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# Complex Ecological Interactions in the Coffee Agroecosystem

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## Keywords

*Coffea arabica*, trophic interactions, trait-mediated indirect interactions, community assembly, spatial ecology, birds, ants, *Azteca*

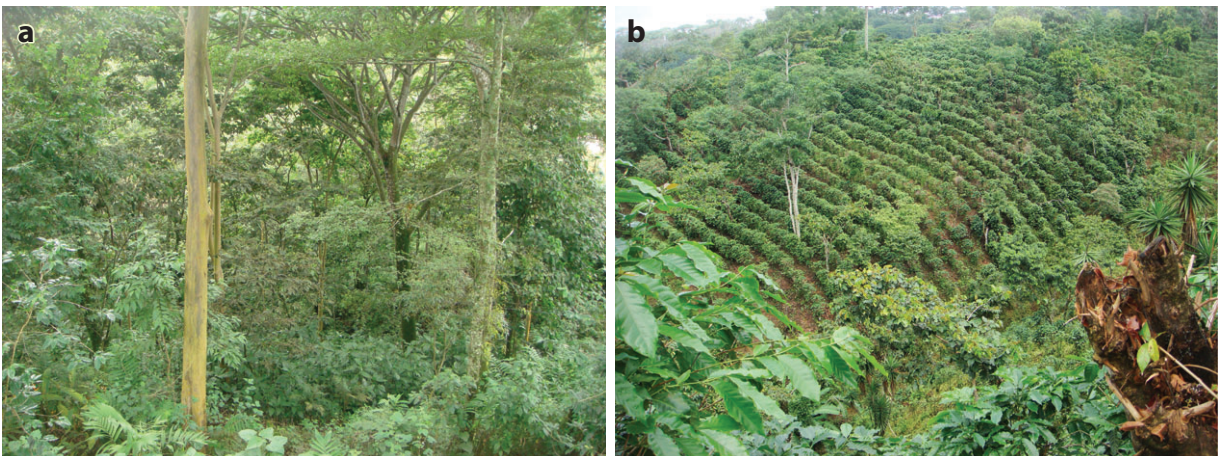
## Abstract

Coffee agroecosystems have become iconic in the study of how agriculture can contribute to the conservation of biodiversity and how biodiversity can deliver ecosystem services to agriculture. However, coffee farms are also excellent model systems for ecological research. Throughout the tropics coffee farms are cultivated using varying numbers and diversity of shade trees, representing a gradient of diversity and complexity, ranging from forest-like “shade coffee” to intensified shadeless “sun coffee.” Here we synthesize ecological research in the coffee agroecosystem focusing on four topics that have received considerable recent attention: (a) trophic interactions (especially vertebrates and ants as predators), (b) trait-mediated indirect interactions, (c) competition and community assembly (mainly birds and ants), and (d) spatial constraints on interactions.

## INTRODUCTION: BIODIVERSITY AND THE STYLE OF COFFEE PRODUCTION

It is not easy to overstate the social and political importance of coffee, from its central role in South Asian colonial history to its influence on the intellectual ferment emerging from eighteenth century coffee houses, to its role today as the world's most important legal stimulant and economic foundation for millions of small family farmers in the tropics and the nations in which they reside. On the negative side, coffee has been associated with habitat loss because it is cultivated in areas that were formerly forests. For example, in Central and South America, coffee plantations comprise 54% of the perennial crops that have replaced cloud and premontane tropical forests (Roberts et al. 2000). Nonetheless, in light of recent reevaluation of agroecosystems and their relationships to conservation (Perfecto & Vandermeer 2010), coffee has come to figure centrally in current narratives about the value of diverse agricultural systems for biodiversity conservation (Perfecto et al. 1996). The view that coffee is important for conservation has emerged largely because of the way in which coffee has traditionally been cultivated in much of the world (Perfecto et al. 1996, Moguel & Toledo 1999, Philpott et al. 2008, Scales & Marsden 2008) (**Figure 1a**). Coffee, originally an understory plant from the highland forests of Ethiopia and Sudan (Anthony et al. 2002), is cultivated with native forest trees and sometimes with other useful trees, such as fruit and nitrogen-fixing trees (Moguel & Toledo 1999, Bandeira et al. 2005), thus traditionally creating a forest-like environment, popularly referred to as shade coffee.

The conservation value of traditional shaded plantations was evident to early naturalists and bird watchers who frequented shaded coffee plantations, noting that the avifauna within plantations was very similar to that of the intact forest (Griscom 1932). In the mid-1980s and early 1990s many governments in Latin America began encouraging the intensification of coffee plantations, leading to the transformation of coffee agroforests to simplified agroecosystems with fewer shade trees (**Figure 1b**) or treeless monocultures, commonly referred to as sun coffee (Rice 1999). Deforestation of coffee agroforests in this region coincided with declining bird populations in North America, and the issue of biodiversity decline as a function of agricultural intensification has ever since been on the minds of thoughtful conservationists. Shortly thereafter, the Smithsonian



**Figure 1**

Examples of coffee farms from Chiapas, Mexico: (a) diverse, shaded coffee and (b) intensive coffee farm with few shade trees. Photo credits: Ivette Perfecto.

Migratory Bird Center started a research program to study the impacts of coffee intensification on migratory bird species (Perfecto et al. 1996; Rice & Ward 1996; Greenberg et al. 1997a,b). There had already been growing concern about the declining bird populations (Brash 1987, Robbins et al. 1989), and the Smithsonian team along with the pioneering work by Borrero (1986) in Colombia provided an explanation that could hardly be ignored. Coffee intensification throughout Mesoamerica and northern South America was resulting in the destruction of wintering habitat for millions of migratory birds. Since then, many studies and several reviews and meta-analyses have been published confirming the important role of traditional shaded coffee plantations as a refuge for biodiversity and from the detrimental impacts of coffee intensification (Perfecto et al. 1996, 2003, 2007; Moguel & Toledo 1999; Staver et al. 2001; Philpott & Dietsch 2003; Donald 2004; Somarriba et al. 2004; Komar 2006; Manson et al. 2008; Philpott et al. 2008; Lin & Perfecto 2012; Caudill et al. 2014, Tadesse et al. 2014). Furthermore, shade trees provide important ecological services in the coffee agroecosystem, such as provision of organic matter, increasing nitrogen in the soil (Beer et al. 1997, Romero-Alvarado et al. 2002), microclimatic regulation, weed suppression, refuge for natural enemies, and many other ecological functions (Soto-Pinto et al. 2000, Staver et al. 2001, Ricketts et al. 2004, Lin 2007, Lin et al. 2008, Van Bael et al. 2008, Vandermeer et al. 2010).

Although our intention here is to review, provide a synthesis of, and reflect on the work done over the past 20 years on the community ecology of this system, it is worth noting that the system itself represents something of a model system of diverse agroforests that have a wide geographic distribution throughout the tropics. From a biogeographic point of view, coffee exists in some of the most important biodiversity hot spots in the world, occupying large areas at mid elevations in the wet tropics (Moguel & Toledo 1999). Its replicate state in so many different sites around the globe makes it almost like an experiment in ecology.

