Ecological Complexity and Pest Control in Organic Coffee Production: Uncovering an Autonomous Ecosystem Service

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Many traditional farmers and environmentalists subscribe to the popular idea that the natural world offers ecosystem services that contribute to the stability, productivity, and sustainability of agriculture. Opponents of this view argue that the farm is not an environment to be stewarded by romantic environmentalists, but rather is a battlefield on which the enemies of production must be vanquished. Contemporary research in ecosystem complexity offers a new platform on which to adjudicate between these two points of view. Through particular network structuring, nonlinearity, and stochasticity, and especially with the added dimension of space, recent theoretical and empirical research reveals that ecological systems persist and generate ecosystem services as a result of complex interacting components. Here we report on our research into the ecological dynamics of a collection of species related to key problems in pest control, a critical ecosystem service in coffee production.

Keywords: ecosystem service, agroecosystem, coffee, complexity

Proponents of sustainable agriculture frequently find solace in a vision of the natural world as inherently harmonious and balanced. From traditional farmers in the tropics to organic farmers in Michigan, producers have a near-universal and evident sense that the natural world offers ecosystem services that contribute to the stability, productivity, and sustainability of their farms. Frequently, this view is regarded as scientifically baseless, hopelessly romantic, and naive; some even argue that it is dangerous because it stands in the way of the technological progress that has provided the world with abundant food for the past 60 years. The farm, some argue, is not an environment to be stewarded by romantic environmentalists, but rather a battlefield on which the enemy, frequently a pest insect or plant pathogen, must be vanquished with the appropriate armaments (mostly pesticides; Russell 2001). This magic-bullet approach to problems that emerge in agriculture has become the sine qua non of industrial agriculture. Those who disagree are often portrayed as "intellectual farmers" who don't really care whether farmers prosper or the people of the world have enough to eat (Evans et al. 2002). They often come across as naive environmentalists who fail to appreciate the possible devastation of pest problems and the consequent need for industrial services to combat these enemies (Collier 2008). Nevertheless, the belief that nature can provide the same services by way of its own balancing act persists (Altieri 1995, Vandermeer 2010), frequently felt in the heart more than known in the head. Indeed, this is a thriving and growing notion among proponents of organic and ecological farming.

Somewhat isolated from the practicalities of pest control, recent research on the theory of ecosystem complexity offers a new platform on which to judge whether this view of nature's beneficence is nothing more than romantic claptrap, or if it indeed has a scientific basis. Networks of ecological interactions are often able to generate a sort of ecological homeostasis even when their microdynamics suggest nothing more than unpredictability and chaos, both formal and metaphorical. Through particular network structuring, nonlinearity, and stochasticity, and especially with the added dimension of space, a great deal of theoretical and empirical research is uncovering a picture of ecological systems that persist as a result of complex, interacting components effectively acting as indirect governors of seemingly inherent instabilities. As we increasingly uncover more of these structures, ecosystems begin resembling the proverbial harmonious provider of ecosystem services, in contrast with the Newtonian machine-in-equilibrium view

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that had been so popular in the early days of the Industrial Revolution. This new view sees the ecosystem not as precisely balanced on the classical engineer's equilibrium point, but more like a spiderweb, achieving structure and resilience from its multiple interconnections. The new scientific ecological view begins to look something like the "harmonious and balanced" view held by the proponents of sustainable agriculture.

One area of research into the ecological dynamics of particular species associated with key pest problems is in the production of coffee. In complex organic coffee systems, intricate interactions among many species result in the dynamic regulation of several potential pest species. The idea of autonomous (or endogenous) pest control as an ecosystem service comes from 10 years of research on a 300-hectare organic farm in the Soconusco region of Chiapas, southern Mexico. This system involves at least 13 components (insects and fungi), six ecological processes (competition, predation, parasitism, hyperparasitism, disease, mutualism), many subtle yet important nonlinearities, and a key role for spatial dynamics. We conclude that the ecological network effectively generates the ecosystem service of buffering coffee production systems against extreme outbreaks of pests and diseases. The complete operation of this system is neither obvious nor straightforward, but rather involves several complicated, dynamic connections that lead to sometimes-surprising system behavior. Nevertheless, the system seems to act in a way that promotes the regulation of several key potential pests in an autonomous, or endogenous, fashion. It might therefore be concluded that in this particular case, the idea of nature's balance should not be demonized as simply romantic claptrap, but rather should be seen as having a solid scientific basis, even if detecting it is not always easy.

The pest problems (four species)

The history of one of the coffee pests is an infamous horror story (McCook 2006). In the early 1800s, Sri Lanka (previously called Ceylon) was occupied by various European powers that, as part of classic colonial strategy, needed to establish a local revenue-generating scheme. Coffee was an obvious cash-crop choice, and it became the gold of the land. The Dutch, and later the British, entered the coffee business in a big way and rapidly implemented an economic model totally dependent on this export commodity. Then, in the middle of the 19th century, disaster struck in the form of a rust disease (figure 1) that appeared to have come out of nowhere (the disease is now thought to have originated in Africa, the original home of coffee). The classic coffee rust *Hemileia vastatrix* was so devastating that after only a few years, coffee production had to be completely abandoned across the entire island. That is why today one hears of Ceylon tea, and not Sri Lankan coffee.

Figure 1. Coffee leaves infested with the coffee rust disease, **Hemileia vastatrix.** *Photograph: John Vandermeer.*

The next part of the rust tale is especially interesting. After the disease's devastating effects in Sri Lanka (and later in Java and Sumatra, too), the rush to bring coffee to the Americas in the late 19th century was accompanied by extreme caution to prevent the transport of the rust disease along with it (Fulton 1984). Despite such care, the disease appeared in Brazil in 1970. Shortly thereafter the rust arrived in Central America and the Caribbean, spawning much concern over its potential devastation. Various dubious phytosanitary methods—including reducing shade cover and planting resistant varieties of coffee—were encouraged throughout the region. The worries ultimately were largely unfounded: Although the rust became (and remains) a nuisance even on remote coffee farms, it did not become the disaster that was feared. Given its very real potential to cause disaster (e.g., in Ceylon, southern India, Sumatra, and Java), the persistence but nondevastation of the coffee rust in Central America warrants explanation (Avelino et al. 2004).

