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The Community Ecology of Herbivore Regulation in an Agroecosystem: Lessons from Complex Systems

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*Whether an ecological community is controlled from above or below remains a popular framework that continues generating interesting research questions and takes on especially important meaning in agroecosystems. We describe the regulation from above of three coffee herbivores, a leaf herbivore (the green coffee scale, *Coccus viridis*), a seed predator (the coffee berry borer, *Hypothenemus hampei*), and a plant pathogen (the coffee rust disease, caused by *Hemelia vastatrix*) by various natural enemies, emphasizing the remarkable complexity involved. We emphasize the intersection of this classical question of ecology with the burgeoning field of complex systems, including references to chaos, critical transitions, hysteresis, basin or boundary collision, and spatial self-organization, all aimed at the applied question of pest control in the coffee agroecosystem.*

Keywords: agroecosystems, ecology, complex systems

Research summaries frequently require a historical backdrop. A quick history of ecology might begin with the idea that Tansley's post-WWI botanical surveys ushered in the modern science of ecology, although its basic vision was articulated half a century earlier by Haeckel, in what was a simple statement recognizable even today in its modern manifestation (Haeckel 1866, Staufer 1957, Tansley 1920, Tilley 2011). The application of mathematics to the field was pioneered by the threesome of Lotka, Volterra, and Gause, in the 1920s (Haydon and Lloyd 1999) and the conceptualization of an ecosystem as a hierarchical energy transfer system by Lindeman in 1942, arguably the foundation on which the Odum brothers successfully launched what we call ecosystems ecology today (Odum 1956, 1959). The famous Hairston and colleagues (1960) paper, perhaps marking the birth of modern community ecology, generated a popular framework that continues generating interesting research questions, all formulated around the central idea that terrestrial communities are regulated by the predators eating the herbivores. Finally, Richard Levins's lifelong commitment to viewing both ecological communities and ecosystems as complex systems presaged the current popularity

of combining recent developments in the field of complex systems with the persistent search for basic framings in community ecology (Levins 1998, Vandermeer and Perfecto 2017). This is the historical skeleton on which the current essay is built, framed within the Hairston and colleagues (1960) hypothesis in the context of Levins's insistence on a complex systems approach.

The most enduring question of Hairston and colleagues (1960) remains popular today, indeed takes on new meaning in the context of modern complex systems. Is a community controlled from above or below, from predators or from competition among herbivores for plant resources (Hunter and Price 1992, Power 1992)? Certainly ecologists have not been credulous to the point of oversimplifying either predator-prey relationships or interspecific competition; however, the simple question "Is control from above or below?" seems a persistent underlying framework for many research programs. The agroecosystem, by its very nature, refuses to entertain this question, at least in its classical form. If the objects of attention (the crops) are overused by the herbivores (which are consequently called *pests*), it is not a system that is regarded as one we should allow to persist (Ong and

Vandermeer 2015). Rather, if the system is to persist at all, the herbivores must be regulated from above. Indeed the standard practical agronomic question “How can we control the pests?” if translated into its true ecological meaning would be “How can we cause the system to switch from control from below to control from above?”

Control from below has come to mean much more than seems to have been the intent of Hairston and colleagues (1960), especially in light of what we now understand about plant chemistry and its relationship to herbivory (Hunter and Price 1992, Hunter 2016). Nonetheless, in this article, we focus on what we think was the initial intent: Either herbivores overconsume their food source and are therefore “controlled,” or herbivores are consumed by their predators and are therefore “controlled.” Given this general notion that control must be from above, we are freed from the standard question (above or below?) and can begin exploring the nature of that control. Although advocates for a more ecologically rational agriculture (including ourselves) persistently argue that the science of ecology should underlie the science of agriculture, we argue that the science itself is in a state of rapid evolution, especially with regard to acknowledging the important contextualization of complex systems. In the present article, we summarize much of the work we have done in the past 20 years, using the coffee agroecosystem as a model system, particularly focusing on the issue of pest control, which is to say control of the herbivore guild from above. Almost 10 years ago, we summarized what we then understood about this system (Vandermeer et al. 2010), wherein we emphasized the importance of ecological complexity in the pursuit of efficient pest regulation. The current work is an update on this research program. Our emphasis then and now is on the irreducibility of the complexities involved in the species assemblage that forms the “above,” perhaps reflecting the ideas of Robert Rosen: A complex system cannot be reduced to a collection of simple ones (Lane 2018, Vandermeer and Perfecto 2018). We describe the regulation of three coffee herbivores, a leaf herbivore, a seed predator, and a plant pathogen, by various players from above, emphasizing the remarkable complexity involved. The intersection of ecology with the burgeoning field of complex systems is evident, and this classical question of ecology is anointed with a well-deserved appreciation of irreducible complexity.

The ecosystem engendering this control from above is a panoply of natural enemies, which is to say the predators and pathogens of the “pests.” They form three distinctly recognizable control-from-above subnetworks, all of which are representable by hypergraphs (Golubski et al. 2016), all of which involve important spatial dynamics, and each of which involves some additional aspect of contemporary theory in the field of complex systems. We treat each of the networks in turn, focusing on the green coffee scale (*Coccus viridis*), the coffee berry borer (*Hypothenemus hampei*), and the agent of the coffee leaf rust disease (*Hemelia vastatrix*).