A variety of topics in community ecology have been intensively studied in this model system. Here we highlight the four that we feel have received the most attention: (*a*) trophic interactions, (*b*) trait-mediated indirect interactions, (*c*) competition and community assembly, and (*d*) spatial constraints on interactions.

## TROPHIC INTERACTIONS

### Vertebrate and Invertebrate Carnivores

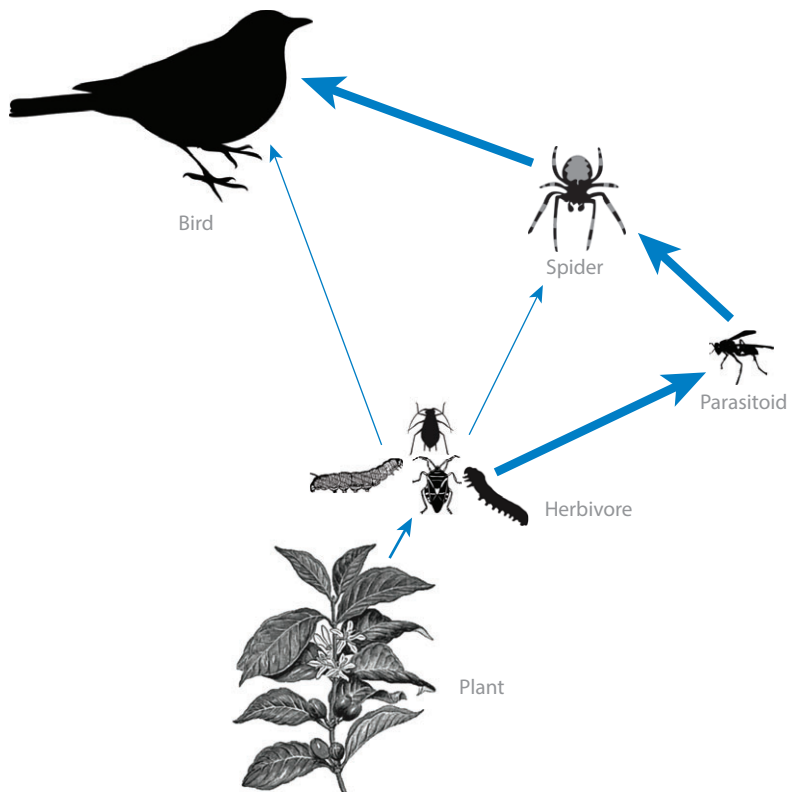
Trophic structures have been a fundamental framework in ecology since Elton's and Lindeman's classic formulations of the food chain and trophic dynamics (Hairston et al. 1960, Pimm & Lawton 1978, Post 2002). Yet a proper analytical framework for dealing with trophic structure remains contested (Pascual & Dunne 2005). In some situations it seems obvious that there is a trophic chain, giving rise to formulations such as the "green world hypothesis" (Hairston et al. 1960). However, in many situations it is hard to distinguish between such clear-cut trophic levels, giving rise to the idea of a food web in which carnivores and top carnivores are not well defined (Paine 1969, Yodzis 2000). Rarely are the categories "primary producer" and "herbivore" thought to be anything other than Lindemanian, but higher trophic categories can be more enigmatic (Dunne et al. 2002). In the coffee agroecosystem there is a rich literature demonstrating the simple fact of a trophic chain (plant eaten by herbivore eaten by carnivore) (Van Bael et al. 2008). Many authors have identified predators of coffee pests, effectively representing a trophic chain from coffee to herbivorous pest to predator of that pest (Barrera et al. 1990, Damon 2000, Jaramillo et al. 2006, De la Mora et al. 2008, Vega et al. 2009, Larsen & Philpott 2010, Gonthier et al. 2013, Classen et al. 2014). For example, Borkhataria and colleagues (2006) excluded lizards in one treatment, demonstrating a

dramatic reduction in herbivorous insects. Greenberg and colleagues (2000) excluded birds (and bats) from individual coffee trees and demonstrated a shift in abundance of large arthropods in the treatment. Exclosure experiments in Jamaica (Johnson et al. 2009, 2010) and Costa Rica (Karp & Daily 2013, Karp et al. 2013) demonstrated that birds (and/or bats) significantly reduced the incidence of the main coffee pest, the coffee berry borer, which translates into an economic value of up to US\$310 per hectare. Reviewing the literature on exclosure experiments in coffee and cacao, Van Bael and colleagues (2008) conclude that top-down effects of birds (and bats) on arthropods are common and strong, including effects on both herbivorous and carnivorous arthropods. In addition, excluding vertebrate predators from coffee plants can decrease fruit set by as much as 9%, dramatically affecting yields (Classen et al. 2014).

A complicating fact of trophic dynamics in most terrestrial ecosystems, including the coffee agroecosystem, derives from a structural constraint. On one hand, arthropods tend to be small but are major components of both herbivore and carnivore categories (Cohen et al. 1993, Emmerson & Raffaelli 2004). On the other hand, vertebrate predators are normally larger and eat both herbivorous and carnivorous arthropods. The consequence of this is that arthropod predators do not generally eat vertebrate predators, but vertebrate predators eat both herbivorous and carnivorous arthropods (Holt & Polis 1997, Karp & Daily 2013). This elementary observation leads to a persistent question, reflecting the contrast between the Lindemanian “food chain” and the more complex “food web” concept of terrestrial trophic interactions: How many “effective” trophic levels are there in a particular system (Hastings & Conrad 1979, Matsuno & Ono 1996, Post 2002)?

Experimental work in the coffee agroecosystem of southern Mexico tested whether the food web involving vertebrate predators and arthropods can be viewed as a simple trophic chain (Perfecto & Vandermeer 2014). Some arthropod herbivores are consumed by both arthropod (beetles, lacewings, wasps, robber flies, ants, and spiders) and vertebrate carnivores (toads, frogs, lizards, bats, and birds). Thus, experimental removal of the vertebrate carnivores (birds and bats) should result in an increase in arthropod carnivores if the system is structured as a trophic chain (if birds and bats are eating more arthropod carnivores than herbivores), but otherwise it should result in an increase in the arthropod herbivores (if predation by arthropod carnivores is stronger than predation by vertebrate carnivores). Contrary to the expected decrease, the number of herbivores increased in the treatment that excluded vertebrate predators. This response has been attributed to the presence of parasitoids, which significantly affect herbivores but are consumed mainly by spiders, especially the web weavers (Ibarra-Núñez 2001), and not extensively by birds, which clearly prefer the larger arthropods (Greenberg et al. 2000, Van Bael et al. 2003, Philpott et al. 2004, Williams-Guillén et al. 2008). Parasitoid numbers decline when birds and bats are both excluded after three and six months, and the parasitoids showed a negative relationship with spiders. It appears that intraguild predation may be implicated, and the increase of herbivores when birds are removed may, at least partially, result from a trophic cascade with five trophic levels (vertebrate predators, spiders, parasitic wasps, herbivores, and plants) (**Figure 2**). Another study in coffee plantations in Costa Rica suggests similar intraguild predation with bats but not with birds (Karp et al. 2014).