The second coffee pest is a far more recent introduction to the mix. The coffee berry borer (*Hypothenemus hampei*) is a small beetle that burrows into coffee berries (figure 2) and that has caused major damage in all coffee-growing regions of the world (Damon 2000). Because of its direct damage to the coffee seed, the borer's impact is immediate, obvious, and severe. Nevertheless, it is not "devastating," as was the coffee rust in Ceylon. What keeps this pest from wreaking the devastation it clearly has the potential to cause?

The third pest is perhaps best described as "pesky" rather than an actual menace. The green coffee scale (*Coccus viridis*) is similar to the familiar scales that plague houseplants (and is sometimes the same species; figure 3). This pest is well known on a wide range of hosts, including coffee and citrus (Bess 1958). On the farm where we conduct most of our work, it is regarded as a nuisance, but not really a pest. Elsewhere it occasionally gains significant pest status (Young 1982).

The fourth pest is a leaf-mining moth (*Leucoptera coffeella*), a species growing in its pest status on the farm (figure 4). This moth is commonly associated with certain

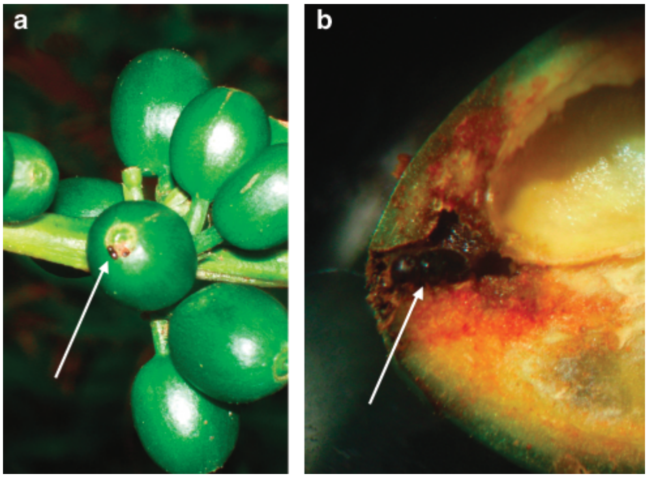

Figure 2. The coffee berry borer, **Hypothenemus hampei.** *(a) A beetle beginning the process of burrowing into the coffee fruit. (b) An individual beetle inside of a cut-away fruit showing the beginning of the fruit rot caused by the borer. Photographs: John Vandermeer.*

Figure 3. The green coffee scale, **Coccus viridis.** *Adults with crawlers (small white individuals) and nymphs. Photograph: John Vandermeer.*

management options; for example, the reduction or elimination of shade trees (Lomeli-Flores et al. 2009). It is also very likely a secondary (or resurging) pest resulting from the use of pesticides (Fragoso et al. 2002). This species too has not yet been devastating, despite the clear potential for it to be so.

All four pest cases have the capacity to repeat the devastation of the rust in Ceylon in the 19th century, yet, at least so far, that has not happened. Something about the ecology of the coffee ecosystem prevents each of these four potential pests from causing ruinous effects. Our research over the past decade leads us to the hypothesis that there is a complex web of ecological interactions that acts as a partial control—an ecosystem service that might be described as "autonomous" or "endogenous" pest management.

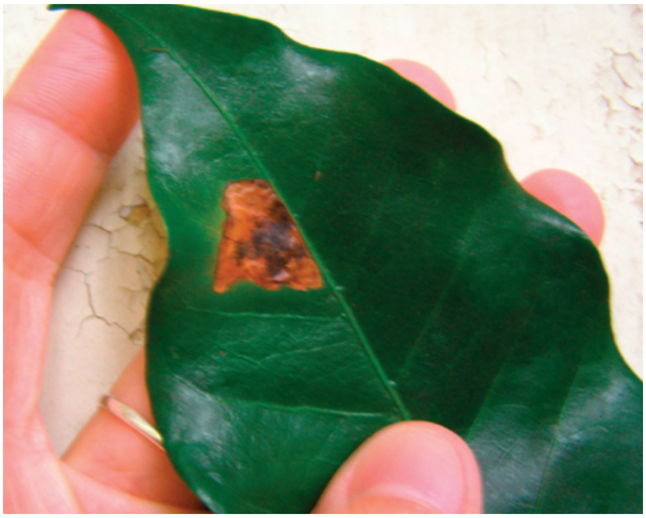

Figure 4. Damage done by the coffee leaf miner, **Leucoptera coffeella.** *Photograph: Stacy Philpott.*

Figure 5. **Azteca instabilis,** *the keystone species of the network. Photograph: Alex Wild.*

The spatial dynamics

The *Azteca* ant (*Azteca instabilis*; figure 5) is well known to neotropical naturalists as the swarming, biting ant that is a close relative to the various species of *Azteca* that occupy the famous *Cecropia* tree, providing the latter protection from herbivores and vines. The *Azteca* ant, unlike its *Cecropia*-associated cousins, is not terribly fussy about what sort of tree it nests in, requiring only the smallest of cavities and sometimes constructing external carton extensions for its growing colonies. Taking a bird's-eye view of the coffee farm these ant nests are not randomly distributed over the farm but occur in distinct clusters (figure 6b). Because the shade trees in which these nests are located are more-or-less uniformly distributed, we have argued that the formation of these clusters is a consequence of biological interactions involving the ants themselves and some other biological forces (Vandermeer et al. 2008). Since we propose that biological interactions cause pattern formation, we include this