As has been reported in numerous venues (Pendergrast 2010), coffee is an unusually important agricultural

commodity. First, it is lauded in popular culture for its drug-based constituents and therefore occupies a special position in international commerce. Second, its role in creating the high-quality matrix that is necessary for biodiversity-friendly landscapes is undeniable (Perfecto and Vandermeer 2015), given proper management. However, not all production styles are equivalent. Although sometimes categorized dichotomously into shade versus sun coffee, there is, in fact, a range of management styles, most of which include some kind of shade trees as part of the system (Moguel and Toledo 1999). Third, it is well worth remembering the importance of trees in agriculture as part of the global agenda of containing the runaway climate change era we currently live in (Nair et al. 2010), especially relevant for shade coffee. Fourth, it is the basis of livelihood for millions of small-scale farmers the world over (Méndez et al. 2011) and important economically for many poor nations.

For the present article, however, the idea of ecosystem services is the normative background of our narrative, especially as regards the important service of pest regulation, or ecologically speaking, controlling herbivores from above. There are three herbivores that need to be regulated, which is to say for which a system of control from above is sought. A key feature of this control is a species of ant, *Azteca sericeasur*, that nests in the shade trees and is either directly or indirectly involved in the regulation of the three coffee herbivores. We begin with an essential feature of the system, the spatial distribution of that species of ant.

The Turing process and the spatial distribution of the ant *Azteca sericeasur*

The ant is oddly nonrandom in its spatial distribution: When you find a nest (almost always in a shade tree), you frequently find another nest nearby, but large sections of shaded farms have no nests at all. Quantitative sampling verifies this simple observable fact (Vandermeer et al. 2008, Jackson et al. 2014, Li et al. 2016), an important feature of the regulation of all three of the herbivores. The question first arises as to where this pattern comes from. There is now substantial evidence that the spatial pattern of the ants is self-organized, which is to say that it emerges from the internal dynamics of the ant population itself, not from any underlying forces such as moisture or temperature or particular vegetation formations (Vandermeer et al. 2008, Liere et al. 2014, Li et al. 2016). The pattern is formed in a complicated fashion by a process similar to that described by Alan Turing in 1952. Turing was interested in chemicals, especially morphogens (proteins involved in the creation of patterns during biological development). In chemistry, a reaction is frequently assumed to be stabilized by the balance between an activation process and a repression process. However, a completely different form of chemical process occurs in a spatially constrained space, the process called *diffusion*. Inject a drop of black ink into a beaker of water, and the instability of the drop isolated from the water gradually turns into a beaker of grey—very stable indeed. It would be