Approaching a similar question about trophic structure, Philpott and colleagues (2004) examined changes in arthropod densities when predation pressure was removed from birds and bats on the one hand and from two species of predatory ants on the other hand in shade trees of a coffee agroforest. Although birds and/or bats had a clear negative effect on arthropods, the two ant species deviated, with one having no effect at all and the other having an effect only in the dry season. Clearly, aggregating top carnivores, whether taxonomically related or not, may lead to a misrepresentation of food web interactions.



**Figure 2**

Suggested trophic structure in a coffee farm. Arrows indicate the transfer of energy. Except for the line connecting herbivores and plants, the thickness of the lines represents experimental determination of the strength of the effects. The main structure is a five-level trophic chain from plant to herbivore to parasitoid to spider to bird. Figure drawn by David Brenner.

Several recent studies have examined the separate roles of birds and bats (Williams-Guillén et al. 2008, Karp & Daily 2013), and these studies generally conclude that both significantly affect arthropods, although cascading effects on coffee yields have not been convincingly demonstrated. In one study (Karp & Daily 2013) the trophic cascades of birds differed significantly from that associated with bats, the former effectively a three-level chain (birds, herbivores, and plants), the latter a four-level chain (bats, arthropod predators, herbivores, and plants). Thus trophic interactions in tropical agroforests, such as coffee and cacao, can be highly complex.

### **A Fungal Disease and Its Natural Enemy**

A completely different set of trophic interactions is presented in the case of coffee diseases, probably the worst of which is the coffee leaf rust disease caused by *Hemileia vastatrix* (Kushalappa & Eskes 1989, Avelino et al. 2012). Historically, this disease has been devastating worldwide, being the main cause of abandonment of coffee as a commercial crop in Sri Lanka, Sumatra, and Java (McCook 2006), as well as causing panic among producers throughout Central America in the 1980s (Schieber & Zentmyer 1984). Contrary to fears, the disease became more of an irritant

than a disaster; farms throughout Latin America almost inevitably showed low levels of infection almost every year and only occasionally experienced epizootic levels (as in 2013; Cressey 2013, Vandermeer et al. 2014).

The importance of natural enemies of the rust has been emphasized by several authors (Kushalappa & Eskes 1989, Andrews 1992). One of those enemies may be the hyperparasite *Lecanicillium lecanii*, known to colonize *H. vastatrix* under laboratory conditions (Eskes et al. 1991) and in the field (Vandermeer et al. 2009, Jackson et al. 2012a,b). In addition, *L. lecanii* routinely attacks the green coffee scale insect (*Coccus viridis*), another pest of coffee (Vandermeer et al. 2009, Rosado et al. 2014).

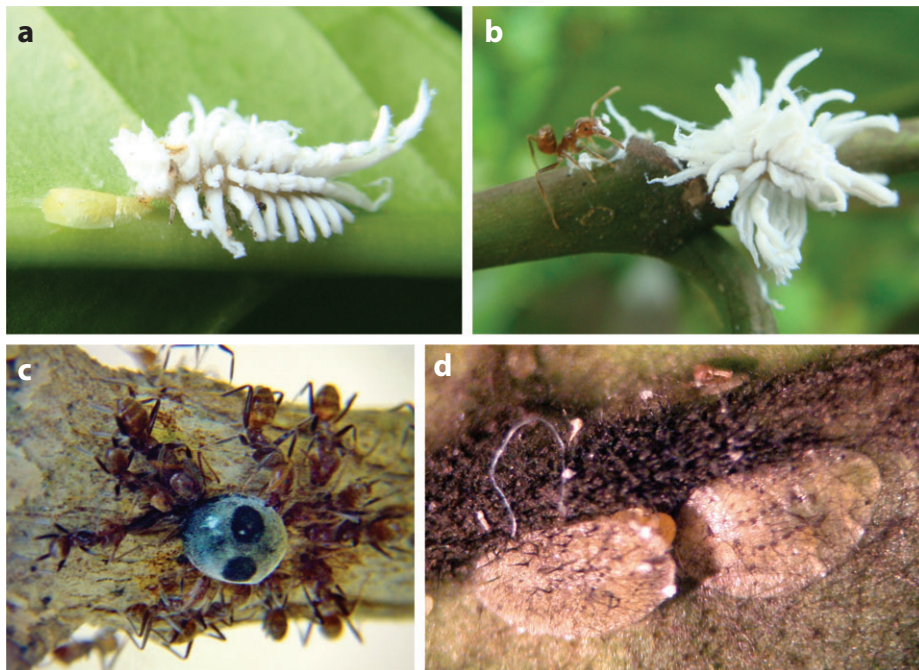
A series of studies (Vandermeer et al. 2009, 2014; Jackson et al. 2012a,b) suggests that the mutualism between green coffee scales (hemipterans) and ants may provide centers of concentrated production of spores of *L. lecanii*, thus contributing to an elevated level of control over *H. vastatrix*. Therefore, there may be partial control of *H. vastatrix* by *L. lecanii*, which is enhanced through the existence of the mutualistic association of the ant *Azteca sericeasur* with the green coffee scale, *C. viridis* (in previous studies, we have referred to *Azteca instabilis*, which is now known to be *A. sericeasur*; J. Longino, personal communication). Thus there is another kind of trophic cascade in the coffee agroecosystem that involves the following: (a) ants provide protection for scale insects against parasites and predators, and (b) the locally concentrated populations of scale insects provide host material for the white halo fungus (*L. lecanii*), which also attacks the coffee rust fungus. The white halo fungus thus acts as a “carnivore” consuming both rust fungus and scale insects. The parasitoids of the scale insects also act as “carnivores,” competing with the white halo fungus for the scale resources. The ant inserts an interaction completely independent of energy transfer but behaviorally altering the trait of parasitism. The food web would make little sense without understanding this key trait-mediated effect.

## TRAIT-MEDIATED CASCADES IN THE AZTECA SYSTEM

In coffee agroecosystems throughout the Neotropics one of the key interactions is the mutualism between arboreal ants in the genus *Azteca* and the green coffee scale, *C. viridis*. Although the ants nest within shade trees, they forage and tend scales on coffee plants near their nests. Extensive research has revealed how a complex ecological network centered on the *Azteca*-green coffee scale mutualism is structured. This network, in addition to the normal energy transferring connections, includes competition, mutualism, predation, parasitism, and disease-host relationships and includes several key trait-mediated interactions. The network also plays a role in the ecosystem service of pest control (Perfecto & Vandermeer 2008, Vandermeer et al. 2010, Pardee & Philpott 2011, Hsieh et al. 2012, Jha et al. 2012, Liere et al. 2012, Jiménez-Soto et al. 2013).

One of the main predators of the green coffee scale that the ants defend against is *Azya orbiger*, a coccinellid beetle (**Figure 3a**). As in other myrmecophilous coccinellids (Päivinen et al. 2003), the larvae of the beetle are protected against ant attack, in this case by waxy filaments (Liere & Perfecto 2008) (**Figure 3b**). Although the larvae are protected, unprotected adult females (**Figure 3c**) must be able to lay unprotected eggs where ants are actively patrolling (i.e., near the concentrations of hemipterans) but must place the eggs where ants cannot find them. One of the main safe sites for oviposition is directly underneath the adult-scale insects (Hsieh et al. 2012, Hsieh & Perfecto 2012) (**Figure 3d**), where ants cannot patrol. But how can the gravid female beetles search for safe sites to lay eggs when under continual attack by the ants? We return to this question later.

