

# Cryptic biodiversity effects: importance of functional redundancy revealed through addition of food web complexity

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**Abstract.** Interactions between predators and the degree of functional redundancy among multiple predator species may determine whether herbivores experience increased or decreased predation risk. Specialist parasites can modify predator behavior, yet rarely have cascading effects on multiple predator species and prey been evaluated. We examined influences of specialist phorid parasites (*Pseudacteon* spp.) on three predatory ant species and herbivores in a coffee agroecosystem. Specifically, we examined whether changes in ant richness affected fruit damage by the coffee berry borer (*Hypothenemus hampei*) and whether phorids altered multi-predator effects. Each ant species reduced borer damage, and without phorids, increasing predator richness did not further decrease borer damage. However, with phorids, activity of one ant species was reduced, indicating that the presence of multiple ant species was necessary to limit borer damage. In addition, phorid presence revealed synergistic effects of multiple ant species, not observed without the presence of this parasite. Thus, a trait-mediated cascade resulting from a parasite-induced predator behavioral change revealed the importance of functional redundancy, predator diversity, and food web complexity for control of this important pest.

**Key words:** Azteca instabilis; biodiversity; biological control; coffee agroforest; ecosystem function; multi-predator effects; Procryptocerus hylaeus; Pseudacteon; Pseudomyrmex simplex; trait-mediated interaction.

## INTRODUCTION

Predators are disproportionately affected by habitat disturbance and loss, and predator diversity declines with agricultural intensification (Bruno and Cardinale 2008). Evidence from empirical studies and meta-analyses indicates that greater richness of natural enemies (predators and parasitoids) often results in enhanced herbivore suppression, especially in agricultural systems (Cardinale et al. 2006a, Letourneau et al. 2009). But increases in predator biodiversity do not always result in declines in herbivore populations or increases in plant productivity in natural or farming systems (Rosenheim et al. 1995). In fact, the impacts of co-occurring multiple predator species on herbivores may depend on the particular interactions between predator species (Vance-Chalcraft et al. 2007) or the degree of functional diversity or redundancy among predator species (Petchey 2003). For example, niche differences between predators such as consumption of prey at different times of the day or seasons, diet complementarity, distinct hunting modes, or foraging styles that facilitate other predator species may result in additive or synergistic effects and risk enhancement for

prey (Losey and Denno 1998, Sih et al. 1998, Hooper et al. 2005, Schmitz 2007). On the other hand, intraguild predation or interspecific interference between multiple natural-enemy species may result in antagonistic effects, and ultimately risk reduction for herbivores (Sih et al. 1998, Finke and Denno 2005, Schmitz 2007, Bruno and Cardinale 2008). Multiple predator species acting together do not always reduce prey to a greater degree than a single efficient predator species (Cardinale et al. 2006a). Thus, understanding the effects of multiple predator species requires a detailed understanding of interactions between predator species, degree of diet overlap, impacts of environmental context, and the surrounding landscape.

Multi-predator effects form part of (often) complex food webs, yet are rarely placed within the context of other interactions. For example, most studies aimed at testing multi-predator effects examine only predator, prey, and plant trophic levels. However, adding vertical diversity within food webs (e.g., a fourth trophic level) may alter biodiversity effects at lower trophic levels (Duffy et al. 2007, Reiss et al. 2009). For instance, adding a top predator or a parasite to a multi-predator system may alter the impacts that those predator species have on herbivores and plants. In the few studies conducted to date, addition of herbivore species can both weaken and strengthen the relationship between biodiversity and ecosystem function (Duffy et al. 2007). But few, if any studies, have examined whether the

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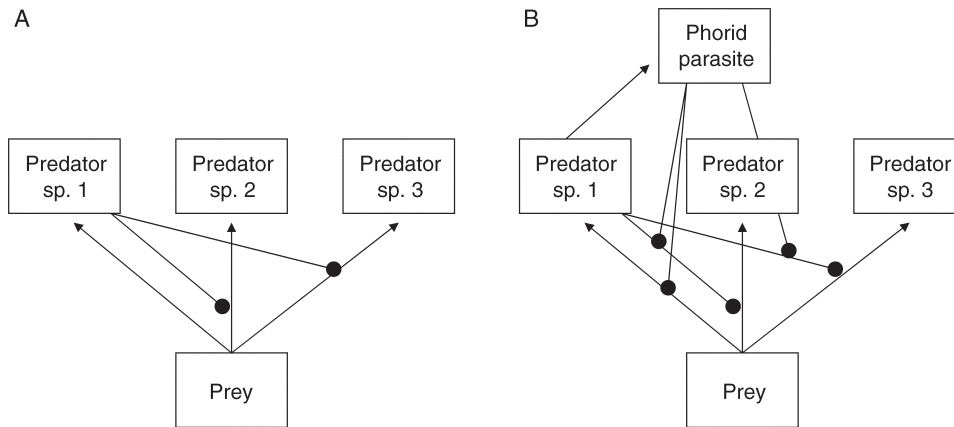


FIG. 1. Hypothetical multi-predator food web in a coffee agroecosystem (A) with and (B) without the presence of a specialist phorid parasite. Without the phorid, the three species of predators (ants) share a common prey resource, and aggression from predator sp. 1 limits the activity of the other two predator species, reducing their effects on prey. In the presence of the specialist phorid parasite, the foraging behavior of predator sp. 1 is reduced, resulting in a trait-mediated cascade that increases activity of predator sp. 2 and sp. 3, while still limiting the prey. Arrows represent direct energy transfer. Circles show trait-mediated effects.

effects multiple predator species on herbivores and plants may be altered by the presence of a larger predator species, or a parasite of one or more predator species. Predators and parasites may modify the behavior, development or physiology of prey resulting in declines in plant damage via trait-mediated indirect interactions (TMII; Werner and Peacor 2003, Preisser et al. 2005). Although TMII are usually discussed in the context of modifications to prey traits, some predators or parasites may have nonconsumptive effects on other predators, resulting in TMII on herbivores (Müller and Godfray 1999, Philpott et al. 2004, Prasad and Snyder 2006, Pardee and Philpott 2011). For example, large carabid beetles do not share prey with smaller predators (carabids and staphylinids), but do modify small predator behavior reducing overall predatory impacts on fly eggs (Prasad and Snyder 2006). If predator behavior is similarly affected by the presence of specialist parasites, this may alter interspecific interactions between predators, and ultimately alter the outcome of experiments aiming to discern the effects of multiple predator species on prey (Fig. 1). Yet, little is known about how multi-predator effects relate to increases in vertical diversity within a community.