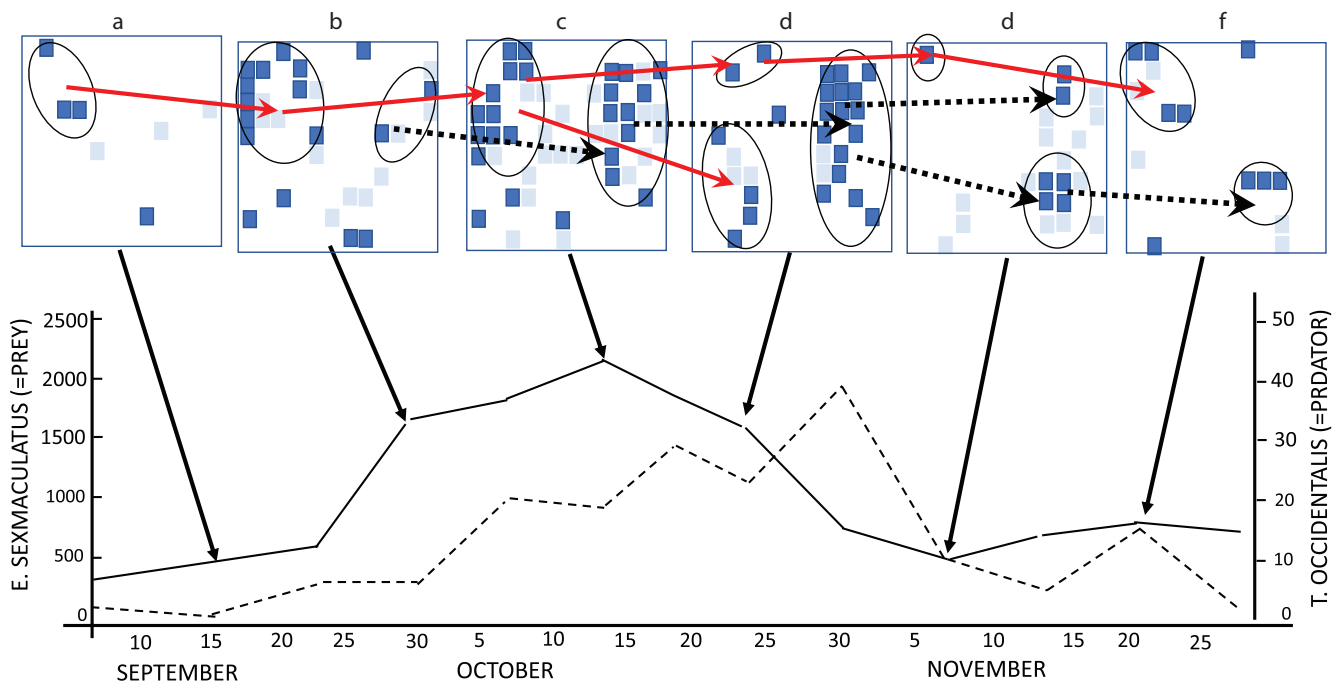


Figure 1. One of three cycles reported by Huffaker in his classic study. The spatial patterns of the densities of the prey on the 10×12 array of oranges are illustrated above the graph, with darker shaded squares corresponding to large local populations, lightly shaded squares to lower populations, and empty squares to zero mites. Note how the formation and dissolution of clusters can easily be imagined in this classic study, reflecting the dynamic patterns expected from a Turing mechanism. We added the oval outlines to emphasize our qualitative interpretation.

natural to think that these two stabilizing processes, activation or repression and diffusion, when combined, would also be stable. What Turing demonstrated was that if the repression force diffused at a rate greater than the activation force, a nonrandom pattern of some sort would develop. The basic idea is that the activating chemical starts the reaction at a specific point in the space but begins its diffusion away from that point immediately. The repressive chemical is eventually produced by the reaction and cancels the effect of the activator, but, because it diffuses at a rate that is greater than that of the activating chemical, it eventually occupies a space where the activator had not yet arrived, therefore canceling the effect of the activator at that point. The results could be spots (e.g., the spots on a leopard's coat) or stripes (e.g., the stripes on a tiger's coat) or some other more complicated form, but the point is simply the qualitative one that a nonrandom pattern would spontaneously develop when these two stabilizing forces were combined. The two stabilizing forces, reaction (activation or repression) and diffusion, combine to form an instability; the whole system is therefore referred to as *diffusive instability* or sometimes *Turing instability*.

Something very similar happens in ecological systems. Evident at a qualitative level but also explored several times mathematically (Alonso et al. 2002), a predator-prey system distributed in space is such a system. The prey as activator and the predator as repressor is the reaction, and the

migration or dispersal of predator and prey is the diffusion. However, an important difference between the ecological and chemical metaphor is that, in the predator-prey situation, it is frequently the case that, at a very local level, the predator and prey form an unstable relationship (perhaps usually), whereas adding diffusion to the mix may result in stabilizing the system. The classic experiments of Huffaker (1958) illustrated this point many years ago (although the insights of Turing were apparently unknown to Huffaker), with two species of mites, one a forager on the surface of oranges, the other a predator on that forager. Huffaker devised a spatial system in which a part of the surface of an orange provided a substrate for the two mites, and the oranges could be arranged in an array to represent a spatial matrix. As frequently cited in ecology textbooks, when predator and prey were isolated on a single orange, the predator would inevitably overeat, first driving the prey locally extinct (on a single orange) and then dying of starvation. In contrast, if a spatial pattern of a number of oranges was presented to the mites, with the possibility of dispersal from one orange to another, a seeming stabilization of the predator-prey system over the whole space occurred.

Although the take-home message of Huffaker's experiment is that environmental heterogeneity can stabilize an inherently unstable system, what is less frequently discussed is Huffaker's observations of the resulting spatial distribution of the mites. In figure 1, we display one cycle