Another key player in the system is a parasitic fly (at least three species in the genus *Pseudacteon*, family Phoridae). In the coffee system the phorid flies that attack *Azteca* are common, and they dramatically change the foraging behavior of the ants (Liere & Larsen 2010), reducing foraging



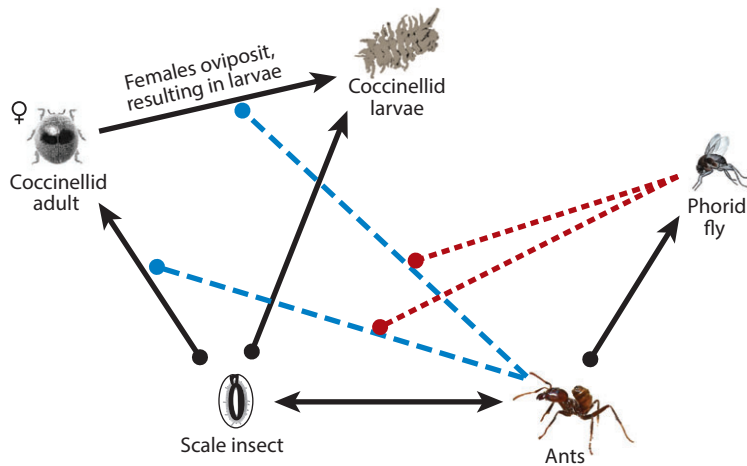
**Figure 3**

Organisms involved in the *Azteca* system: (a) larvae of *Azya orbigera* eating the green coffee scale (*Coccus viridis*); (b) a worker of *Azteca sericeasur* trying to attack a larva of *A. orbigera* but being unable to kill it; (c) workers of *Azteca sericeasur* attacking and killing an adult *A. orbigera*; (d) eggs of *A. orbigera* hidden under green coffee scale (*Coccus viridis*). Photo credits: (a,b,d) Ivette Perfecto and (c) Shinsuke Uno (printed with permission of S. Uno).

activity by as much as 50% (Philpott et al. 2004, Philpott 2005). Indeed, the ants display an unusual behavior when under attack by the phorids, either rushing back to the closest nest entrance or assuming a catatonic posture seemingly protecting the anterior thorax—the oviposition site of the fly (Mathis et al. 2011, Mathis & Philpott 2012). Furthermore, this characteristic behavior is generalized over a rather large area (at least a linear meter distance from the source of the attack), indicating a chemical communication among ant individuals to warn of imminent phorid attack. Adult beetle residence time on a coffee branch is, not surprisingly, strongly correlated with ant activity (Liere & Larsen 2010). Beetles that would otherwise be restricted in residence time are partly released from that restriction when the phorids arrive (Liere & Larsen 2010), thus resolving the problem of locating safe oviposition sites (Hsieh et al. 2012). Phorid flies locate concentrations of foraging ants by recognizing an ant pheromone (1-acetyl-2-methylcyclopentane, released from the pygidial gland; Mathis et al. 2011) that the ants produce when disturbed. Once near the ants, phorids cannot oviposit unless they see movement on the part of an individual ant (Mathis et al. 2011), suggesting the adaptive significance of the ant's catatonic behavior.

This basic natural history places this system as an example of a trait-mediated cascade (Hsieh et al. 2012). Yet it is not clear how the beetles find these high-quality patches and then manage to know that the ants have adopted their protective position. A series of olfactometer experiments demonstrated that both female and male beetles are attracted to the green coffee scale, but only female beetles are attracted to ant pheromones (Hsieh et al. 2012). More importantly, female





**Figure 4**

Diagram indicating direct (black solid lines) and trait-mediated indirect (dashed lines) interactions. Blue dashed lines are first-order trait-mediated indirect interactions, and red dashed lines are second-order trait-mediated indirect interactions. Arrows are positive effects, and solid dots are negative effects. Photo credits: Ivette Perfecto.

beetles (but not the males) are attracted to ants only when the ants are under attack by phorid flies, and the attraction to ant pheromones is manifested only when females are gravid (Hsieh et al. 2012). Because beetle larvae have restricted movements and are attacked by several parasitoids (Liere & Perfecto 2008), there is clear pressure for female beetles to oviposit in ant-tended areas, where high prey density and low risk of parasite attack are secured. However, the aggressive behavior of ants apparently renders female beetles incapable of ovipositing in these high-quality areas. The olfactometer experiments described above suggest that female beetles avoid this problem by being able to detect some kind of “phorid alert” pheromone released by *Azteca* ants, thus allowing them to take advantage of low ant activity periods to search for safe oviposition sites. This system is an example of cascading trait-mediated indirect interactions facilitated by the ant’s chemical communication system (Figure 4).

In addition to attacking adult coccinellid beetles, *Azteca* ants remove any herbivores from where they are actively foraging and also attack coffee berry borers (*Hypothenemus hampei*), coffee’s most damaging insect pest (Jiménez-Soto et al. 2013), making it difficult for the borers to make their way into coffee fruits to lay eggs. However, when *Azteca* ants are under attack from phorid flies, and in the catatonic state, coffee berry borers can invade just as many coffee fruits as when no ants are protecting coffee plants (Pardee & Philpott 2011). The effects of phorids are not entirely negative, however, when other ants, such as arboreal twig-nesting ants, are present. *Azteca* ants have negative impacts on other species of ants; yet, when they are being attacked by phorids, other ant species have significantly greater access to food resources (Philpott 2005). This extends to biological control of the coffee berry borer, as demonstrated with lab experiments. Pairs or trios of functionally redundant ant species (*Azteca sericeasur* plus *Pseudomyrmex simplex* or *Procrystocerus bylaeus* or both) have synergistic protective effects for the coffee by preventing attacks by the borer; however, these synergistic effects are only evident where phorids are present (Philpott et al. 2012). In effect, as *Azteca* behavior is limited to a great extent by the phorids, other ant species, normally attacked by the *Azteca*, increase their predatory activities, thus maximizing negative effects on this globally important coffee pest. In sum, the trait-mediated effects result in complex networks

of interactions that provide pest control and maintain a diversity of organisms in shaded coffee farms.

## COMPETITION AND COMMUNITY ASSEMBLY

As noted in the introduction, many ecological studies in coffee agroecosystems focus on biodiversity and the ecosystem services provided by the diverse array of species that use coffee agroecosystems. However, a number of these studies have, at least implicitly, connected with some of the classic notions of community structure and have analyzed species assemblages and competitive interactions, providing insights for more general ecological principles. The majority of the studies that take this approach are studies of bird and ant assemblages. In what follows, we provide a synthesis of that literature.