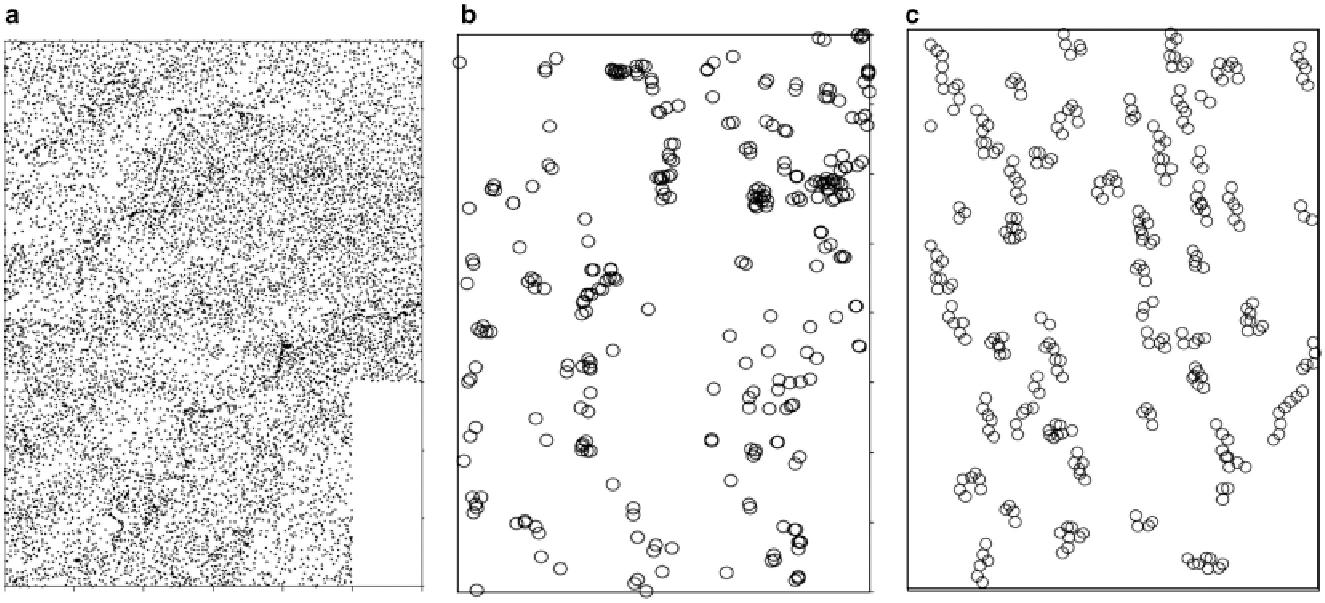

Figure 6. Distribution of (a) the 11,000 shade trees and (b) positions of the ant nests in a 45-hectare plot. Note that in (b), a 20-meter circle has been drawn around each tree with a nest, the presumed area of foraging influence for each nest, and the area chosen to decide cluster membership. (c) An artificial distribution of nests (or areas of foraging influence) that would not follow a power law, but would have a central tendency (the mean cluster size is about 8).

pattern within the general idea of self-organization in the sense that no outside force causes the spatial pattern—it is caused by the biological interactions themselves.

The existence of a self-organized pattern is strongly supported by the distribution of the sizes of the ant clusters. In particular, rather than having a central tendency (figure 6c), the distribution of cluster sizes closely follows a power function, which is normally taken as evidence of self-organization (Pascual and Guichard 2005). Given the nest clustering (figure 6b) and the evidence that the clustering is self-organized (i.e., follows a power function), it makes sense to ask which biological interactions cause this clustering. A variety of theoretical studies have shown that a spatially specific force that causes local expansion of a population, coupled with some sort of negative density dependence, leads to spatial clusters of the individuals in the population (Pascual et al. 2002). This dynamic outcome reflects the original insights of Turing (1952), who showed in a chemical reaction how an activator and repressor, diffusing at different rates, could form rigid structures in an otherwise homogeneous medium. Various ecological models have shown similar phenomena (Alonso et al. 2002, Pascual et al. 2002). For example, to model the system of nest cluster formation (figure 6b), we constructed a cellular automata model in which an abstract space was viewed as a homogeneous checkerboard of cells, each of which could be occupied according to simple rules. First, each cell that did not have a nest at one point in time would receive a nest based on the occupancy of the eight surrounding cells (reflecting the reality that this species is known to increase nest numbers through the budding of individual nests). Second, each cell that did have a nest would have that nest disappear based on the same occupancy of nearby cells (reflecting the reality that several potential antagonists are related to the ant nests in a density-dependent fashion). In other words, we constructed an abstraction that mimicked the local expansion of nests, plus some force that caused the disappearance of nests on the basis of their local abundance. This model usually resulted in a spatial distribution in which clusters of nests followed a power function (Vandermeer et al. 2008).

The model reflects the reality that the ant is polygynous and regularly forms new nests by "budding," wherein one of the queens takes some brood with her and moves to a nearby tree, forming a nest there. This is evidently the "expansion" part of the self-organization of the system. However, if this were the only force in the system, the ant would eventually occupy all of the shade trees, which it clearly does not (of 11,000 trees, only about 300 are occupied by an ant nest). Some sort of negative force (similar to Turing's repressor) must therefore be involved. One of the key negative forces affecting this ant species is a parasitic fly in the family Phoridae (in the genus *Pseudacteon;* hereafter referred to as the "phorid fly"), a small fly that attacks worker ants by laying an egg on their bodies. When the egg hatches, the developing larva migrates to the head, where it grows by eating the contents of the ant's head. Just before pupation, the fly causes the remainder of the ant's head to fall off (thus the nickname "decapitating fly"), and the pupa, from which the new adult fly emerges, develops inside the ant's empty head capsule. From intensive surveys we have established that this fly attacks the ants in a nest density–dependent fashion (Vandermeer et al. 2008, Philpott et al. 2009). That is, nests located within a high-density cluster are more likely to be attacked by this parasitoid than nests located in lower-density clusters. This is precisely the sort of force that is expected in the basic self-organizing process we described earlier: The ant expands its nest by budding the nest in a single tree and sending out queens and broods to other trees nearby, but when a group of trees all have ant nests, it attracts the phorid fly parasitoid. The result is that the high-density clusters of nests are preferentially attacked and consequently disappear—the ants either die or move on to other trees.

These spatial dynamics lead to a specific spatial pattern, as noted earlier—one that seems to be a requirement for a major natural enemy of one of the pests in the system, the green coffee scale. The lady beetle, *Azya orbigera* (figure 7a, 7b), is a major predator of this pest and we judge it to be the main reason that the coffee scale is not normally at pest levels in the system. Adult beetles fly throughout the coffee farm and are able to detect either the odor of the scale insects or the odor of the chemicals coffee plants emit when they are attacked by the scale. Under predation of the beetle, the green coffee scale never reaches pest status. Paradoxically, the beetle remains common enough in the plantation to keep the scale insect in check, even though the beetle larvae are severely attacked by parasitic wasps. The rate of parasitism on the beetle larvae is so high that one might conclude that this beetle population simply cannot survive on the farm, but it does, and it controls one of the potential pests.

