three anonymous reviewers greatly improved the manuscript. G. Ibarra-Núñez and El Colegio de la Frontera Sur in Tapachula provided logistical support. We thank the Peters family for permission to work on their farm. This study was funded by NSF no. DEB-9981526 to I.P., the Helen Olsen Brower Fellowship in Environmental Science of the University of Michigan, and an NSF Graduate Research Fellowship to S.P.

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