In coffee agroecosystems, suites of predators prey on an important coffee pest, the coffee berry borer (CBB; *Hypothenemus hampei*, Coleoptera), but the behavior of one aggressive predator species is altered by the presence of a fourth trophic level: namely, a specialist parasite. The CBB is the most economically damaging pest of coffee, and is a tiny beetle (<1 mm) that burrows into the coffee fruits where it lays eggs, thus making the coffee beans unsuitable for export (Damon 2000). Several species of parasitic wasps (Barrera et al. 1990, Damon 2000), birds (Kellermann et al. 2008), and possibly lizards (Borkhataria et al. 2006, Kellermann et al. 2008) attack the CBB. In addition, arboreal twig-

nesting and ground-foraging ants prevent the borer from damaging coffee berries and also remove adult CBB once inside the fruits (Armbrecht and Gallego 2007, Larsen and Philpott 2010). The canopy dominant ant, *Azteca instabilis*, prevents CBB from entering coffee fruits (Pardee and Philpott 2011) and the abundance of an *A. instabilis* mutualist, the coffee green scale (*Coccus viridis*), negatively correlates with CBB attacks (Perfecto and Vandermeer 2006). In addition, several species of arboreal twig-nesting ants prey on the CBB, and these ant species may compete for food resources or influence colonization processes of other species (Vandermeer et al. 2010). Thus, ant impacts on the CBB may not combine in a simply additive fashion in the field. Workers of *A. instabilis* are aggressive toward ground-foraging and arboreal twig-nesting ant species in the community limiting the foraging activity and nest establishment of other ant species (Philpott 2005, Philpott 2010). Yet, *A. instabilis* is parasitized by three undescribed species of specialist phorid parasites (*Pseudacteon* spp.), therein adding a fourth trophic level to the system. Phorids reduce *A. instabilis* foraging behavior by about half, and limit attacks by *A. instabilis* on the CBB and other herbivores (Philpott et al. 2004, Pardee and Philpott 2011). During attacks, and for at least 90 min after an attack, other predators, such as ants and beetles, are able to gain more access to food resources shared with *A. instabilis* (Philpott 2005, Liere and Larsen 2010), thus making it possible that the presence of the vertical diversity within this system alters multi-predator effects of these interacting ant species.

We investigated how the predatory activities of multiple species of ants interact to affect the CBB and whether adding vertical diversity to the system (e.g., specialist parasites of one predator species) altered multi-predator interactions or ultimately resulted in cascading effects on an economically important pest

TABLE 1. Experimental laboratory treatments with and without phorid parasites showing sample sizes during 2009 and 2010.

Treatment†	Predator species‡	Phorid§	Sample size		
			2009	2010	Total
Control	none	no	24	38	62
Single predator	<i>Azteca instabilis</i>	no	26	31	57
Single predator	<i>Pseudomyrmex simplex</i>	no	9	24	33
Single predator	<i>Procrystocerus hylaeus</i>	no	7	28	35
Single-predator total			42	83	125
Two predators	<i>A. instabilis</i> + <i>P. simplex</i>	no	10	33	43
Two predators	<i>A. instabilis</i> + <i>P. hylaeus</i>	no	6	24	30
Two predators	<i>P. simplex</i> + <i>P. hylaeus</i>	no	4	28	32
Two-predator total			20	85	105
Three predators	<i>A. instabilis</i> + <i>P. simplex</i> + <i>P. hylaeus</i>	no	5	25	30
Single predator with phorid	<i>A. instabilis</i>	yes	26	34	60
Two predators with phorid	<i>A. instabilis</i> + <i>P. simplex</i>	yes	6	27	33
Two predators with phorid	<i>A. instabilis</i> + <i>P. hylaeus</i>	yes	5	33	38
Two-predator phorid total			11	60	71
Three predators with phorid	<i>A. instabilis</i> + <i>P. simplex</i> + <i>P. hylaeus</i>	yes	5	35	40

† All arenas included 20 individuals of the coffee berry borer (*Hypothenemus hampei*).

‡ Arenas with *A. instabilis* contained 20 individuals; arenas with *P. simplex* and *P. hylaeus* contained individuals from one occupied dry coffee twig.

§ Two female phorids were added to each arena, and phorids added were an unknown mix of three *Pseudacteon* morphospecies.

species and plant damage. We examined relationships between the canopy dominant ant, *A. instabilis*, two species of arboreal twig-nesting ants, *Pseudomyrmex simplex* and *Procrystocerus hylaeus*, the specialist parasites of the *A. instabilis* (three species of *Pseudacteon*), and the coffee berry borer in shaded coffee agroecosystems in Chiapas, Mexico. We asked the following questions: (1) Do *A. instabilis*, *P. simplex*, and *P. hylaeus* differ in their effects on the CBB? (2) Do single-, two- or three-species combinations of ants differ in their impacts on the CBB? (3) Does presence of the fourth trophic level (*Pseudacteon* spp. phorid flies) result in an emergent change in the relative effectiveness of single-, two- or three-species combinations of ants in predation on the CBB? We examined multiple-predator effects in a coffee agroecosystem and the influence of adding a fourth trophic level on these multi-predator effects. We determined that ants are effective predators of the CBB, and that multiple predators did not enhance predatory impacts. Yet, in the presence of a specialist parasite, predatory effects of *A. instabilis* were limited. Only in the presence of this parasite was the effect of multiple predators significant. Thus, our results suggest that the importance of predator diversity is only revealed within a more complex food web.

#### METHODS

We conducted research on a 280-ha coffee farm in Chiapas, Mexico, during May–July 2009 and 2010. The study site, Finca Irlanda, is a shaded coffee farm, located at 15°11' N, 90°20' W, between 950 and 1150 m. On the farm, *A. instabilis* is a dominant, arboreal keystone species that significantly affects many species in a complex food web (Vandermeer et al. 2010). More than 30 species of ants occupy dry hollow coffee twigs on the farm, and interact with each other and with *A. instabilis* when searching for nest sites and food

resources. We selected the twig-nesters *Pseudomyrmex simplex* and *Procrystocerus hylaeus* for experiments because they are the two most frequently encountered species and nest occupation of the two species is limited by *A. instabilis* (Livingston and Philpott 2010, Philpott 2010). Thus, there is a potential that each of these species affects the CBB, and that they interact with each other in a meaningful way.

To examine the effects of phorid flies on CBB predation by multiple species of ants, we conducted laboratory experiments. We used 16 60 × 60 × 60 cm insect arenas (Bug Dorm-2 Insect Tent, Bug Dorm Store, Taichung, Taiwan) for observations. For each trial, we placed 20 CBB, a coffee branch with 10 undamaged berries and between 4 and 9 leaves in an arena, and then assigned arenas to 1 of 12 treatments (Table 1). Treatments included all combinations of 1 to 3 ant species; treatments with *A. instabilis* were replicated with and without phorid flies. We did not include phorids in treatments without *A. instabilis*, as preliminary observations indicated phorids do not modify the behavior of the CBB or of other ant species. After 24 h, we counted the number of fruits with CBB damage. There were between 30 and 62 replicates of each treatment due to differences in availability of certain species of ants in the field (Table 1). A maximum of 16 trials was conducted per day. Not all treatments were replicated daily, but at least 6 treatments were replicated on a given day. At the time experiments were conducted, we believed there was only one species of *A. instabilis*-attacking phorid at our study site. However, there are three phorid morphospecies that attack *A. instabilis* at the study site (B. Brown, *personal communication*). Because we did not have this knowledge at the time experiments were conducted, we did not differentiate between phorid species. Thus, laboratory experiments with field-collected phorids report the effects of an

unknown mix of the three phorid species on the behavior of *A. instabilis* and interactions with other ant species. To date, we have no reason to suspect that the composition of phorids used in trials changed during the course of the experiment, as phorids were collected from the same sites over a relatively short time frame.