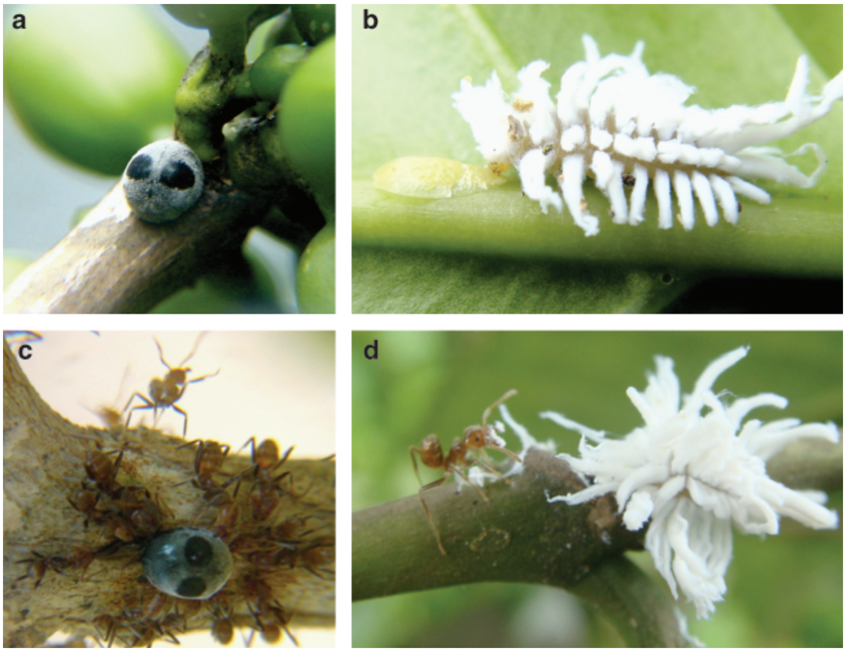

*Figure 7. The lady beetle predator (*Azya **orbigera***) of the green coffee scale. (a) adult, (b) larva eating a scale insect, (c) adult beetle being attacked by* **Azteca** *ants, (d)* **Azteca** *ant with mandibles filled with the waxy filaments of the beetle larvae. Photographs: Shinsuke Uno (a and c), Ivette Perfecto (b and d).*

Recall that the spatial pattern is characterized by clusters of ant nests (figure 6b). These ants are mutualistically associated with the green coffee scale, which is the beetle's major prey. In the form of a classical ant-hemipteran mutualism, *Azteca* offers the scale insects protection from their natural enemies in exchange for the honeydew the scales produce. Thus, what we might expect, and indeed what we invariably see, is a high concentration of scale insects in the areas where the ant nest clusters occur. Beetle larvae produce waxy protuberances on the surfaces of their bodies (figure 7b) such that they look like little puffballs on the surface of a leaf. When an ant attempts to attack a beetle larva, its mandibles become gummed up by the waxy protuberances, and the ant is thus unable to divert the beetle larva's voracious appetite (figure 7d).

Bear in mind that part of the mutualistic advantage the ants give to the scale insects results from the ants' behavior—they run around and scare away the parasitic wasps. Ironically, as the ants are scaring away the wasps that are trying to attack scale insects, they inadvertently scare away the wasps that are trying to attack the beetle larvae. Thus the ants protect the beetle larvae from their main natural enemies, an unintended consequence of ants' efforts to scare off any flying insect they see (Liere and Perfecto 2008).

As a result, beetle adults are not able to survive very well within the clusters of ant nests (the ants harass them, preventing them from eating [figure 7c]), and beetle larvae are not able to survive very well outside of the clusters of ant nests (they are regularly attacked by parasites). The existence of clusters of ant nests in a matrix of nest-free areas permits the beetle population to survive—the adults eating scales (and thus controlling them) as they fly around the whole plantation, but laying their eggs preferentially where there are concentrations of scale insects, which, of course, is where the ant nest clusters are, such that the ants protect their larvae from the parasites and provide them with plenty of scale insects. The ant occupies only about 3% of the shade trees on the farm, but provides the service of supporting the natural enemy of the green coffee scale over the entire farm.

Spatial dynamics reconsidered

The clusters of ant nests undoubtedly create the conditions necessary for the beetle to persist. However, the clusters' initial origin is not completely certain. The underlying spatial dynamics include the tendency of ants to occasionally expand their nests to occupy nearby trees coupled with some density-dependent negative effect—a negative effect seemingly caused by the phorid parasite. But there are other forces that could also have a negative impact on the ants. In particular, any natural enemy of the scale insects, which are mutualists with the ants, would provide a potential repressive mechanism that indirectly affects the ants (i.e., by reducing the survivorship of the ant's mutualists). One such force is a disease of the scale insects caused by the fungus *Lecanicillium lecanii*, popularly known as the white halo fungus disease (figure 8). This disease seems to occur sporadically throughout the farm, yet becomes epizootic (i.e., epidemic) only when the scale insects are locally very abundant. However, the scale insects reach such a level of abundance only when they are under the protection of the ants. Therefore, the white halo fungus disease could very well act in the same way that we propose the phorid fly acts, albeit in a more indirect way, through the scale insects (Jackson et al. 2009).

We emphasize that the effect of the fungus on the ant is indirect (the fungus negatively affects scales, which themselves positively affect ants; therefore, the fungus has an indirect, negative effect on the ants). But if we argue that the indirect effect of the fungus could be responsible for the repressive action that creates the self-organization of ant cluster sizes, we must equally consider other natural enemies of the scales—most importantly, the beetles. Clearly, the beetles could be acting the same way as the fungus from the point of view of spatial organization (they are predators on the food of the ants). There is irony here in that the beetle population derives its stability from the spatial distribution of the ants. Could it be that the beetle population is responsible for the spatial pattern that is necessary for its own survival? We have approached this question using a simple population model involving beetle larvae, beetle adults, scale insects, and ants. If the beetle's vital rates (mortality, birth rates, etc.) are set such that the ant completely takes over the plantation (in the computer model), the beetle itself goes extinct (since the adult beetles cannot find enough food). On the other hand, if the vital rates are arranged such that the ant goes extinct, the beetle also goes extinct (since the larval beetles cannot find enough food). But if those vital rates are set such that the beetle causes the ant to form clusters, the beetle population persists and keeps the scale insect under control. Thus, a population (the beetle) creates dynamic conditions that cause a completely different population (the ants) to become distributed in clusters in space, and those clusters are essential for the survival of that population. The beetle creates the conditions for its own survival!

Figure 8. The white halo fungus disease, caused by the fungus* Lecanicillium lecanii*, attacking the green coffee scale. Photograph: John Vandermeer.

As fascinating as this arrangement is, a feature of the beetle's biology leaves us with a bit of a conundrum. Larval beetles must be located among patrolling ants, but adults cannot survive for longer than a couple of minutes among those ants. So how do the beetles manage to deposit their eggs among the patrolling ants? Furthermore, ants rapidly prey upon the exposed beetle eggs; because of ant predation, female beetles must oviposit carefully, and frequently place eggs beneath the scale insects, or sometimes in old, waxy residues of previous pupae (of their own species). But ovipositing females require some time to locate good sites, which is simply not possible where the ants are foraging so aggressively. How is this resolved?