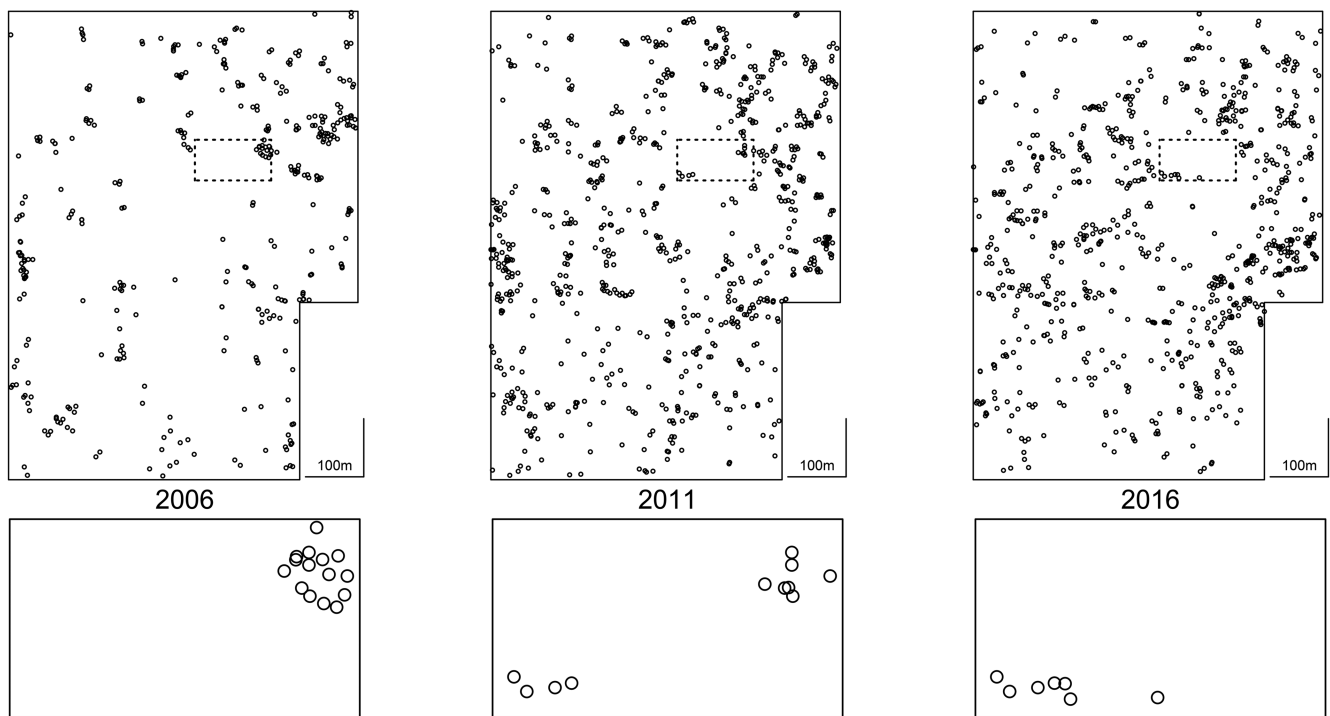


Figure 2. Distribution of shade trees containing nests of *Azteca sericeasur* over a 10-year period. Each circle is a single shade tree containing a nest. There are approximately 7,000–11,000 total shade trees in the plot (depending on the year), but only the ones containing an *Azteca* nest are plotted. The rectangles outlined with dashed lines in the upper graphs are magnified below to illustrate the dynamic nature of the system. In 2006, in this small—approximately 1.5-hectare—subgraph, there is a single cluster of 15 nests in the upper right-hand corner. In 2011, that cluster had dissipated into a less dense cluster of seven nests, and a new cluster of four nests had appeared in the lower left-hand corner. In 2016, the upper right-hand corner cluster has disappeared entirely, and the lower left cluster had expanded to include seven nests.

of the three-cycle predator–prey system he observed in the spatially distributed system, along with the spatial pattern of the foraging mites. Note the emergence and disappearance of clusters. In the spatial pattern in figure 1a, one can visualize (we have added oval outlines to aid in visualizing our interpretation) that a single cluster seems to be forming. Figure 1b shows that initial cluster growing and the possible formation of a second cluster. In figure 1c, the two clusters have grown considerably. In figure 1d, the largest cluster seems to have split into two smaller clusters, whereas the other cluster seems to have expanded slightly. In figure e, the two smaller clusters that came from the first cluster seem to be disappearing and the second cluster seems to have split in two. In figure f, two of the clusters remain. Although this interpretation of Huffaker’s data is qualitative (and certainly questionable), it serves to illustrate the basic process of cluster dynamics that is expected from a spatial system emerging from the Turing mechanism (Ong et al. 2018). It is furthermore worth noting that, in the present example, as well as in Turing dynamics in general, the spatial pattern occurs even though the physical space in which the processes occur is uniform or, at least, distinct from the patterns formed.

In the coffee agroecosystem, we have argued (Vandermeer et al. 2008, Li et al. 2016) that the *Azteca* nest pattern is

formed in a similar fashion. The repression agent is thought to be a parasitic fly, *Pseudacteon* spp., in the family Phoridae (Philpott et al. 2009). The fly oviposits on the back of the ant’s head, and its larva penetrates the head capsule, there developing to the point that the head of the ant falls off of the body (hence the name “decapitating fly”) and a new fly emerges to mate and repeat the cycle. As a local population of ant nests builds up from single (or a few) queens taking a part of the colony to a new shade tree (the activator), spatial clusters are formed. As the clusters become larger, they are targets for the phorid flies, either because the flies are attracted from far away or they build up local populations within the area of the nest cluster. Either way, the flies act as the repressor in the system. The result is a patchy distribution of ants. In figure 2, we show the nest distribution for 3 of the 12 years of the study and enlarge one section (about 1.5 hectares) of the data to illustrate how clusters form and dissipate over time. We note that the general qualitative dynamics of the formation and dissolution of patches, such as the Huffaker mite example above, resonates quite well with the basic expectations of the Turing process. We further note that the dynamic details associated with the cluster scalings that we discussed earlier (Vandermeer et al. 2008) seem to repeat themselves in subsequent years,