All insects used for laboratory experiments were collected in the field. We collected CBB by opening dry fruits to extract individuals. Nests of *P. simplex* and *P. hylaeus* were collected during destructive surveys of dry coffee twigs. We placed entire twigs containing nests of *P. simplex* or *P. hylaeus* into arenas assigned to twig-nesting ant treatments. We did not count the numbers of individuals per nest used in experiments, but *P. simplex* twigs contain, on average,  $31.74 \pm 4.04$  (mean  $\pm$  SE) workers and *P. hylaeus* twigs contain, on average,  $16.09 \pm 2.8$  workers (S. M. Philpott, unpublished data). *A. instabilis* workers were collected from colonies nearby to the field station and transported to the laboratory. We added  $\sim 20$  individuals of *A. instabilis* to treatment groups with *A. instabilis*. We thus used an additive, rather than replacement, design to examine for the effects of multi-predator species. We chose an additive design to mimic the field density of these ants on a single coffee plant. Even though *A. instabilis* can limit colonization of other twig-nesting ant species, it is common to find two or all three of these species together on coffee plants, especially when phorid flies are present. We also chose the additive design to be able to more effectively test for nonadditive effects of the three predator species.

We compared the number of fruits attacked by CBB in two ways. To compare the individual effects of each ant species acting alone, we used a general linear model to compare mean number of fruits attacked in arenas with *A. instabilis*, *P. simplex*, or *P. hylaeus* or without ants. We included treatment and year as main factors, a treatment by year interaction effect, number of fruits attacked by the CBB as the dependent variable, and individual observations as replicates. Second, to examine the multi-predator effects of ants (one, two, or three species present) and the impacts of phorids on multi-predator effects, we pooled data from all single-predator and two-predator treatments for a total of seven treatments (Table 1). Again, the model included treatment and year as main effects, a treatment by year interaction, number of fruits attacked by the CBB as the dependent variable, and individual observations as replicates. We then compared the mean number of fruits attacked by the CBB in treatments with one, two, or three ant species with and without phorids, and in controls with general linear models. We determined pairwise differences among treatments with Tukey's post hoc tests.

We also tested for nonadditive effects of multiple predators both in the presence or absence of phorid flies. We first calculated expected predation rates (e.g., numbers of fruits with CBB; ln-transformed) for all

combinations of two or three predator species in the presence or absence of phorids. We used a multiplicative risk model (Eq. 1) because it corrects for the problem of consuming prey twice (Soluk 1993, Sih et al. 1998, Nilsson et al. 2006). For two-predator treatments we calculated expected predation as

$$E_{\text{CBB}_{1+2}} = \text{CBB}_1 + \text{CBB}_2 - (\text{CBB}_1 \times \text{CBB}_2) \quad (1)$$

where  $E_{\text{CBB}_{1+2}}$  is the expected numbers of CBB in fruits in two-predator treatments, and  $\text{CBB}_1$  and  $\text{CBB}_2$  are the numbers of CBB in fruits in single-predator treatments. We modified this equation (Eq. 2) following Nilsson et al. (2006) to calculate expected values for the three-predator treatment as

$$\begin{aligned} E_{\text{CBB}_{1+2+3}} = & \text{CBB}_1 + \text{CBB}_2 + \text{CBB}_3 - (\text{CBB}_1 \times \text{CBB}_2) \\ & - (\text{CBB}_1 \times \text{CBB}_3) - (\text{CBB}_2 \times \text{CBB}_3) \\ & + (\text{CBB}_1 \times \text{CBB}_2 \times \text{CBB}_3) \end{aligned} \quad (2)$$

where  $E_{\text{CBB}_{1+2+3}}$  is the expected number of CBB in fruits in the three-predator treatment, and  $\text{CBB}_1$ ,  $\text{CBB}_2$ , and  $\text{CBB}_3$  are the mean observed numbers of CBB in fruits with the individual predators. The last term ( $\text{CBB}_1 \times \text{CBB}_2 \times \text{CBB}_3$ ) is added because the correction should not be made twice for the same prey individual (Nilsson et al. 2006). For expected predation in predator combinations without phorids, we used observed CBB values for *A. instabilis* without phorids. For expected predation in predator combinations with phorids, we used observed CBB values for *A. instabilis* with phorids. Then, we compared expected vs. observed values of numbers of CBB attacking fruits with one-tailed *t* tests. If the observed numbers of CBB in fruits deviated from expected ( $P < 0.05$ ), this indicated a nonadditive effect. Because, in our experiment, the response variable is the number of attacked fruits, higher than expected numbers (positive values) indicate risk reduction and lower than expected numbers (negative values) indicate risk enhancement.

We predicted that ants would interact with one another in an aggressive manner, leading to reduced effects on the CBB in multi-predator arenas. In order to quantify interactions between species, we conducted separate aggression trials. We placed one individual of each ant species (all two and three species combinations) into Petri dishes (50 mm diameter  $\times$  11 mm) and observed interactions. We observed each ant combination during eight 15-min trials. We scored each time that ants responded to an ant of another species in the following way as: (1) touching antennae, (2) flaring its mandibles, (3) biting, (4) removing a limb, or (5) killing the other ant (Torres et al. 2007), and noted which ant was the recipient of the aggressive action. We then tabulated a mean aggression score of each ant species toward each other, and compared mean aggression scores between species, and between two- and three-