To answer this question, we must return to some fundamental features of the biology of the fly parasite that attacks the ant, the phorid. As in so many other cases in nature, this parasitoid uses chemical clues to locate its ant host (Mathis et al. 2010). In this case, phorids are attracted to the ants' alarm pheromones. The phorid, however, is unable to locate individual ants by odor alone. Overwhelmed by the high concentration of pheromone spread over a large group of ants, the phorid cannot pinpoint its particular target of oviposition unless it can see that particular target move (Mathis et al. 2010). That is, the phorids use the pheromone cue to locate the general vicinity of ant activity, but then use visual cues to locate individual ants to parasitize. The ants counter this behavior in two ways. When a phorid is sensed in the vicinity, foraging ants either (a) scurry back to their nest; or (b) assume a sort of catatonic state, with their heads reared backward and front legs raised into the air. Indeed, if a phorid gets too close to one of these "catatonic" individuals, it risks itself becoming the prey, as the ant quickly attacks any phorid that gets within a couple of millimeters of its outstretched front legs. Thus there is a continuous "dance" in which the ants exit the nest and use alarm pheromones to attract more individuals to help tend the scale insects—consequently attracting phorids—but then retreat or go catatonic when the phorids arrive.

It is clear that the ants not only detect the presence of phorids (and then take their defensive action) but also communicate with one another (in the same foraging area): When a phorid is present, it is not just the ant under attack that goes catatonic, but many of the ants surrounding her. Such behavior indicates that ants are using another communicative pheromone, distinct from the general alarm pheromone, to warn one another of the presence of the phorids—the "phorid pheromone." In a way

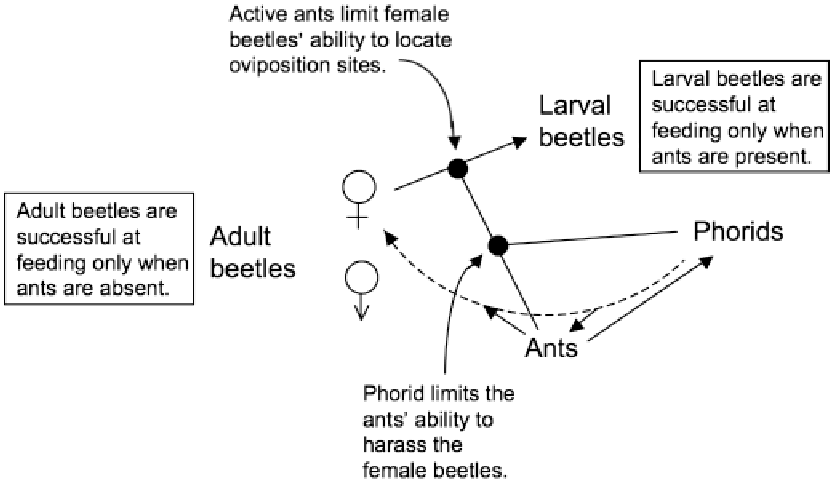

Figure 9. Subweb illustrating the complex nonlinear interactions between the beetles, the ants, and the phorids. Arrowheads indicate positive effects, solid circles indicate negative effects. The negative effects attached to lines rather than variables indicate an "effect on an effect," or what is called a trait-mediated indirect effect (e.g., the ants negatively affect the beetles' ability to locate oviposition sites). Note the "cascade" of trait-mediated indirect effects, in which the phorids affect the ants' ability to affect the beetles' ability to find oviposition sites. Dotted line illustrates the indirect effect of phorids in causing the ants to release a pheromone to which the female beetles are attracted.

not previously noted in the ecological literature, the beetle becomes involved in this dance. Recall that the female beetle must get her eggs into an area that is protected by ants, but the ants do not permit her enough time to locate proper oviposition sites. Remarkably, the female beetles (but not the males) are attracted to the phorid pheromone produced by the ants. That is, female beetles apparently take advantage of the pheromone produced by the ants in response to phorid attacks to find places within the protectorate of the ants but where the ants have been temporarily disabled (Perfecto et al. 1996). In this way the beetle is able to get its larvae into an area where it will both benefit from the protection of the ants and have a ready source of its main food, the green coffee scale. This rather complex set of nonlinear interactions is illustrated in figure 9.

The question, then, of whether it is the phorid or the beetle that causes the nest cluster formation in the ants may be poorly formulated in the end. The ultimate cause may be the complex interaction of beetle and fly (figure 9). It is worth noting that this arrangement (figure 9) involves what has been referred to as a cascade of indirect effects (Liere and Larson 2010), what is formally a complex nonlinear connection in the ecological network. That is, the rate at which the female beetle lays eggs is lowered by the actions of the ant, but the rate at which the ant lowers that rate is itself lowered by the presence of the phorids (see figure 9). This sort of double, or cascading, indirect effect is probably very common in ecological networks, although the general theoretical consequences of such an effect are largely unexplored in the literature.

The coffee rust disease

The coffee rust disease has had a major impact on the history of both the coffee industry and imperialism itself: Coffee was the major crop in Ceylon, Java, and Sumatra during colonial times; thus, it supported the empires of both Holland and Britain. The disease caused the entire industry to collapse, with reverberations worldwide, given the importance of coffee in world trade even then (it is far more important today). That collapse and its dramatic consequences were caused by the pathogenic fungus *H. vastatrix*, the coffee rust. With such a history it is not surprising that the fungus remains a contemporary concern for coffee producers and countries that produce coffee.

From our perspective, the interesting ecological question is why this disease, so devastating in the past in Asia, has not been so in the Americas. There is now substantial evidence to link at least part of the control of this disease to the complex web of interactions surrounding the *Azteca* ant. And that link, surprisingly, arises from the disease that attacks scale insects.

The white halo fungus disease that attacks scale insects, caused by the fungus *L. lecanii*, is well known to be an antagonist of coffee rust (figure 10). Evidence now points to a spatially explicit antagonism between coffee rust and white halo fungus. Spores from *L. lecanii* are residual in the soil where the disease has been epizootic; that is, in areas of trees occupied by *Azteca*. From these loci, the spores disperse

Figure 10. The white halo fungus, **Lecanicillium lecanii,** *attacking the cause of the coffee rust disease,* **Hemileia vastatrix.** *Photograph: John Vandermeer.*

locally to attack the coffee rust (Vandermeer et al. 2009). However, these local concentrations of *L. lecanii* spores are associated with their epizootic attack on the green coffee scale, which happens only when the scale is locally abundant, which in turn happens only when the scale is under protection by ants (mainly the *Azteca* ant).