### Competition and Foraging in Bird Assemblages

For coffee agroforests, the first subject to receive a large amount of attention in the area of ecology and conservation was birds. Several studies have reviewed the impacts of coffee intensification on bird abundance, richness, and community composition (e.g., Greenberg et al. 1997a,b; Johnson 2000; Roberts et al. 2000; Perfecto et al. 2003; Komar 2006; Philpott et al. 2008). Many have documented changes in resource use, foraging behavior, and roost selection based on differences in availability and stability of fruit and floral resources (Carlo et al. 2004, Peters & Nibbelink 2011, Bakermans et al. 2012), epiphytes (Cruz-Angón et al. 2008), and distance to forest fragments (Luck & Daily 2003, Jirinec et al. 2011). Coffee farms have been used as laboratories for understanding how sex and age influence bird foraging behavior (Jones et al. 2000) and how foraging strata influence infestation of birds by mite parasites (Dietsch 2008). Furthermore, coffee agroforests have been used to examine differences in foraging behavior in solitary foragers versus members of mixed-species flocks and to test whether flock-related foraging shifts differ with habitat type (Latta & Wunderle 1996, Pomara et al. 2003). Here, we focus on summarizing what has been learned about competition and foraging in bird communities via studies in coffee agroforests by specifically examining work on competition between migrant and resident birds, aggression, and home range, as well as competition between avian insectivores and ants.

Shaded coffee farms are easily divided into two distinct foraging strata, the understory layer that is primarily composed of coffee plants and the shade-tree layer that can sometimes be a single layer dominated by a nitrogen-fixing legume or a multistrata canopy. Understanding how birds use these different foraging strata and interactions between bird species in different vegetation layers has been an important focus of bird studies in coffee, especially because of the relative ease with which foraging maneuvers can be observed in coffee compared with more complex forest habitats. For example, in Chiapas, Mexico, Jedlicka et al. (2006) examined the foraging behavior of one resident bird species (the rufous-capped warbler, *Basileuterus rufifrons*) during both the wet season (summer), when migratory birds are absent from coffee farms, and the dry season (winter), during which hundreds of migratory birds forage in shaded coffee farms. They found that these insectivorous warblers spent a similar amount of time foraging in the canopy and understory in the summer but had higher capture rates in the canopy. However, in the winter, migratory birds dominated the canopy layer while the warblers shifted foraging such that >80% of maneuvers were in the understory. Furthermore, the warblers were less successful at capturing prey in both the canopy and understory during the winter. There were significant changes in the abundance of canopy arthropods during the wet and dry seasons with significantly fewer large arthropods available in the canopy during the dry season. This change in arthropod abundance may have

precipitated the change in foraging by the rufous-capped warblers. Yet this study may also provide evidence that there is a niche shift on the part of this warbler species to avoid competition with the neotropical migrants that dominate the shade-tree canopy.

A recent study conducted in coffee farms in Jamaica tested whether habitat type, prey availability, and tree strata influenced the degree of aggression from insectivorous black-throated blue warblers (*Setophaga caerulescens*). Smith et al. (2012) radio-tagged several warblers and then tested their response to decoy intruders in coffee farms (both shade-tree strata and coffee layer) and in nearby forests (understory layer). They documented differences in aggression based on habitat type and strata, with the highest aggression being displayed by black-throated blues against the conspecific decoy in the shade-tree canopy, followed by those in the forest understory and coffee layer. Arthropod abundance in the habitat types and strata followed the same pattern, with highest insect abundance being found in the shade-tree canopy, followed by the forest understory and coffee layer. In addition, they found that several explanatory variables influenced the degree of aggression of the black-throated blue warblers—including sex, home-range size, proximity to the center of the home range, habitat, food supply, and presence of another aggressive bird in the area. Importantly, this study used natural variation in the abundance of insects in different strata within coffee farms (the arthropod-rich shade-tree canopy versus the leaves of a chemically well-defended crop plant) to demonstrate that the black-throated blue warblers more aggressively defend areas with greater food supply.

Coffee farms have also been used as model systems for examining competitive interactions between insectivorous birds and ants that forage on canopy trees. The same ant species described in detail above, *Azteca sericeasur*, is aggressive not only to insects but also to other organisms. Philpott et al. (2005) examined how much the presence of *A. sericeasur* on coffee shade trees would influence the foraging of birds, including insectivores. They compared bird foraging (including number and duration of visits) between two species of shade trees with and without nests of *A. sericeasur*. They found that the presence of ants on shade trees did not affect the number of bird individuals or species that visited shade trees; however, ant presence did shorten the length of visits for all birds, and specifically for insectivores, but only on *Alchornea latifolia* shade trees. Two interesting patterns result from this finding. It appears that *A. sericeasur* is not directly aggressive to birds, deterring them from visiting shade trees, and therefore ants likely do not influence birds via interference competition. However, the reduction in time spent foraging on some trees with *A. sericeasur*, and the specific response of insectivores (where other guilds were not affected) indicates that *A. sericeasur* may affect bird foraging via exploitative competition, reducing the arthropod abundance sufficiently to lower the time birds spend foraging on certain shade trees. The response on *A. latifolia* trees, but not the *Inga* spp. shade trees examined, is likely because ant colonies are larger and stronger on those trees (Philpott et al. 2005).

### Competition and Foraging in Ant Assemblages

Ant community assembly and ant diversity are strongly impacted by several characteristics, including abiotic factors associated with changes in vegetation (Kaspari & Weiser 2000, Albrecht & Gotelli 2001, Ribas et al. 2003), temperature or moisture conditions (Perfecto & Vandermeer 1996, Kaspari & Weiser 2000), changes in nest availability (Armbrecht et al. 2004), and changes in food availability and distribution (Kaspari et al. 2000, Blüthgen et al. 2004). In addition, species interactions may drive assembly, as competition from native and non-native ants can affect nest recruitment and resource acquisition (Holway et al. 2002, Parr & Gibb 2010).

Ants may be affected by environmental requirements or filters such that certain ant species thrive only in certain environments. Differences in shade quality or temperatures, for example,

may limit ant foraging or survival, as exemplified in an experimental manipulation of both shade and leaf litter that dramatically affected the nature of competition interactions among ground-foraging species in a Costa Rican shade coffee system (Perfecto & Vandermeer 1996). Similarly, as discussed further below, availability of appropriate nesting sites is at least occasionally limiting. For example, the diversity of tree species from which hollow twigs were derived was a major determinant of the species diversity of the ants occupying them (Armbrecht et al. 2006) in the leaf litter of a shaded coffee farm in Colombia.

Although such environmental filters are well known to be important, it is nevertheless a major assumption of most ant biologists that competitive interactions among ant species frequently determine community structure (see Parr & Gibb 2010, Cerdá et al. 2013 and references therein). Extensive studies of community assembly of ants in the coffee agroecosystem reveal that both environmental filtering, which is frequently associated with nesting opportunities (Philpott & Foster 2005, Armbrecht et al. 2006), and competitive interactions are likely involved (Perfecto 1994; Perfecto & Vandermeer 1996, 2013). Here we divide that literature into two general groupings, ants that generally nest in the ground or leaf litter, broadly construed, versus ants that nest in hollow cavities, generally referred to as twig-nesting ants. The first, we suggest, are structured largely through competition for feeding resources, whereas the second are structured more through competition for nesting sites.