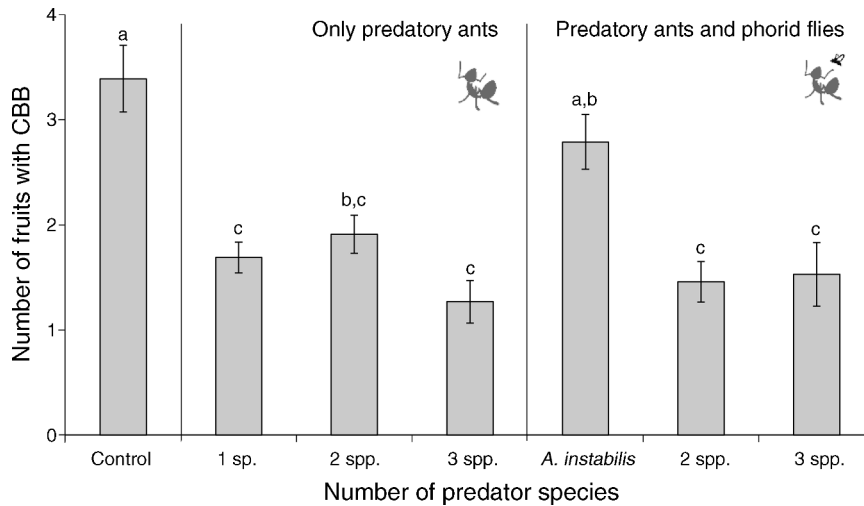


FIG. 2. Mean number of fruits attacked by the coffee berry borer (CBB) in insect arenas with one, two, or three species of predatory ant in the presence or absence of specialist *Pseudacteon* spp. phorid flies. The three predator species examined were *Azteca instabilis*, *Pseudomyrmex simplex*, and *Procryptocerus hylaesus*. Data for individual single-, two-, and three-species treatments were pooled for analysis. The column for one species with phorid only shows data from treatments with *A. instabilis* with phorids. Error bars show  $\pm$ SE, and lowercase letters indicate significant differences ( $P < 0.05$ ) between treatments.

species replicates with general linear models. We included ant pair and the number of species in Petri dishes as main factors, included an ant pair by number of species interaction, used the mean aggression score as the dependent variable, and individual observations as replicates. We determined pairwise differences with Tukey's post hoc tests. All statistical tests were conducted with SPSS v. 16 (SPSS 2010).

### RESULTS

In treatments without phorids, all combinations of ant species reduced CBB attacks compared with controls. All ant species, when alone, limited attacks of the CBB on coffee fruits ( $F_{3,179} = 10.84$ ,  $P < 0.001$ ). On average, CBB attacked  $3.39 \pm 0.32$  (mean  $\pm$  SE) fruits when alone, and only about half as many when *A. instabilis* ( $1.67 \pm 0.23$  fruits,  $P < 0.001$ ), *P. simplex* ( $1.73 \pm 0.28$  fruits,  $P = 0.001$ ), or *P. hylaesus* ( $1.69 \pm 0.26$  fruits,  $P < 0.001$ ) were present in insect arenas. The effects of individual ant species did not differ from one another ( $P > 0.05$ ). Effects of ant species on the CBB did not differ by year ( $F_{1,179} = 0.03$ ,  $P = 0.868$ ), nor did we observe a year by treatment interaction ( $F_{3,179} = 0.76$ ,  $P = 0.515$ ). All two- and three-species combinations of ants limited attacks by the CBB, but there were no differences depending on number of ant species present ( $F_{6,480} = 9.92$ ,  $P < 0.001$ ; Fig. 2). For those treatments without phorids, one-third to half as many fruits were attacked by the CBB in treatments with one ant species ( $P < 0.001$ ), two ant species ( $P < 0.001$ ), and three ant species ( $P < 0.001$ ) than in the control. There were no differences in effects of ants on CBB where one, two, or three ant species were present ( $P > 0.619$  for all pairwise comparisons).

In the presence of phorid parasites, in contrast, attacks by the CBB were reduced only in treatments with multiple ant species (Fig. 2). In most treatments with ants and phorid parasites, there were fewer fruits attacked by the CBB than in the control (Fig. 2). There were half as many fruits attacked in arenas with two ant species with phorids ( $P < 0.001$ ), and three ant species with phorids ( $P < 0.001$ ) than in control arenas. The notable exception was that a similar number of CBB attacked fruits in control arenas and in arenas with *A. instabilis* and phorids ( $P = 0.546$ ). In other words, the presence of phorid parasites limited the effectiveness of *A. instabilis* as a predator. Importantly, then, there were fewer fruits attacked by the CBB in arenas with phorids and two ( $P < 0.001$ ) or three ( $P < 0.015$ ) ant species than when phorids and *A. instabilis* were alone. A similar number of fruits were attacked by the CBB in arenas with two or three ant species with or without phorids ( $P > 0.283$  for all pairwise comparisons). There were no differences in CBB reduction with multiple species with and without phorids by year ( $F_{1,480} = 2.89$ ,  $P = 0.090$ ), or a year by treatment interaction ( $F_{3,480} = 11.91$ ,  $P = 0.077$ ).

In some cases, effects of multiple predator species were nonadditive and phorid presence altered multipredator effects. The number of fruits attacked by the CBB did not differ from expected for any pair of two predator species in the absence of phorid flies (*A. instabilis* + *P. simplex*,  $t = -0.744$ ,  $df = 42$ ,  $P = 0.461$ ; *A. instabilis* + *P. hylaesus*,  $t = -1.78$ ,  $df = 29$ ,  $P = 0.086$ ; *P. simplex* + *P. hylaesus*,  $t = -0.218$ ,  $df = 31$ ,  $P = 0.829$ ; Fig. 3). In contrast, the effects of *A. instabilis* plus one other ant species were nonadditive in the presence of the phorid flies (Fig. 3). Both with *A. instabilis* and *P. simplex* ( $t = -2.464$ ,  $df = 32$ ,  $P = 0.019$ ) and with *A.*

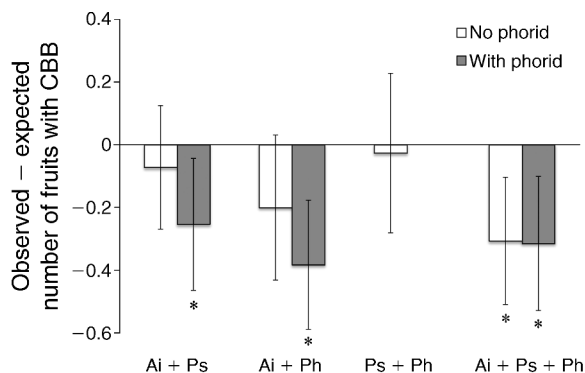


FIG. 3. Observed minus expected numbers of coffee berry borers (CBB; ln-transformed) in fruits in the presence of two or three species of predatory ants and with or without phorid flies. Bars (mean values) with 95% confidence intervals (CI) that do not overlap zero are not significantly different from expected. Bars with CI that do not overlap zero show nonadditive risk enhancement for prey. Asterisks indicate significant deviance from expected ( $P < 0.05$ ) as determined with one-tailed  $t$  tests. Species abbreviations are as follows: Ai, *Azteca instabilis*; Ps, *Pseudomyrmex simplex*; Ph, *Procryptocerus hyleaus*.

*instabilis* and *P. hyleaus* ( $t = -3.776$ ,  $df = 37$ ,  $P = 0.001$ ), there were fewer than expected CBB in coffee fruits, indicating synergistic, risk-enhancing effects of the two predator species. In treatments both with and without phorid flies, the effects of three predator species were nonadditive. There were fewer than expected CBB per fruit with three predators without phorids ( $t = -3.101$ ,  $df = 29$ ,  $P = 0.004$ ) and with phorid flies ( $t = -2.975$ ,  $df = 39$ ,  $P = 0.005$ ) indicating synergistic, risk-enhancing effects of the three predator species.