Waiting for *Azteca*

The process of cluster pattern formation, described above, consists of two general forces: Individual ant nests have a tendency to expand from a tree to neighboring trees in response to some pressure, thought to be the phorid-beetle combination or the white halo fungus, or perhaps some combination of all of the negative density-dependent forces. As this negative pressure builds, a given ant nest is under pressure to "split," whereby one or more of the queens in the nest (recall that *Azteca* ants have multiple queens) will leave the nest to form a new nest in a neighboring tree. For establishment, a new nest needs first an adequate tree to nest in, and second, a food source, which is mainly the green coffee scale. However, when not under the protection of the *Azteca* ants, the green coffee scale is driven to very low local population densities by its own natural enemies, especially the lady beetle. Consequently, the general population density of green coffee scales is normally very low, and it is rather difficult to even find scales on coffee bushes unless the *Azteca* ants are present. Yet, when the *Azteca* ants seek a new tree for a new nest, they need to find not only a suitable tree in which to build the nest but also they must find a local concentration of scale insects for food. If such local concentrations are not around, the *Azteca* ants would have to wait until a single scale insect was dispersed into a close-by coffee bush and built up a significant population. This could take a prohibitively long period of time.

The solution to this problem comes from some of the other ants in the system. There are at least five other ant species that tend the scale insects. But these other ants are unable to protect the scale insects as efficiently as the *Azteca* ants. For example, we have encountered coffee bushes with more than 3000 scale insects when *Azteca* ants are present, but we find only 50 to 100 scale insects when they are under protection of one of the other species. (Where scale insects are not under the protection of any ants at all, it is difficult to find even a single individual.) One of the most important of these "other" species is a member of the genus *Pheidole*, which we have not yet been able to identify. Its local field name is *Pheidole* ctp (a Spanish acronym), and it nests in the ground but forages vigorously on coffee bushes, frequently tending the scale insects, although not nearly as efficiently as *Azteca* ants. The presence of *Pheidole* ctp thus acts as a kind of indirect mutualist for the *Azteca* ants over the long term, in that it creates small localities of relatively dense coffee scales that the *Azteca* ants can later use when they are in the process of finding a new nest site.

Given the potential importance of *Pheidole* ctp in the pattern-formation process, it is useful to consider its effects on other elements of the system. In particular, because it has the ability to forage both on the ground and in the trees, it seems to be at an advantage when in competition with other arboreal foragers; when *Pheidole* ctp is foraging on a coffee bush, only rarely are any of the other arboreal foragers found. In particular, there is a suite of about 5 to 10 species of arboreal ants that nest in hollow twigs and are affected by both *Pheidole* ctp and *Azteca* ants. These twig nesters seemingly are able to persist mainly in bushes that are not dominated by either *Pheidole* ctp or *Azteca* ants, although the negative effect of the *Azteca* ants is far greater than that of *Pheidole* ctp.

More important, *Pheidole* ctp is not able to withstand the competitive pressure of another ground-nesting ant, a small species with a high nest density, *Pheidole protensa*. It is unknown what tips the balance in favor of which species of *Pheidole*, but *P. protensa* is virtually incapable of foraging arboreally, and is unable to provide the local scale abundance that *Azteca* ants need for their own nest expansion. So, where *P. protensa* dominates on the ground, *Pheidole* ctp is unavailable to tend the scales, therefore indirectly linking the ground-foraging ant community with the nest-cluster pattern formation of the *Azteca* ants. The precise importance of this particular function is difficult to evaluate completely, but given the well-known concept that very small ecological interactions can have very large ecological consequences (e.g., McCann et al. 1998, Vandermeer and Pascual 2006), this component of the system could be important, and is currently under study.

Ants as predators

The subtle connections of various species in the network extend to yet another guild that turns out to be an important element in the ecosystem service of pest control. Arboreal-foraging ants, the most evident example of which is *Pheidole* ctp, as noted above, seem to exert competitive pressure on another group of ants: those that nest in hollow twigs. One of the predominant species of this latter guild is *Pseudomyrmex simplex*, although about 10 other species have similar habits. *Pseudomyrmex simplex* is a small ant and predator, feeding on small insects, including the green coffee scale. Usually, when *Pheidole* ctp is foraging on a coffee bush, *P. simplex* and the other twig nesters are rare as foragers, presumably because of competitive pressure from *Pheidole* ctp and similar ants (we refer to this group of ants as the ctp group). Species of the ctp group tend to dominate large areas (e.g., a circle of radius 15 meters).

So the overall ant story can be tentatively summarized as (a) the *Azteca* ants are extremely dominant where they occur, driving several general pest-control processes, as discussed earlier, but they occur only in about 3% to 5% of the farm; (b) the ground-nesting, arboreal-foraging ants (the ctp group) tend sucking insects, especially the green coffee scale, and prey upon whatever small arthropods they come across; (c) the ground-nesting, ground-foraging ants (the *P. protensa* group, of which *P. protensa* itself is overwhelmingly dominant) strongly compete for nest sites and generally engage in a process of scramble and contest competition with one another and with the ctp group; and (d) the arboreal-nesting (mainly in hollow twigs), arboreal-foraging ants (the *Pseudomyrmex* group) compete for both nest sites and food with one another and for food resources with the ctp group.

Given these complex interactions among more than 80 species of ants, there are many specific complexities involved, but the basic function of the network that is implicated in the ecosystem service of pest control can be tentatively summarized as follows: (a) *Azteca* ants create a "no-ant zone" in which other ants are not capable of surviving, at least for long; (b) the ctp group nests on the ground but forages in coffee bushes, creating competitive pressure against (c) the arboreal nesting ants. At the same time, the (d) ground-nesting, ground-foraging ants create competitive pressure for the ctp group. All of this is illustrated in figure 11.