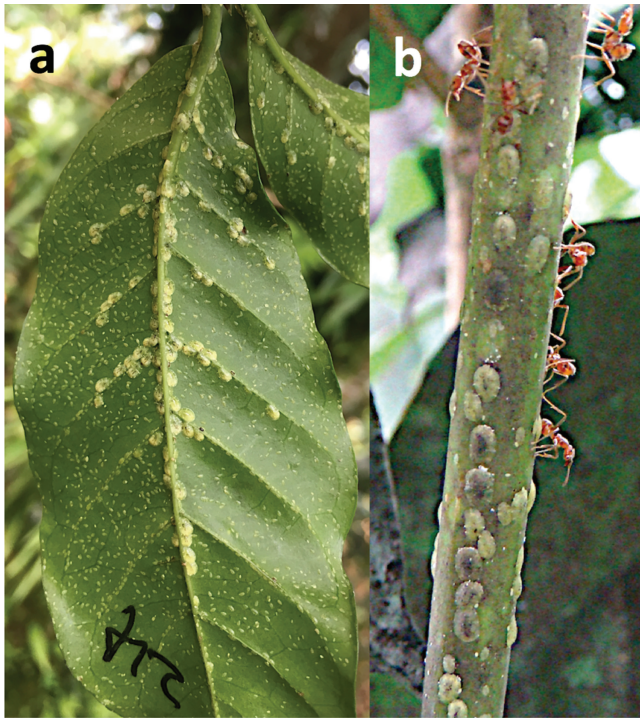


Figure 3. The green coffee scale, *Coccus viridis*. (a) Note adults concentrated on the main vein of the leaf and first instar larvae, crawlers, some of which have already begun feeding along a secondary vein, others of which have yet to settle down and may be blown away by wind, the main form of dispersal of the species. (b) Ants, *Azteca sericeasur*, tending the scale insects on a coffee branch. Photographs: Ivette Perfecto.

following a special pattern of self-organization (Pascual and Guichard 2005).

The consequences of this clustered distribution of ant nests are diverse and complicated, as will be evident from our subsequent narrative, but can be summarized with a reversion to earlier observations about environmental heterogeneity. Tansley and Chipp noted in 1926:

“It is really the whole of the living organisms together, plus the inorganic factors working on them, which make up... a ‘system.’ But such a ‘system’ considered fundamentally... must include the ‘inorganic’ factors of the habitat and these obviously cannot be considered as ‘members’ of the community, and if we take the inorganic factors as external, why not biotic factors such as grazing animals?”

These and other early ecologists certainly recognized patchiness in the environmental scaffolding on which ecological communities sit. Historically, it is likely the case that the massive vegetative surveys that energized the development of ecology in the early twentieth century tacitly assumed that ubiquitous edaphic and climatologically

produced patches determined regular combinations of plant species. These physical patches clearly made intelligible many particulars of plant distributions, and to the present day, there is a tendency to ask what the underlying edaphic factors are that prejudice one species as opposed to another or one species complex over another. However, the prescient observations of Tansley and Chipp (1926) bring to the table the possibility that the biological interactions themselves create the heterogeneity, what we have referred to as a *pilot pattern* (Vandermeer and Jackson 2018), similar to the important idea of *niche construction* (Odling-Smee et al. 1996, Vandermeer 2008) but with a key interspecific and spatial element: Species group X creates the spatially explicit conditions for species group Y to exist.

This framing is convenient for the present summary. The clustered distribution of the *Azteca* ants indeed does provide an essential environmental heterogeneity on which the other systems operate. However, we add to this narrative the idea that the species group providing the pilot pattern must operate in a distinct time frame from the other systems operative within it, a restriction that seems to be relevant at least for the systems we report in the present article. The pilot pattern formed by the *Azteca*–phorid complex must be experienced by the rest of the relevant organisms as parallel to the old idea of edaphic or climatological factors—relatively permanent compared with the dynamical changes of the systems living within the pattern (Vandermeer and Jackson 2018).

The green coffee scale: Critical transition and hysteresis

As is frequently noted, the green coffee scale insect is a persistent but relatively benign coffee herbivore, only rarely reaching important pest status, although with clear potential to do so (figure 3). A casual walk on a coffee farm reveals what appears to be a regulating factor. Searching coffee bushes, one finds scale insects here and there and, importantly, a small species of beetle that is evidently feasting on them (Liere and Larsen 2010, Liere and Perfecto 2014, Liere et al. 2014, Ong and Vandermeer 2014). The predatory beetle is *Azya orbiger*, in the family Coccinellidae. Without a doubt, this observation can easily lead to the conclusion that the relatively rare scale insect is kept under control by the relatively common coccinellid beetle. But a closer look reveals a dramatic variability: Some bushes are very heavily laden with the scale insects, and some have none at all.

There is another classical ecological notion that emerges in this system. Surrounding the tree in which an *Azteca* nest is located is a region containing coffee plants that are routinely patrolled by the *Azteca* ants that were described above. The ants harvest the sweet secretions the scale insects produce and, in turn, scare away or kill the natural enemies seeking to attack the scales (figure 3b), a well-known mutualism (Vandermeer and Perfecto 2006, Rivera-Salinas et al. 2018). Because the coffee bushes located near the shade trees that contain *Azteca* nests are where the scale insect is at least