All ants were aggressive toward other ants, but the degree of aggression differed by species. *A. instabilis* was

the only ant that killed another individual (one *P. simplex* and one *P. hyleaus*). Furthermore, *A. instabilis* was more aggressive toward both *P. simplex* ( $P < 0.001$ ) and *P. hyleaus* ( $P < 0.001$ ) than *P. simplex* and *P. hyleaus* were toward *A. instabilis* individuals ( $F_{5,84} = 52.32$ ,  $P < 0.001$ ; Fig. 4). There were no differences in aggression depending on whether two or three ant species were present ( $F_{1,84} = 3.12$ ,  $P = 0.081$ ), nor was there an interaction between interspecies aggression and number of species present ( $F_{5,84} = 0.61$ ,  $P = 0.692$ ).

DISCUSSION

Parasitic phorid flies are specialist parasites of ants that have widespread influences on ants and other insects. More than 20 genera of phorids attack at least 22 genera of ants across five subfamilies (Mathis and Philpott 2012). Phorids limit foraging activity of host species (Feener and Brown 1992, Orr et al. 1995, Folgarait and Gilbert 1999, Morrison et al. 2000, Philpott et al. 2004) and thereby alter interspecific competitive interactions (LeBrun and Feener 2002, LeBrun 2005, Philpott 2005), maintain dominance-discovery trade-offs (LeBrun and Feener 2007), and potentially adjust ant competitive hierarchies (Feener 2000). Phorids can also limit protein acquisition of ant colonies, leading to decreases in colony size (Mehdiabadi and Gilbert 2002). Because of these strong effects on ant communities, phorid flies have been released as biological control agents of some invasive ant species, including *Solenopsis invicta* in the southern United States (e.g., Porter et al. 2004). However, phorid presence does not always change the outcome of interspecific contests (Morrison 1999, 2000, Morrison et al. 2000, Orr et al. 2003). In addition, reduction of ant foraging by phorids can limit host ant predatory abilities

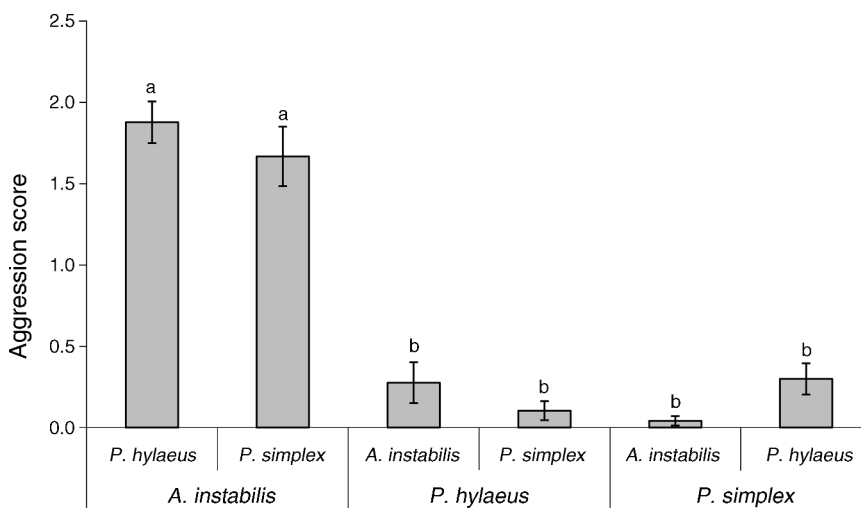


FIG. 4. Mean aggression score between interacting individuals of three different ant species. The species name on the lower row of the title shows the ant performing the aggressive behavior. The ant species on the upper row was the recipient of the aggressive behavior. A higher aggression score shows more aggressive behavior. Error bars show standard error, and different lowercase letters indicate significant differences ( $P < 0.05$ ) between treatments.

(Philpott et al. 2004), and can influence interactions between ants and their mutualists and predators of ant mutualists (Liere and Larsen 2010). Here, we report that phorid flies, via their impacts on host ants, can also alter the outcome of multi-predator effects, strengthening the idea that phorids have strong effects on insect communities.

Predator richness often enhances prey risk, and here, we found that three co-occurring ant species did prey on the CBB, but that increasing the number of predator species did not further reduce CBB attacks on fruits. In general, negative interactions between natural enemy species, including intraguild predation, cannibalism, hyperparasitism, and interspecific aggression, can limit the effects of multiple predator species on prey (Rosenheim et al. 1995, Schmitz 2007, Letourneau et al. 2009), reducing the likelihood of finding additive or synergistic effects on prey. Certainly, many studies have documented nonadditive effects and risk reduction for prey with multiple predators (Schmitz 2007, Bruno and Cardinale 2008, Letourneau et al. 2009). Generally, risk reduction or nonadditive effects for prey are attributed to increased interference among predator species (Wilby et al. 2005, Cardinale et al. 2006b) and, alternatively, to a high degree of habitat or behavioral similarity (Schmitz 2007). Yet, recent meta-analyses of multiple-predator studies report that, in the majority of cases examined (between 20% and 69.5%), increased predator diversity increases herbivore suppression (Halaj and Wise 2001, Schmitz 2007, Letourneau et al. 2009). However, nearly all studies that have examined multiple-predator effects in both laboratory and natural settings have used combinations of natural enemies from a wide taxonomic array (e.g., combining spiders with carabids, or ladybeetles with parasitoids). Our study focuses exclusively on three species of ants, a single insect family. Although ant diets (Davidson et al. 2003) and recruiting behaviors (Hölldobler and Wilson 1990) vary greatly, it is possible that the narrow taxonomic band of predators included may limit the degree of complementarity among predators or increase the amount of interspecific aggression. Thus, in addition to predator identity (Wilby et al. 2005, Straub and Snyder 2006), the taxonomic diversity (at the level of order or family, rather than species) of predator organisms examined may be important. Competition is common in ant communities (Parr and Gibb 2010), and we found a high degree of interspecific aggression among the ant species examined in this study. *A. instabilis* especially was highly aggressive toward the other two ant species, and this aggressive behavior likely limited the overall predatory activity of other ant species. It is easy to imagine that, while with other ant species, these three species will spend some time interacting with the other ant species rather than preying on the CBB, and thus reducing the potential for prey risk enhancement in treatments with multiple predators.