**Community assembly in ground-foraging generalist ants.** The general spatial patterns seen with ground-foraging ants are frequently thought to result from interspecific competition (Parr & Gibb 2010). Part of the evident spatial structure is the existence of mosaics (Leston 1978, Armbrecht et al. 2001, Davidson et al. 2003) in which patches of dominant species are arranged in space something like a jigsaw puzzle. Ground-foraging ants on coffee farms seem also to form this mosaic spatial pattern; various species form patches that are relatively discrete, with each species occupying its own space and the patches fitting together almost as if they were pieces in a jigsaw puzzle (Majer & Queiroz 1993, Perfecto 1994, Perfecto & Vandermeer 2013). Studies in coffee farms suggest that much of the spatial pattern of ground-foraging ants is indeed a consequence of the underlying structure of competitive interactions among the various species (Perfecto & Vandermeer 2013), although that structure is not simple.

**Community assembly in twig-nesting ants.** For both arboreal ants that nest in hollow trees or shrub twigs and leaf litter ants that inhabit hollow twigs on the ground, the size, number, or diversity of available twigs may be an important determinant of community structure. For arboreal ants in coffee agroforests, hollow coffee twigs and shade-tree twigs and branches comprise the vast majority of available nest sites, and there can be considerable variation in the size of twigs available. However, in the coffee plants themselves, most ants prefer to nest in similar-sized twigs (Livingston & Philpott 2010). Although one larger ant species, *Procryptocerus bylaeus*, occupied twigs with larger cavities in the field and selected larger twigs in choice experiments in the lab, nine other species examined showed no difference in the mean nest size occupied (Livingston & Philpott 2010).

Nest availability also strongly varies, and competition for nesting resources may be an extremely important determinant of community structure and contribute to community assembly processes in tropical communities. Work in coffee farms has enabled learning the importance of diversity, quality, and size of nesting resources for community assembly. Ants compete for nesting resources, and among indications of nest limitation in ants are the occupation of a large fraction of available resources, takeovers of nests by different colonies or species, and occupation of artificial nests (Philpott & Foster 2005 and references therein). Coffee agroforests that differ in shade structure,

and therefore in the overall availability of nest sites, have been used to demonstrate the importance of nest-site limitation for ants, and the fact that nest-site limitation can contribute to a loss of ant diversity (Philpott & Foster 2005). In a comparison of two different coffee farms varying in the amount of shade, nest-site limitation was stronger in farms with less shade. In addition, increasing the number of artificial nests in high-shade coffee farms resulted in a large increase in the number of species colonizing twig nests, but there were less dramatic increases in richness in low-shade sites (Philpott & Foster 2005). Thus nest limitation, but also other processes (i.e., dispersal or recruitment limitation) must be important drivers of community assembly in large, intensively managed farms. In coffee agroforests in Colombia, nest-site limitation is important for twig-nesting ants both on coffee plants and in the leaf litter. With a similar technique, Armbrrecht et al. (2006) added artificial nests to coffee plants and added artificial nests and leaf litter in forests and in three coffee systems varying in shade management to examine the bottom-up influences of resources on ant assembly. Both litter addition and twig addition increased the number of ant colonies, indicating that ant colonies in these habitats are litter- and nest-limited. The numbers of ant species colonizing resources did not increase with litter or twig addition but did increase with increasing shade in coffee farms, a similar result to that found in Mexico (Philpott & Foster 2005).

Nest diversity may also be important in determining the numbers of species that can colonize and survive in tropical environments. In Colombia, Armbrrecht et al. (2004) tested whether the diversity of nesting resources affected colonization by litter-dwelling ants. They collected branches of eight species of shade trees and drilled holes in the branches so that they would resemble natural hollow twigs found in the leaf litter. They then placed the nests in bags and added the bags to the leaf litter on the ground in either single-species bags, containing eight twigs of the same tree species, or mixed bags, containing one twig of each of eight tree species. They found that the mixed bags were colonized by a significantly greater diversity of ants but not for the reasons expected. Whereas it was expected that different species of ants would select different species of twigs, leading to an increase in ant diversity in mixed bags, they instead found that most ant species preferred the mixed bags, but not due to strong tree-species and ant-species associations. Thus, diversity in a nesting resource greatly influenced ant assembly and led to a more diverse ant community.

Ecological interactions with other species, such as dominant ants or parasites, may also contribute to the structure and maintenance of ant communities. The presence of aggressive, dominant ants may influence the foraging by arboreal ants and may also limit their abilities to colonize new areas as well as limit their access to food resources and perhaps survival once they are established. But little experimental work has documented the importance of arrival and survival processes for ant communities (Andersen 2008). Two interesting studies in coffee farms have documented the importance of aggression from canopy-dominant ants on twig-nesting ants that belong to a different nesting guild. *A. sericeasur* ants are aggressive toward many types of arthropods, including even birds. In a manipulative field experiment, Philpott (2010) added artificial nests on coffee plants with *A. sericeasur* foragers and on coffee plants without *A. sericeasur* foragers to assess their impact on nest colonization. Fewer nests (43–54% fewer) were colonized by twig-nesting ant species when *A. sericeasur* were present, and six out of ten common species occupied significantly more artificial nests placed on plants without *A. sericeasur*. Nest colonization increased with tree density (consistent with results presented above), indicating that both abiotic and biotic factors are contributing to assembly processes for this community. The presence of *A. sericeasur* can also dramatically alter the foraging behaviors of established colonies. In a clever experiment to test the influences of the *A. sericeasur*–*C. viridis* or ant-scale mutualism on foraging by *A. sericeasur* and other arboreally foraging ant species, MacDonald et al. (2013) sprayed scale insect populations near clusters of *A. sericeasur* nests with an aqueous solution of *L. lecanii*, a fungal parasite of the scale insects. The

*L. lecanii* killed significant numbers of scales and resulted in increases in the foraging of other ant species (including seven species of arboreal twig-nesting ants) proportional to the reduction in the numbers of *A. sericeasur* foraging on coffee plants. Thus *A. sericeasur* likely affects not only arrival but also survival of the twig-nesting ant colonies in coffee farms. As an aside, the same sorts of reductions in foraging by *A. sericeasur* are also experienced frequently when they are under attack by *Pseudacteon* spp. phorid flies, resulting in similar increases in resource access for twig-nesting ant species (Philpott et al. 2012). Such manipulative experiments have rarely been conducted in natural habitats, highlighting the role of coffee farms as model systems for ecological tests.

Coffee farms have also provided a natural laboratory for simultaneously testing multiple hypotheses for community assembly. Livingston & Philpott (2010) used twig-nesting ants to investigate drivers of community assembly, including nest-site preferences; environmental filters, such as nest-site abundance and disturbance by *A. sericeasur*; influences of competition among ant species; and stochastic dispersal. They examined co-occurrence patterns of 25 twig-nesting ant species and used a “core/satellite” approach to address dispersal heterogeneity among species in the community (Hanski 1982). Species were divided into four groups: (a) core species that are common at both local and regional scales, (b) regional dominants that are found globally and dominant locally, (c) local dominants that are dominant locally but not well distributed globally, and (d) satellite species that are neither dominant locally nor well distributed. According to theory, competition among core species should result in overdispersed co-occurrence patterns (Ulrich & Zalewski 2006), whereas dispersal effects should result in random or aggregated co-occurrence for satellite species. Several patterns emerged from the field analysis. First, >60% of twigs were occupied, demonstrating strong nest-site limitation. Second, most ant species inhabited similar-sized twigs, all species examined had proportionally similar responses to gradients in nest-site abundance, and *A. sericeasur* presence had little influence on richness or composition of ants occupying coffee twigs. Thus, Livingston & Philpott concluded that species sorting through environmental filters plays a minor role. Third, all ant species showed random patterns of co-occurrence with respect to each other in the absence of the “core” species, *Pseudomyrmex simplex*. But in the presence of *P. simplex*, regional dominants, local dominants, and satellite species showed aggregated patterns of co-occurrence with respect to one another. Thus, *P. simplex* likely plays an important role in “assembling” the community by providing a core metapopulation into which the other species fall. Fourth, there was evidence for priority effects, as two ant species of equal competitive rank (determined with lab trials) rarely co-occurred. Taken together, these data provide support for a competitive meta-community structure and suggest that competition for nest sites should be the dominant species interaction in this community.