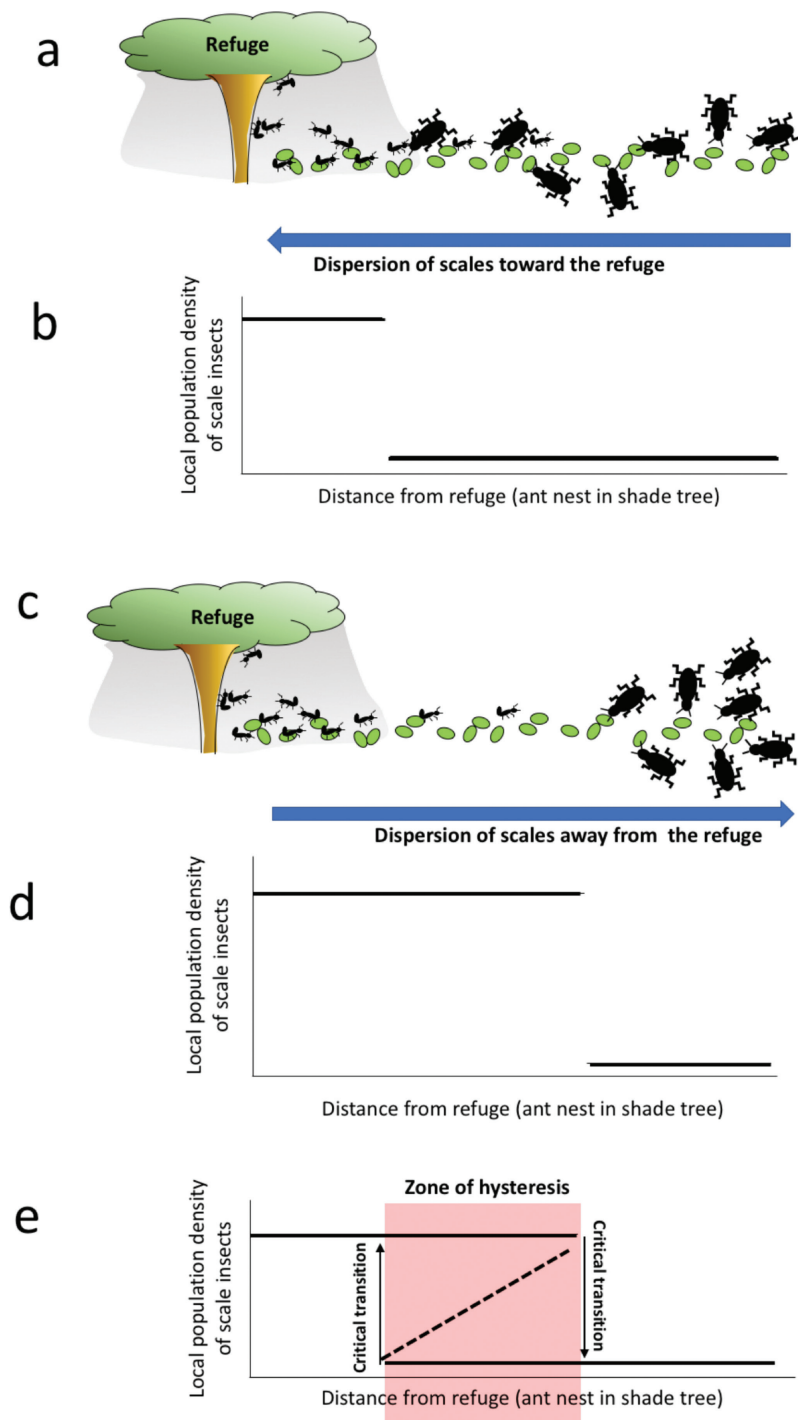


Figure 4. Theoretical pattern expected from the combination of Azteca ants creating a refuge for the scale insects and the adult predatory beetle (*Azya orbiger*) responding spatially. (a) When dispersing from far from the refuge toward the refuge, the local presence of the beetle “follows” the scales to very near to the edge of the refuge. (b) The population density as a function of the distance to the nest expected from the story in panel (a). (c) When dispersing from within the refuge to far away from the refuge, it is unlikely that any beetle predators will “follow” the dispersal route, resulting in (d) the population density as a function of the distance to the nest expected from this alternative story. (e) Combining the two expected population patterns results in a graph illustrating the phenomenon of hysteresis.

partially protected from the predatory beetle and various parasitoids, this area represents a refuge for the scale insect. It is therefore tempting to conclude that the ant itself is an indirect herbivore on the coffee (by protecting the scales, which are herbivores, the basic idea of the friend of my enemy is my enemy). Although such is the case at a very local level (e.g., the level of an individual coffee bush), because of the complexities induced by the beetle predator, such is not the case at a larger scale. The ants effectively provide an area of high food availability for the beetle. Furthermore, the ants protecting the scale insects also, inadvertently, protect the beetle larvae from its own parasitoids, providing an effective refuge for the beetle as well (Liere and Perfecto 2014). Predator-prey systems that contain a refuge are well studied in theoretical ecology (Murdoch 1969, Abrams and Walters 1996), usually with an emphasis on their stabilizing properties.

Expanding our view to a larger spatial scale, we deduce an evident contradiction from easily observable patterns. The scale insects are inevitably eaten by the predatory beetle (there are other predators—Iverson et al. 2018, Uno 2007—but, by far, the most common is *A. orbiger*) unless they are protected by the ants. However, the ants cannot provide protection if they have not yet created a foraging pattern at the site where the scales are located. Therefore, the scale insect is unable to form a successful population unless under protection from the ants but is unable to attract the ant protection unless it builds up at least a small population. This pattern is well known in ecology as an Allee effect: An organism cannot form a successful population unless a critical number of individuals first become established, a mechanism generally understood to frequently be involved with the idea of critical transitions.