However, when in the presence of phorid flies, all combinations of two and three ant species had higher than expected, synergistic effects on the CBB. Thus, we did find that adding vertical diversity (e.g., a specialist parasite of one predator species) and associated interactions to the experimental food web altered emergent multi-predator effects. Presence of the phorid flies induced nonadditive, risk-enhancing effects of *A. instabilis* acting with another ant species. In addition, the presence of the phorid flies illustrated the importance of functional redundancy in the community. The combined effects of *P. simplex* and *P. hyleaus* on the CBB were additive and not significantly different from expected effects. This is what we expected based on the limited degree of aggression that they showed toward one another. In addition, because the two species did not have synergistic effects, they likely have similar foraging times and locations. Despite that *A. instabilis* was highly aggressive toward the other two species, effects of *A. instabilis* plus another species were also additive. This indicates that the two species are likely complementary in other ways such that interspecific interference (that would lead to antagonistic effects) is possibly buffered by some other behavioral or foraging difference. This hypothesis is supported by the findings that *A. instabilis* plus another species have synergistic effects on the CBB. What appears to be occurring is that in the presence of the phorid fly, *A. instabilis* activity is reduced, and the interspecific aggression toward other ant species and the CBB is limited, but not altogether eliminated. The other ant species increase their foraging activity compensating for the reduced attacks on the CBB by *A. instabilis*. It is likely that the ant species in this case are at least to a degree functionally redundant or complementary. It is possible, for example, that with phorids, there is specifically enhanced predation by the non-*A. instabilis* species during the daytime. Phorid flies are only active during the day (e.g., Morrison 1999); thus, we may assume that interactions between the ant species in treatments with phorid flies differed during the day and night. Specifically, the other ant species were likely less often attacked by *A. instabilis* during the day. In sum, adding vertical diversity to the experimental design revealed the importance of predator diversity. Addition of another trophic level (vertical diversity) created a trait-mediated cascade whereby a parasite changes the behavior of a competitively dominant predator, thereby releasing the other predator species. Many empirical studies of multi-predator effects focus on resource capture rather than behavioral modifications of prey (Hooper et al. 2005, Steffan and Snyder 2010, but see Preisser et al. 2005). This is true despite that nonconsumptive effects produce strong trait-mediated effects in a number of systems (Werner and Peacor 2003, Steffan and Snyder 2010). Here, a behavioral modification of workers of *A. instabilis* by phorid flies reveals the importance of biodiversity for pest control services.

Of course, our results are from a laboratory study, and effect sizes of multiple predator species on prey may be enhanced in the laboratory compared with field studies (e.g., Letourneau et al. 2009). Our observations and previous studies indicate, however, that behaviors of the species involved, and their interactions with one another are similar in the field and laboratory. For example, we isolated 20 *A. instabilis* workers from their colony to measure their impact on the CBB and other ants. *A. instabilis* are aggressive, indiscriminate ants that respond to competitors and prey in a similar fashion (Liere and Perfecto 2008). They communicate primarily with chemical signals, and just one ant can elicit a behavioral response in a large number of individuals. Further, in many field studies (e.g., Vandermeer et al. 2002, Philpott et al. 2004, Philpott 2005), we have observed that an isolated group of *A. instabilis* workers (on a single coffee branch) negatively impacts herbivores as quickly as when on a tree trunk near to the *A. instabilis* nest. Likewise, the effect of *Pseudacteon* spp. phorids on *A. instabilis* is similar in laboratory and field settings. Phorids reduce *A. instabilis* foraging behavior by about half in both the field and the laboratory (Philpott et al. 2004, Liere and Larsen 2010). Finally, the response of the ants to the CBB appears to be similar in both the lab and the field. *A. instabilis* generally respond to introduced or encountered insects by carrying them to the edge of leaves and dropping them off plants, or causing insects to fall off (Philpott et al. 2004, Liere and Larsen 2010). In the laboratory, twig-nesting ants do kill CBB and take them inside of their nests (Larsen and Philpott 2010); we have also observed these ants expel CBB from coffee leaves in both the field and the laboratory. It bears pointing out that all ant species have been observed to carry CBB to their nests, and drop CBB from plants onto the ground. Thus, ant effects on the CBB are likely via both direct predation, and nonconsumptive effects that may nonetheless have strong impacts on prey population dynamics (Werner and Peacor 2003, Steffan and Snyder 2010). The observed impacts on the CBB are similar in both the laboratory and the field. We are confident that our laboratory observations are similar to actual encounters in coffee agroecosystems.

These findings have interesting theoretical and practical applications. First, this study demonstrates that vertical diversity is important in multi-predator interactions, and that the number of trophic levels present can alter the interpretation and outcome of multi-predator effects. There is a large literature describing how adding or removing trophic levels (top-down and bottom-up effects; vertical diversity) can have widespread effects in food webs (Hairston et al. 1960, Fretwell 1977, Hunter and Price 1992). Similarly, the number of studies documenting how species diversity within a given trophic level can alter community structure and ecosystem function is now quite large (Cardinale et al. 2006a, b, Bruno and Cardinale 2008). Only recently

have ecologists examined the impacts of manipulating the number of trophic levels (vertical diversity) in concert with manipulating the number of species in a single trophic level (horizontal diversity; e.g., Duffy et al. 2005, 2007, Reiss et al. 2009, Srivastava and Bell 2009). To our knowledge, only a few other studies have manipulated vertical and horizontal diversity and compared the response of ecosystem functions. For example, Srivastava and Bell (2009) manipulated species diversity of detritivores and the presence or absence of their predators, and then measured the diversity of other organisms within bromeliad plant aquatic food webs. They found that the diversity of detritivores only impacted the diversity of ciliates in the absence of detritivore predators. In another study, Gamfeldt et al. (2005) manipulated species diversity at both primary producer and primary consumer trophic levels and measured the productivity of the two trophic levels. They found that productivity at each trophic level was impacted differently by changes at other trophic levels (Gamfeldt et al. 2005). These studies, and ours, form a growing set of results that imply that emergent effects may result from interactions between vertical and horizontal diversity, and show the importance of diversity to ecological function across multiple trophic levels. Further empirical and theoretical studies are needed to elucidate expectations and generalizations across interactions between vertical and horizontal diversity.

On a practical level, understanding how addition of vertical diversity influences multiple-predator effects may have important implications for designing successful biological control strategies, and understanding more fully how agricultural and landscape intensification will result in changes in ecosystem services. For example, consider the biological control potential of a single ant species in the system. *A. instabilis* is considered a keystone species in this system, with strong effects on several components of the insect food web, and has been implicated in maintaining low populations of scale insects and other common pests (Vandermeer et al. 2010, Liere 2011). One option might be using the *A. instabilis* as a biological control agent in coffee agroecosystems, especially given that, apparently (without considering the effects of an additional trophic level), the ant is equally as effective as other species, and may deter the other ant species from preying on the CBB. Yet, phorids reduce *A. instabilis* activity. Despite that phorids reduce the abilities of *A. instabilis* to prey on the CBB in the laboratory, there is not a negative relationship between the number of phorid attacks around an *A. instabilis* colony and the number of fruits attacked by the CBB (Pardee and Philpott 2011). This is likely due to compensatory predation by other ant species when phorids are attacking workers of *A. instabilis*. Because ants such as *A. instabilis* also limit activities of insectivorous birds (Philpott et al. 2005), and can reduce densities of spiders (Halaj et al. 1997), activity of

additional non-ant predators may be affected by the vertical diversity of predators and their parasites within coffee agroecosystems. Thus, when considering an additional trophic level, predator diversity is important in limiting the number of attacks by this important coffee pest, therefore lending support to the idea that both herbivore activity may be limited and coffee yields may be increased where predator diversity is higher.