In a follow up paper, Livingston et al. (2013) used an expanded data set, coupled with data on dispersing alates (winged ants), to examine evidence for species sorting (trade-offs in species performance across habitats) and mass effects (source-sink dynamics between habitats of differential quality). They used data on twig-nesting ants from natural twig nests in five microhabitat types in a shaded coffee agroecosystem (coffee twigs in high-, medium-, and low-shade environments, shade-tree twigs from medium-shade coffee, and tree twigs from a natural forest) and coupled this with data on artificial nest occupation and numbers of alates caught in light traps. They then used community similarity and a variance decomposition to partition community variance into spatial and environmental components. Twig-nesting ant communities were distinct in each of the five microhabitats, and dissimilarity among communities was largely driven by changes in relative abundance of dominant and subdominant species but also by extensive turnover in the rare species. Space and environment together predicted 24.5% of the variation in the ant community, and space and environment explained unique fractions of the variance, indicating that both species sorting and mass effects are likely important drivers in this community. Alate abundance

for a species was correlated with colony abundance of species, indicating that microhabitats are dominated by internal dispersal. Finally, ant richness in artificial nests was higher than that in natural nests in coffee; however, natural nests had higher richness than artificial nests in shade trees and in the forest. Thus, abundances of the dominant and subdominant species are predominant in community dynamics, and dispersal of rare species from the canopy or adjacent forest patches may support mass effects into coffee microhabitats. To summarize, evidence to date for this twig-nesting ant community suggests that environmental filtering at the level of the nest may not occur but that some differences in habitat may impact ant assembly. Furthermore, dispersal and competition appear to be highly important in this community.

## SPATIAL CONSTRAINTS ON INTERACTIONS

It has long been known more generally that various intrinsic biological dynamics are capable of producing spatial patterns even in a landscape that is homogeneous according to the environmental conditions (Klausmeier 1999, Vandermeer et al. 2008). The question arises, for any nonrandom spatial pattern, whether the pattern is caused by exogenous (broadly speaking, underlying habitat patchiness) or endogenous (broadly speaking, biological aspects of the organism independent of the habitat) factors. The coffee agroecosystem has served as a model system for the study of spatial ecology (Perfecto & Vandermeer 2008) regarding both the generation of spatial patterns (Philpott 2006, Vandermeer et al. 2008, Perfecto & Vandermeer 2013, Jackson et al. 2014) as well as the consequences of spatial patterns for species interactions and ecosystem services (Vandermeer & Perfecto 2006; Vandermeer et al. 2009, 2010; Jackson et al. 2012a,b; Liere et al. 2012; MacDonald et al. 2013).

### Self-Organization in *Azteca* Ants

*Azteca sericeasur* nests in trees and is common in the Mesoamerican tropics, where it is frequently encountered on casual walks in the forest. However, discerning any spatial pattern of its colonies in a tropical forest is inevitably obstructed by the heterogeneity of the habitat. In a 45-ha plot regular surveys revealed that *Azteca* colonies were distributed neither randomly nor uniformly within the plantation. Rather, they were strongly clustered (Vandermeer et al. 2008). Examining a variety of environmental factors, such as slope, identity of nesting tree, and size of nesting tree, showed that nothing external to the ant population was correlated with the clusters, suggesting that the underlying biology of the ant was potentially the source of a self-organized pattern.

The basic biology of the ant is not unusual for a species that has multiple queens and may be quite general for species that acquire most of their energy from hemipterans (Davidson et al. 2003). After a queen establishes a colony in a tree, the colony may grow to the point that new nests are established in neighboring trees, evidently one part of the mechanism whereby patchiness is generated. However, unabated new nest formation would obviously result in a continuous expansion of colonies, which means that some force must limit this expansion. Turing's concept of diffusive instability is a useful metaphor (Klausmeier 1999), with the tendency of the ants to disperse to neighboring trees equivalent to the "activator" of the system. However, there must also be some "suppressor," otherwise the ants would simply disperse (diffuse) over the whole farm. The ant has several direct and indirect natural enemies, any one of which, or any combination thereof, could form the basis for the control that must occur to prevent the ant from taking over every shade tree in the plantation. One possibility we have suggested is that the phorid flies, known to reduce ant foraging activity, act as one suppressor. The reduction of foraging activity in the presence of phorids suggests that the latter could cause an ant colony to disappear, by either dying

of starvation or being so harassed that the queen moves the nest to another site (MacDonald et al. 2013).

A simple cellular automata (CA) model based on the natural history of the system captures the essential features of the clustering patterns of this ant (Vandermeer et al. 2008, Jackson et al. 2014). Furthermore, it has frequently been suggested that this sort of dynamic should lead to a power function distribution of the sizes of the clusters (e.g., Kéfi et al. 2011). As expected, the distribution of cluster sizes in our plot does follow a power function, as do the cluster sizes predicted by the CA model (Vandermeer et al. 2008, Jackson et al. 2014). It thus may be the case that the spatial pattern of the *Azteca* ants in coffee plantations forms by the same general rules that govern the formation of the spots of the jaguar or the stripes of the tiger, as suggested by the fundamental Turing process (Goodwin 2001).

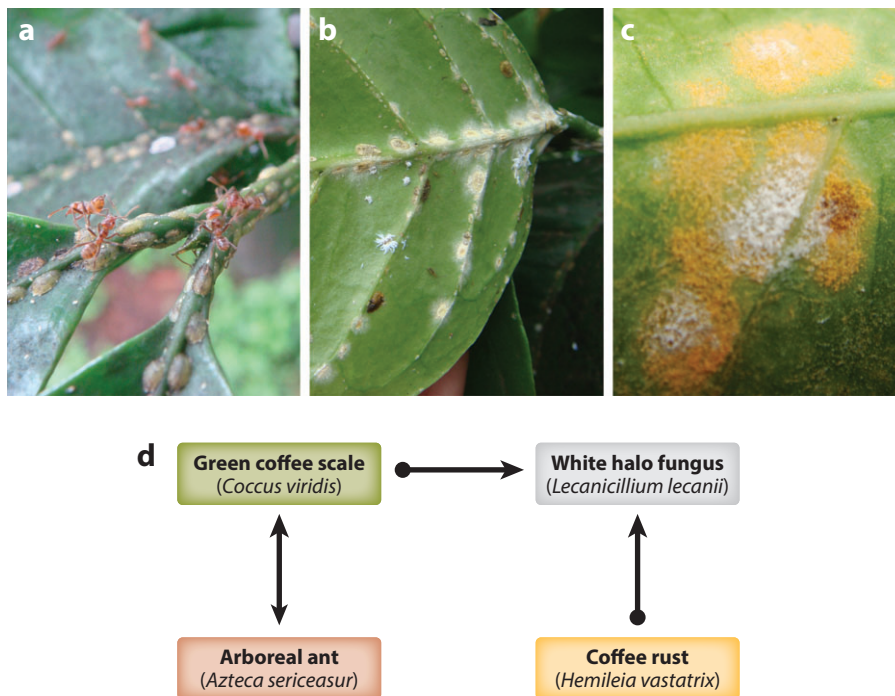
## Spatial Constraints on Other Organisms