In figure 4, we illustrate the system with a cartoon diagram approximately summarizing a simple population model (details can be found in Vandermeer and Perfecto 2019). On one hand, as the dispersion of scales moves from a

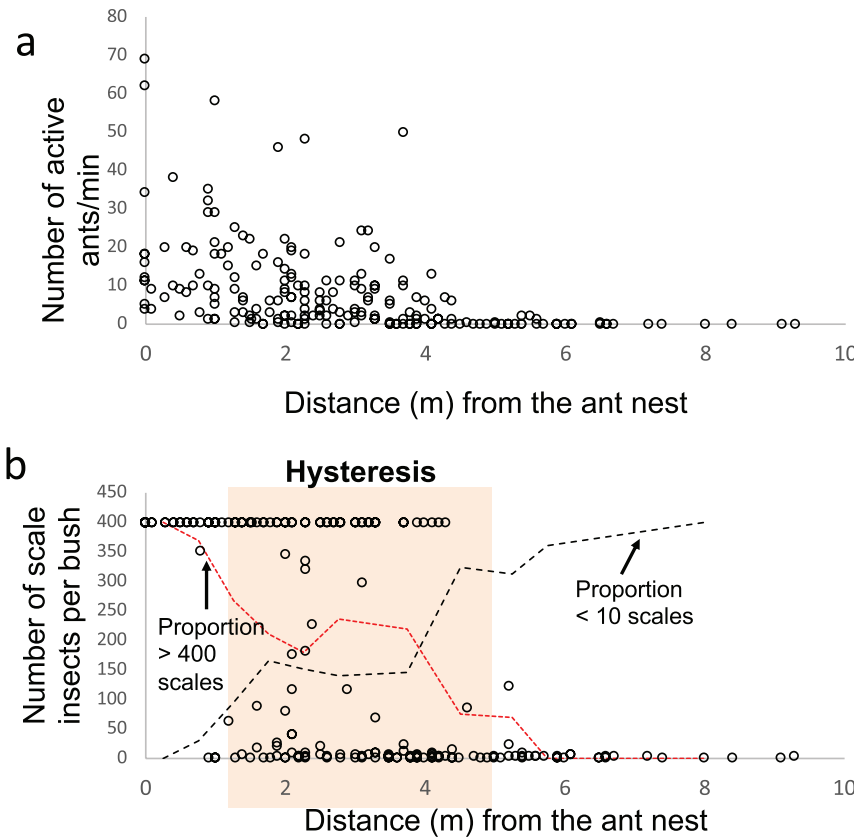


Figure 5. Results from observations on 211 coffee bushes surrounding 20 Azteca nests in 2018 (within an area of approximately 30 meters, on a shade coffee farm in southern Mexico, Finca Irlanda). (a) Activity of Azteca ants (the number of individuals crossing a fixed point on a branch in 1 minute) as a function of the distance from the ant nest (the effective refuge for the scale insects is where the ants are active). (b) The number of scale insects per bush. All points at 400 are greater than or equal to 400. The two categories of proportion of bushes with more than 400 scales and less than 10 scales are also indicated with the connected lines for binned data. The data were summarized from Vandermeer and Perfecto (2019).

position far removed from the refuge (ant nest) toward it, the adult beetle predators that have already located the scales will tend to move with it, until they encounter the protective ants (i.e., find themselves entering the refuge), as is presented in figure 4a. A snapshot at some particular time therefore might look like the pattern in figure 4b. On the other hand, as the dispersion of scales moves from a position within the refuge away from it, the encounter with the beetle predators will not occur until the scales are far removed from the refuge, as is presented in figure 4c. A snapshot at some particular time therefore might look like the pattern in figure 4d. Finally, combining the pattern of figure 4b with that of figure 4d, we obtain the combined graph presented in figure 4e. Note that there is a broad region in which the scales could be very high while at the same time could be very low, effectively depending on where the scales are dispersing from, a structure typically referred to as hysteresis.

Selecting 20 different shade trees containing *Azteca* nests, we examined all coffee bushes within 2 meters of the nest and a number of bushes further removed (the actual number depended on the particular site and the availability of trees nearby). We estimated the activity of *Azteca* ants on each of the bushes before counting the scale insects, to get an estimate of where the actual refuge was located (figure 5a). Note that the ant activity within 1 meter of the nest was high for almost all bushes surveyed (indeed, not a single bush had zero activity), although positions greater than 1 meter away were highly variable, with some bushes having high activity levels and others having none. Further than 4 meters from the nest, ant activity was effectively nonexistent, and bushes further than about 4 meters from the nest were completely out of the refuge. Plotting the number of bushes with a saturated density of scale insects (i.e., more than 400 scales) and those with less than 10 scales, we obtain a pattern (figure 5b) corresponding quite closely to what is expected from the hysteretic pattern predicted by the theoretical considerations (figure 4e; Vandermeer and Perfecto 2019).