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#### LITERATURE CITED

- Armbrecht, I., and M. C. Gallego. 2007. Testing ant predation on the coffee berry borer in shaded and sun coffee plantations in Colombia. *Entomologia Experimentalis et Applicata* 124:261–267.
- Barrera, J. F., P. S. Baker, J. E. Valenzuela, and A. Schwarz. 1990. Introduction of two African parasitoid species to Mexico for biological control of the coffee borer *Hypothenemus hampei* (Ferrari) (Coleoptera: Scolytidae). *Folia Entomologica Mexicana* 79:245–247.
- Borkhataria, R., J. Collazo, and M. Groom. 2006. Additive effects of vertebrate predators on insects in a Puerto Rican coffee plantation. *Ecological Applications* 16:696–703.
- Bruno, J. F., and B. J. Cardinale. 2008. Cascading effects of predator richness. *Frontiers in Ecology and the Environment* 6:539–546.
- Cardinale, B. J., D. S. Srivastava, E. Duffy, J. P. Wright, A. L. Downing, M. Sankaran, and C. Jouseau. 2006a. Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature* 443:989–992.
- Cardinale, B. J., J. J. Weis, A. E. Forbes, K. J. Tillman, and A. R. Ives. 2006b. Biodiversity as both a cause and consequence of resource availability: a study of reciprocal causality in a predator-prey system. *Journal of Animal Ecology* 75:497–505.
- Damon, A. 2000. A review of the biology and control of the coffee berry borer, *Hypothenemus hampei* (Coleoptera: Scolytidae). *Bulletin of Entomological Research* 90:453–465.
- Davidson, D. W., S. C. Cook, R. R. Snelling, and T. H. Chua. 2003. Explaining the abundance of ants in lowland tropical rainforest canopies. *Science* 300:969–972.
- Duffy, E., B. J. Cardinale, K. E. France, P. B. McIntyre, E. Thébault, and M. Loreau. 2007. The functional role of biodiversity in ecosystems: incorporating trophic complexity. *Ecology Letters* 10:522–538.
- Duffy, J. E., J. P. Richardson, and K. E. France. 2005. Ecosystem consequences of diversity depend on food chain length in estuarine vegetation. *Ecology Letters* 8:301–309.
- Feener, D. H., Jr. 2000. Is the assembly of ant communities mediated by parasitoids? *Oikos* 90:79–88.
- Feener, D. H., Jr., and B. V. Brown. 1992. Reduced foraging of *Solenopsis geminata* (Hymenoptera: Formicidae) in the presence of parasitic *Pseudacteon* spp. (Diptera: Phoridae). *Annals of the Entomological Society of America* 85:80–84.
- Finke, D. L., and R. F. Denno. 2005. Predator diversity and the functioning of ecosystems: the role of intraguild predation in dampening trophic cascades. *Ecology Letters* 8:1299–1306.
- Folgarait, P. J., and L. E. Gilbert. 1999. Phorid parasitoids affect foraging activity of *Solenopsis richteri* under different availability of food in Argentina. *Ecological Entomology* 24:163–173.
- Fretwell, S. D. 1977. The regulation of plant communities by food chains exploiting them. *Perspectives in Biology and Medicine* 20:169–185.
- Gamfeldt, L., H. Hillebrand, and P. R. Jonsson. 2005. Species richness changes across two trophic levels simultaneously affect prey and consumer biomass. *Ecology Letters* 8:696–703.
- Hairton, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. *American Naturalist* 94:421–425.
- Halaj, J., D. W. Ross, and A. R. Moldenke. 1997. Negative effects of ant foraging on spiders in Douglas-fir canopies. *Oecologia* 109:313–322.
- Halaj, J., and D. Wise. 2001. Terrestrial trophic cascades: how much do they trickle? *American Naturalist* 157:262–281.
- Hölldobler, B., and E. Wilson. 1990. *The ants*. Harvard University Press, Cambridge, Massachusetts, USA.
- Hooper, D. U., et al. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* 75:3–35.
- Hunter, M. D., and P. W. Price. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology* 73:724–732.
- Kellermann, J. L., M. D. Johnson, A. M. Stercho, and S. C. Hackett. 2008. Ecological and economic services provided by birds on Jamaican Blue Mountain coffee farms. *Conservation Biology* 22:1177–1185.
- Larsen, A., and S. M. Philpott. 2010. Twig-nesting ants: the hidden predators of the coffee berry borer. *Biotropica* 42:342–347.
- LeBrun, E. G. 2005. Who is the top dog in ant communities? Resources, parasitoids, and multiple competitive hierarchies. *Oecologia* 142:643–652.
- LeBrun, E. G., and D. H. Feener, Jr. 2002. Linked indirect effects in ant-phorid interactions: impacts on ant assemblage structure. *Oecologia* 133:599–607.
- LeBrun, E. G., and D. H. Feener, Jr. 2007. When trade-offs interact: balance of terror enforces dominance discovery trade-off in a local ant assemblage. *Journal of Animal Ecology* 76:58–64.
- Letourneau, D. K., J. A. Jedlicka, S. G. Bothwell, and C. R. Moreno. 2009. Effects of natural enemy biodiversity on the suppression of arthropod herbivores in terrestrial ecosystems. *Annual Review of Ecology, Evolution, and Systematics* 40:573–592.
- Liere, H. 2011. Complex interactions and ecosystem function: Auto-regulation of an insect community in a coffee agroecosystem. University of Michigan, Ann Arbor, Michigan, USA.
- Liere, H., and A. Larsen. 2010. Cascading trait-mediation: disruption of a trait-mediated mutualism by parasite-induced behavioral changes. *Oikos* 119:1394–1400.
- Liere, H., and I. Perfecto. 2008. Cheating on a mutualism: Indirect benefits of ant attendance to a coccidiphagous coccinellid. *Environmental Entomology* 37:143–149.
- Livingston, G. F., and S. M. Philpott. 2010. A metacommunity approach to co-occurrence patterns and the core-satellite