This relatively complicated guild structure of approximately 80 species of ants is important for four reasons. First, as indicated previously, the ctp group effectively maintains a residual population of scale insects that the *Azteca* ants seemingly need to move their nests. As we have already described, nest moving is a key element in the spatial structure formation, which, in turn, is important for maintenance of at least two key natural enemies in the system (the lady beetles and the white halo fungus). Second, the ants in the *Pseudomyrmex* group are known predators of the leaf miner (de la Mora et al. 2008)—the *Azteca* ants, however, seem not to be as efficient, although they are generalist predators (Vandermeer et al. 2002) and do indeed prey on the leaf miner at least occasionally (Lomeli-Flores 2009). Third, the *Azteca* ants (Perfecto and Vandermeer 2006) and the ants in the *Pseudomyrmex* group (Larsen and Philpott 2010) are predators of the coffee berry borer. Fourth, the ants in the *P. protensa* group may be important predators of the berry borers in old seeds that fall to the ground and provide refuge for the berry borers during times when berries are not available (Armbrecht and Perfecto 2003). This fourth predatory function is inferred on the basis of evidence from Colombia, but we have no reason to believe that it does not also happen in Mexico.

Conclusions

We summarize this entire interaction network in figure 12. Two elements stand out: First, the network is suggestive of a "small-world" structure with strong clustering and short paths, albeit much of the connectivity of the major cluster is in the nature of higher-order nonlinear effects, reflecting the importance of the *Azteca* ant as a keystone species, mainly through the higher-order effects. Second, the integrity of the web is at least partly a result of the spatial structure

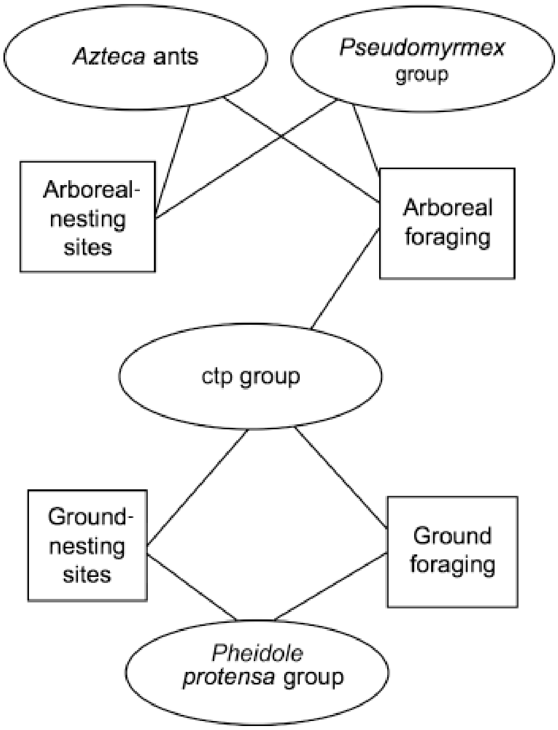

Figure 11. Hypothesized relationships among the four major guilds of ants in the system.

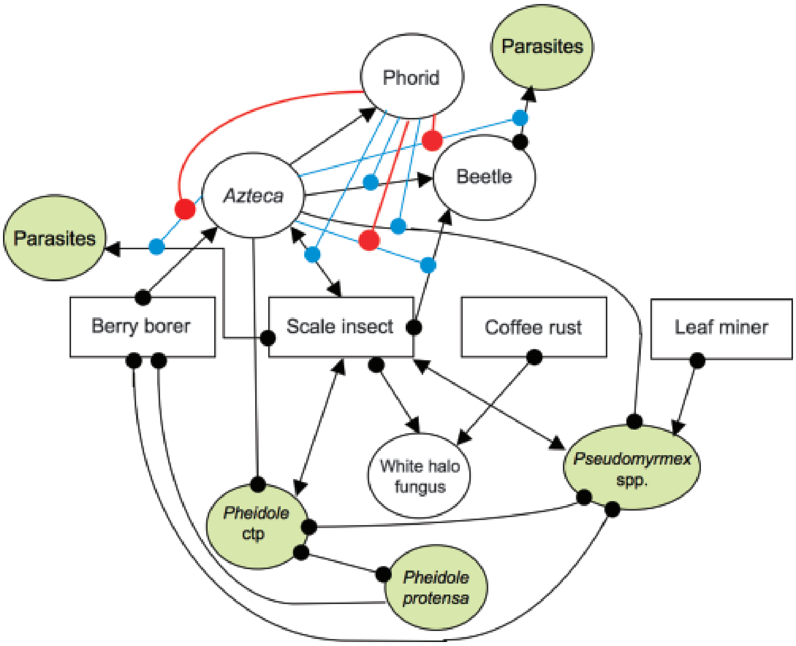

Figure 12. Simplified version of the interaction network that results in autonomous pest control. The four pests are shown in rectangles and the elements involved in their control in ovals (shaded ovals indicate a species group rather than a single species). Negative effects are shown with a small circle at the end of the connector and positive effects with an arrowhead. Indirect effects are shown as small circles (negative effect) affecting a different connector (an effect on an effect). Indirect effects of order one are indicated in blue. Indirect effects of order two are indicated in red.

of the system, which itself appears to be an example of self-organization—the tendency of the *Azteca* ants to, on one hand, move their nests in a density-dependent fashion, and on the other hand, to have their nests attacked by some negative force also in a density-dependent fashion.

The existence of such an ecosystem service emanating from ecological complexity is especially critical in this particular agroecosystem, not only because coffee is so important in international trade and supports millions of small farmers worldwide but also because its shaded nature has been intensively studied as a component in creating high-quality matrices in fragmented habitats for the purpose of biodiversity conservation (Perfecto et al. 1996, Philpott et al. 2008). It is now well documented that a variety of taxa find refuge in shaded coffee farms, sometimes at diversity levels approaching local natural habitats. Demonstrating the ecosystem service function of this biodiversity adds to our understanding of the importance of this type of ecosystem.

The farm on which most of this work was accomplished is an organic farm that has been in production for almost 100 years (more complete descriptions can be found in Vandermeer et al. 2008 and Philpott et al. 2009). The organisms involved in the interaction web are well known to be associated with coffee, but their points of origin are not always known. The rust disease almost certainly comes from Africa, the lady beetle is known throughout the neotropics, the white halo fungus is common throughout the tropics, and most of the ants appear to be native to southern Mexico. Although almost all the work reported in this article was done on this farm, our view is that interaction webs of this sort will prove common in agroecosystems in general, repeating a theme that is certainly not unusual in the field of ecology. Yet we are unsure of how the specifics will work out at many different levels. For example, we know that all of the components of our basic system exist in coffee plantations in the Antilles, with the exception of the *Azteca* ant. Since we argue that this species is keystone in the system, the question naturally arises, What happens to the system when *Azteca* is removed? We hope further research will find the answer to this question.