**Ant–coccinellid beetle interaction.** As noted above, the relationship between *A. sericeasur* and the hemipteran *C. viridis* is a classic mutualism (Jha et al. 2012). While tending the scales, the ants also protect them from natural enemies, including parasitoids and at least two coccinellid predators, *Azya orbiger*a and *Diomus* sp. (A. Iverson, personal communication). It is notable that these two coccinellid beetles appear to divide the habitat spatially, with *Diomus* sp. able to feed on scales when they are separated in space from the local scale densities surrounding *A. sericeasur* nests while *A. orbiger*a concentrate on those local densities near *A. sericeasur* nests. Other ants are involved in tending the scales [especially the arboreal foraging but ground nesting *Pheidole synanthropica* (Jiménez-Soto et al. 2013), but including perhaps a dozen other species] but only on coffee plants that are not occupied by *A. sericeasur* (Perfecto & Vandermeer 2013).

As is generally the case, coccinellid predators of hemipterans tended by ants face a dilemma; though adults can fly some distance to locate the isolated hemipterans that are not tended by ants, larvae are less mobile and need local concentrations of hemipterans to survive. However, the only place those high concentrations occur is where they are tended by ants. Consequently, the larvae of the coccinellid beetles, faced with the aggressive behavior of the protective ants, have evolved protective mechanisms against the ants, as noted above. In the network contained in the coffee system, *Diomus* larvae appear to engage in chemical mimicry that renders them invisible to the ants (Vantaux et al. 2010), and *A. orbiger*a larvae are covered with waxy filaments, creating a barrier to ant attack (Liere & Perfecto 2008). This arrangement provides a spatially explicit form of biological control in that the adult beetles range widely and consume hemipterans over a large area, but the larvae require the local concentrations of hemipterans that are provided only when under protection from ant mutualists, an ecosystem service provided by a simple level of ecological complexity (Vandermeer et al. 2010, Liere et al. 2012). This also represents a spatially explicit community organization in that the ant *P. synanthropica* tends the same hemipterans, but never generates an extremely high density of the latter. The consequence is that when *A. sericeasur* searches for an alternative nesting site to escape its enemies, the residual concentrations of *C. viridis* supported by *P. synanthropica* provide them with an initial population of this key hemipteran mutualist. The alternative predator, *Diomus* sp., is spatially restricted to these less dense congregations of hemipterans but also participates in their overall control. Thus a spatially explicit organization of these interactions generates a unique community structure.

**Coffee rust spatial pattern.** As discussed in the section on trophic interactions, one of the main biological control agents of *H. vastatrix* (the disease agent that causes the coffee rust) is the white halo fungus, *L. lecanii*, which is commonly found in coffee plantations, especially associated





**Figure 5**

Pictures and diagram of the relationships among the arboreal ant, the green coffee scale, the white halo fungus, and the coffee rust. (a) The ant, *Azteca sericeasur*, tending green coffee scales in coffee; (b) green coffee scales attacked by the white halo fungus; (c) coffee rust attacked by the white halo fungus; (d) diagram showing the mutualism between the ant and the green coffee scale, the predator-prey relationship between the white halo fungus and the green coffee scale, and the predator-prey relationship between the white halo fungus and the coffee rust. The arrowheads indicate positive effects, and the closed circles indicate negative effects. Photo credits: (a,b) Ivette Perfecto and (c) John Vandermeer.

with the hemipteran *C. viridis* when tended by *Azteca* ants (Vandermeer et al. 2009; Jackson et al. 2012a, 2012b; MacDonald et al. 2013). Because of this basic natural history (**Figure 5**), an obvious expectation is that the coffee rust disease incidence should be negatively correlated with the presence of ant nests because it is only under the protection of ants that *C. viridis* reaches densities high enough to attract the epizootics of the white halo fungus. This is precisely what was found at three spatial scales. First, at a scale of 15 m, we reported a negative correlation between rust incidence and the distance to a coffee plant in which an epizootic of the white halo had killed all the hemipterans the previous year (Vandermeer et al. 2009). Second, rust incidence data from plots approximately 50 m × 50 m show a negative correlation between rust incidence and coffee plants close to *Azteca* nests, although the  $R^2$  value was low, suggesting that many other factors affect the incidence of the disease (Vandermeer et al. 2009, Jackson et al. 2012a). Finally, rust incidence data at a large scale (~45 ha) similarly show a weak negative correlation between rust incidence and *Azteca* sites (Vandermeer et al. 2009, 2014).

It is notable that discerning the effect of *L. lecanii* first was facilitated by its relationship to the ant/hemipteran mutualism and thus its expected spatial pattern owing to the association of the latter with *Azteca* ants. At least eight other fungal pathogens are known through laboratory assessments to attack the causal agent of the coffee rust disease (Carrión & Rico-Gray 2002;

Vandermeer et al. 2009, 2014), yet finding spatial correlations that would indicate effectiveness in the field is not possible because of a lack of known spatial associations with other organisms.

The essential ecological features of this disease are implicated in spatial ecology due to long-distance dispersal by wind, local dispersal by touch and splash, mycoparasites, and other potential antagonists, and the need for a droplet of water for germination (Kushalappa & Eskes 1989, Avelino et al. 2012). The essential sociopolitical features include economic and political forces that cause coffee farming to either be undertaken or abandoned in a whole region, producing yet a larger spatial component of the system (Vandermeer & Rohani 2014).

## CONCLUSION

The coffee agroecosystem constitutes a model system of diverse agroforests with a wide geographic distribution throughout the tropics. It is especially important because coffee exists in some of the most important biodiversity hot spots in the world (Perfecto et al. 1996, Moguel & Toledo 1999). Almost like experimental replicates, the coffee agroecosystem exists with a similar vegetative backbone around the globe, making it almost like an experiment in ecology. And the various ecological complexities reviewed herein support the basic idea that the coffee agroecosystem is something of a model system, enabling the study of basic ecological questions. Our coverage has been limited to four particular themes: (a) trophic interactions, (b) trait-mediated indirect interactions, (c) competition and community assembly, and (d) spatial constraints on ecological interactions and their consequences. There is an enormous collection of ecological issues beyond these four themes awaiting detailed empirical and theoretical study. The coffee agroecosystem is, we believe, a potential model ecosystem for the study of population, community, and systems ecology, providing a somewhat more experimental framework than similar natural vegetation types.

## DISCLOSURE STATEMENT

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