- hypothesis in a community of tropical arboreal ants. *Ecological Research* 25:1129–1140.
- Losey, J. E., and R. F. Denno. 1998. Positive predator–predator interactions: enhanced predation rates and synergistic suppression of aphid populations. *Ecology* 79:2143–2152.
- Mathis, K. A., and S. M. Philpott. 2012. Current understanding and future prospects of host selection, acceptance, discrimination, and regulation of phorid fly parasitoids that attack ants. *Psyche* article 895424. <http://dx.doi.org/10.1155/2012/895424>.
- Mehdiabadi, N. J., and L. E. Gilbert. 2002. Colony-level impacts of parasitoid flies on fire ants. *Proceedings of the Royal Society Biological Sciences B* 269:1695–1699.
- Morrison, L. W. 1999. Indirect effects of phorid fly parasitoids on the mechanisms off interspecific competition among ants. *Oecologia* 121:113–122.
- Morrison, L. W. 2000. Mechanisms of *Pseudacteon* parasitoid (Diptera: Phoridae) effects on exploitative and interference competition in host *Solenopsis* ants (Hymenoptera: Formicidae). *Annals of the Entomological Society of America* 93:841–849.
- Morrison, L. W., E. Kawazoe, R. Guerra, and L. E. Gilbert. 2000. Ecological interactions of *Pseudacteon* parasitoids and *Solenopsis* ant hosts: environmental correlates of activity and effects on competitive hierarchies. *Ecological Entomology* 25:433–444.
- Müller, C. B., and H. C. Godfray. 1999. Indirect interactions in aphid–parasitoid communities. *Research in Population Ecology* 41:93–106.
- Nilsson, E., P. Hertonsen, M. Stenberg, J. Brodersen, K. Olsson, P. Stenroth, T. Lakowitz, C. Brönmark, P. Nyström, and A. R. McIntosh. 2006. Facilitation and interference among three predators affect their consumption of a stream-dwelling mayfly. *Freshwater Biology* 51:1507–1514.
- Orr, M. R., D. L. Dahlsten, and W. W. Benson. 2003. Ecological interactions among ants in the genus *Linepithema*, their phorid parasitoids, and ant competitors. *Ecological Entomology* 28:203–210.
- Orr, M. R., S. H. Seike, W. W. Benson, and L. E. Gilbert. 1995. Flies suppress fire ants. *Nature* 373:292–293.
- Pardee, G. L., and S. M. Philpott. 2011. Cascading indirect effects in a coffee agroecosystem: Effects of parasitic phorid flies on ants and the coffee berry borer in a high-shade and low-shade habitat. *Environmental Entomology* 40:581–588.
- Parr, C. L., and H. Gibb. 2010. Competition and the role of dominant ants. Pages 77–96 in L. Lach, C. L. Parr, and K. L. Abbott, editors. *Ant ecology*. Oxford University Press, New York, New York, USA.
- Perfecto, I., and J. Vandermeer. 2006. The effect of an ant–Hemipteran mutualism on the coffee berry borer (*Hypothenemus hampei*) in southern Mexico. *Agriculture, Ecosystems, and Environment* 117:218–221.
- Petchey, O. L. 2003. Integrating methods that investigate how complementarity influences ecosystem functioning. *Oikos* 101:323–330.
- Philpott, S. M. 2005. Trait-mediated effects of parasitic phorid flies (Diptera: Phoridae) on ant (Hymenoptera: Formicidae) competition and resource access in coffee agro-ecosystems. *Environmental Entomology* 34:1089–1094.
- Philpott, S. M. 2010. A canopy dominant ant affects twig-nesting ant assembly in coffee agroecosystems. *Oikos* 119:1954–1960.
- Philpott, S. M., R. Greenberg, and P. Bichier. 2005. The influence of ants on the foraging behavior of birds in an agroforest. *Biotropica* 37:467–470.
- Philpott, S. M., J. Maldonado, J. Vandermeer, and I. Perfecto. 2004. Taking trophic cascades up a level: behaviorally-modified effects of phorid flies on ants and ant prey in coffee agroecosystems. *Oikos* 105:141–147.
- Porter, S. D., L. A. Nogueira de Sá, and L. W. Morrison. 2004. Establishment and dispersal of the fire ant decapitating fly *Pseudacteon tricuspis* in North Florida. *Biological Control* 29:179–188.
- Prasad, R. P., and W. E. Snyder. 2006. Diverse trait-mediated interactions in a multi-predator, multi-prey community. *Ecology* 87:1131–1137.
- Preisser, E. L., D. I. Boknick, and M. F. Benard. 2005. Scared to death? The effects of intimidation and consumption in predator–prey interactions. *Ecology* 86:501–509.
- Reiss, J., J. R. Bridle, J. M. Montoya, and G. Woodward. 2009. Emerging horizons in biodiversity and ecosystem functioning research. *Trends in Ecology and Evolution* 24:505–514.
- Rosenheim, J. A., H. K. Kaya, L. E. Ehler, J. J. Marios, and B. A. Jaffee. 1995. Intraguild predation among biological-control agents: Theory and evidence. *Biological Control* 5:303–335.
- Schmitz, O. J. 2007. Predator diversity and trophic interactions. *Ecology* 88:2415–2426.
- Sih, A., G. Enlund, and D. Wooster. 1998. Emergent impacts of multiple predators on prey. *Trends in Ecology and Evolution* 13:350–355.
- Soluk, D. A. 1993. Multiple predator effects: prediction combined functional response of stream fish and invertebrate predators. *Ecology* 74:219–225.
- SPSS. 2010. IBM SPSS statistics for MacOS. Release 19.0.0. SPSS, Chicago, Illinois, USA.
- Srivastava, D. S., and T. Bell. 2009. Reducing horizontal and vertical diversity in a food web triggers extinctions and impacts functions. *Ecology Letters* 12:1016–1028.
- Steffan, S. A., and W. E. Snyder. 2010. Cascading diversity effects transmitted exclusively by behavioral interactions. *Ecology* 91:2242–2252.
- Straub, C. S., and W. E. Snyder. 2006. Species identity dominates the relationship between predator biodiversity and herbivore suppression. *Ecology* 87:277–282.
- Torres, C. W., M. Brandt, and N. D. Tsutsui. 2007. The role of cuticular hydrocarbons as chemical cues for nestmate recognition in the invasive Argentine ant (*Linepithema humile*). *Insectes Sociaux* 54:363–373.
- Vance-Chalcraft, H. D., J. A. Rosenheim, J. R. Vonesh, C. W. Osenberg, and A. Sih. 2007. The Influence of intraguild predation on prey suppression and prey release: a meta-analysis ecology 88:2689–2696.
- Vandermeer, J., I. Perfecto, G. Ibarra-Núñez, S. Philpott, and A. Garcia-Ballinas. 2002. Ants (*Azteca* sp.) as potential biological control agents in shade coffee production in Chiapas, Mexico. *Agroforestry Systems* 56:271–276.
- Vandermeer, J., I. Perfecto, and S. M. Philpott. 2010. Ecological complexity and pest control in organic coffee production: uncovering an autonomous ecosystem service. *Bioscience* 60:527–537.
- Werner, E. E., and S. D. Peacor. 2003. A review of trait-mediated indirect interactions in ecological communities. *Ecology* 84:1083–1100.
- Wilby, A., S. Villareal, L. Lan, K. Heong, and M. B. Thomas. 2005. Functional benefits of predator species diversity depend on prey identity. *Ecological Entomology* 30:497–501.