In the end, this model system suggests that the vision of the natural world as harmonious and balanced is wrong if we naively accept an unreconstructed Newtonian world view of balance—ecosystems are not like a marble coming to rest at the bottom of an inverted cone. However, through the spatially explicit complexity of myriad interactions, many of which are multiply nonlinear, a higher notion of balance emerges—not the balance of Newton, but rather the balance of a shifting sand dune whose detailed structure changes minute to minute, but whose fundamental nature as a "sand dune" is never in doubt. Our understanding becomes not the crude, positivist logic that must identify a singular enemy to conquer, and a magic bullet with which to do so, but rather the holistic vision of a new kind of "balance" emerging from the very complexity that traditional farmers intuitively understood from the beginning.

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References cited

Alonso D, Bartumeus F, Catalan J. 2002. Mutual interference between predators can give rise to Turing spatial patterns. Ecology 83: 28–34.

Altieri MA. 1995. Agroecology: The Science of Sustainable Agriculture. Westview.

Armbrecht I, Perfecto I. 2003. Litter ant's diversity and predation potential in two Mexican coffee matrices and forest fragments. Agriculture, Ecosystems and Environment 97: 107–115.

Avelino J, Willocquet L, Savary S. 2004. Effects of crop management patterns on coffee rust epidemics. Plant Pathology 53: 541–547.

Bess HA. 1958. The green scale *Coccus viridis* (green) (Homoptera: Coccidae) and ants. Proceedings of the Hawaiian Entomological Society 16: 349.

Collier P. 2008. The politics of hunger: How illusion and greed fan the food crisis. Foreign Affairs 87: 67–79.

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.

De la Mora A, Livingston G, Philpott SM. 2008. Arboreal ant abundance and leaf miner damage in coffee agroecosystems in Mexico. Biotropica 40: 742–746.

Evans N, Morris C, Winter M. 2002. Conceptualizing agriculture: A critique of post-productivism as the new orthodoxy. Progress in Human Geography 26: 313–332.

Fragoso DB, Guedes RNC, Picanco MC, Zambolim L. 2002. Insecticide use and organophosphate resistance in the coffee leaf miner *Leucoptera coffeella* (Lepidoptera: Lyonetiidae). Bulletin of Entomological Research 92: 203–212.

Fulton RH, ed. 1984. Coffee Rust in the Americas. American Phytopathology Society.

Jackson D, Vandermeer J, Perfecto I. 2009. Spatial and temporal dynamics of a fungal pathogen promote pattern formation in a tropical agroecosystem. Open Ecology Journal 2: 62–73.

Larsen A, Philpott SM. 2010. Twig-nesting ants: The hidden predators of the coffee berry borer in Chiapas, Mexico. Biotropica 42: 342–347.

Liere H, Larsen A. 2010. Cascading trait-mediation: Disruption of a trait-mediated mutualism by parasite-induced behavioral modification. Oikos. doi:10.1111/j.1600-0706.2010.17985.x

Liere H, Perfecto I. 2008. Cheating on a mutualism: Indirect benefits of ant attendance to a coccidophagous coccinellid. Ecological Entomology 37: 143–149.

Lomeli-Flores JR, Barrera JF, Bernal JS. 2009. Impact of natural enemies on coffee leafminer *Leucoptera coffeella* (Lepidoptera: Lyonetiidae) population dynamics in Chiapas, Mexico. Biological Control 51: 51–60.

Mathis K, Philpott SM, Moreira RF. 2010. Parasite lost: Chemical and visual cues used by *Pseudacteon* in search of *Azteca instabilis*. Journal of Insect Behavior. Forthcoming.

McCann K, Hastings A, Huxel GR. 1998. Weak trophic interactions and the balance of nature. Nature 395: 794–798.

McCook S. 2006. Global rust belt: *Hemileia vastatrix* and the ecological integration of world coffee production since 1850. Journal of Global History 1: 177–195.

Pascual M, Guichard F. 2005. Criticality and disturbance in spatial ecological systems. Trends in Ecology and Evolution 20: 88–95.

Pascual M, Manojit R, Guichard F, Flierl G. 2002. Cluster size distributions: Signatures of self-organization in spatial ecologies. Philosophical Transactions of the Royal Society B 357: 657–666.

Perfecto I, Vandermeer J. 2006. The effect of an ant-hemipteran mutualism on the management of the coffee berry borer (*Hypothenemus hampei*) in southern Mexico. Agriculture Ecosystems and Envronment 117: 218–221.

Perfecto I, Rice RA, Greenberg R, van der Voort ME. 1996. Shade coffee: A disappearing refuge for biodiversity. BioScience 46: 598–608.

Philpott SM, et al. 2008. Biodiversity loss in Latin American coffee landscapes: Review of the evidence on ants, birds, and trees. Conservation Biology 22: 1093–1105.

Philpott SM, Perfecto I, Vandermeer J, Uno S. 2009. Spatial scale and density dependence in a host parasitoid system: An arboreal ant, *Azteca instabilis*, and its *Pseudacteon* phorid parasitoid. Environmental Entomology 38: 790–796.

Russell E. 2001. War and Nature: Fighting Humans and Insects with Chemicals from World War I to *Silent Spring*. Cambridge University Press.

Turing AM. 1952. The chemical basis of morphogenesis. Philosophical Transactions of the Royal Society B 237: 37–72.

Vandermeer J. 2010. The Ecology of Agroecosystems. Jones and Bartlett.

Vandermeer J, Pascual M. 2006. Competitive coexistence through intermediate polyphagy. Ecological Complexity 3: 37–43.

Vandermeer J, Perfecto I, Ibarra Nuñez G, Phillpott S, Garcia Ballinas A. 2002. Ants (*Azteca* sp.) as potential biological control agents in shade coffee production in Chiapas, Mexico. Agroforestry Systems 56: 271–276.

Vandermeer J, Perfecto I, Philpott SM. 2008. Clusters of ant colonies and robust criticality in a tropical agroecosystem. Nature 451: 457–459.

Vandermeer J, Perfecto I, Liere H. 2009. Evidence for hyperparasitism of coffee rust (*Hemileia vastatrix*) by the entomogenous fungus, *Lecanicillium lecanii* through a complex ecological web. Plant Pathology 58: 636–641.

Young GR. 1982. Recent work on biological control in Papua New Guinea and some suggestions for the future. Tropical Pest Management 28: 107–114.

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