A further complication enters with a more complete natural history understanding of the beetles and their larvae. Although the adult beetle can fly and therefore forage over long distances for its food source, the larvae are largely restricted to terrestrial movement; that is, they are restricted in space (Jha et al. 2012). Female beetles therefore must choose their oviposition sites in such a way that the larvae will mature in an environment that contains a locally abundant food source. One major food source for predatory beetles is the general kinds of insects that are relatively sessile and suck the juices from plants, precisely the characteristics of the green coffee scale. They are easy targets for predators because they are normally slow moving and have few defenses. The problem for a potential predator is that they are very frequently defended by ants, precisely in areas where they are good sources of food for a beetle larva. Consequently, a whole group of beetles has evolved the habit of seeking out ants and ovipositing in areas where ants are abundant and defending the hemipterans. These myrmecophilous beetles must obviously have a strategy of protecting their larvae from the aggressive action of the ants and of enabling oviposition in sites of high ant activity (Hsieh et al. 2012, Liere and Perfecto 2014). In the case of the beetle

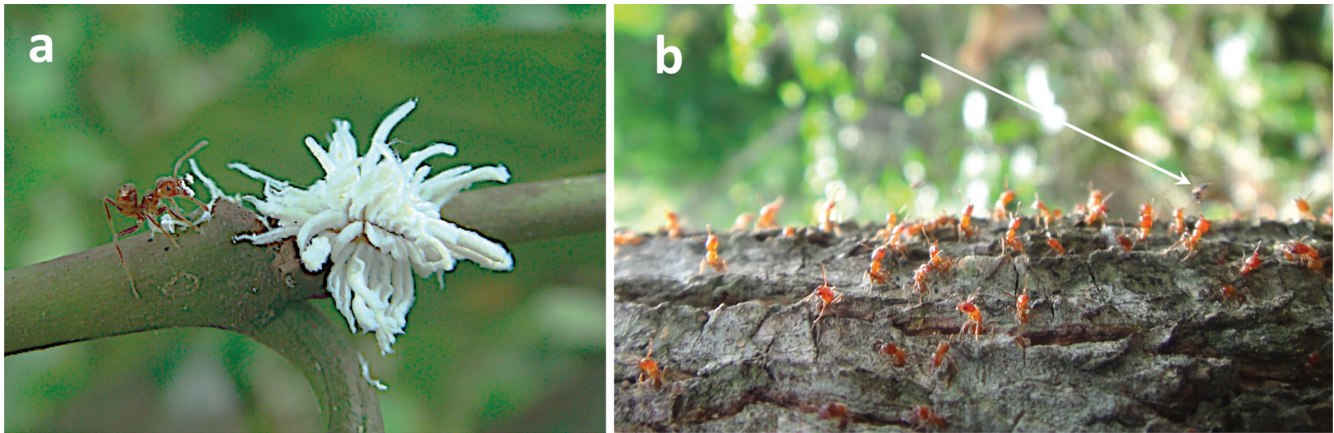


Figure 6. The mechanisms whereby the beetle predator avoids the protective activity of the ant. (a) Beetle larvae with long waxy filaments protected from an *Azteca* worker who just had her mandibles gummed up by the wax after making the mistake of trying to attack. (b) A phorid fly (indicated by the arrow) hovers above the *Azteca* ants, inducing their characteristic behavior of elevating their body in a semicatatonic state with mandibles open. Photographs: (a) Ivette Perfecto. (b) John Vandermeer.

A. orbigera, the larva is covered with waxy filaments that tend to stick in the ants' mandibles whenever they try to attack it (figure 6a). But more importantly, female beetles take advantage of an unusual behavioral pattern of the ants in order to oviposit where the scales are abundant (figure 6b). When a phorid fly attacks an ant, that ant exudes a pheromone that effectively says to the other ants in the general vicinity "Look out! Phorids attacking," and the surrounding sisters all adopt a sort of catatonic posture, heads up, mandibles open, and stationary (figure 6b; Liere and Larsen 2010, Hsieh and Perfecto 2012, Hsieh et al. 2012). Although the phorid is able to detect the alarm pheromones of the ant and is therefore attracted to it, it is unable to actually oviposit on the ant unless it sees some movement (Mathis et al. 2011, Mathis and Philpott 2012, Mathis and Tsutsui 2016). Therefore, not only the ant under potential phorid attack, but also the sisters surrounding her assume this semistationary posture, a result of the very specific pheromone that alerts all ants in the vicinity that a phorid is lurking about. Remarkably, the adult female beetle is able to detect and react to this specific chemical, apparently using it as a cue that the time is propitious to enter into the ant-protected zone to sneak in some ovipositions (Hsieh and Perfecto 2012, Hsieh et al. 2012). Therefore the phorid, in addition to being an important player in the Turing process that forms the basic spatial structure of the system, imposes a trait-mediated indirect interaction (Werner and Peacor 2003), in which the effect of the ant on the beetle (and other elements; see below) is reduced.

There is more to this story: first, from simple theoretical considerations and, second, from some evident natural history observations of the system. The theoretical considerations emerge from the knowledge that the refuge is dynamic. That is, past ecological theory has shown that when a prey species is able to retreat from its predator in a fixed refuge space, the basic instabilities of the predator-prey

arrangement can be cancelled. But, in the present example, the refuge is effectively a pattern formed by another element in the system (Vandermeer and Jackson 2018), the *Azteca* ant. And the *Azteca* ant is dynamic in the system, increasing its numbers (nests) in proportion to the resources it gains (the scale insects). If the scale insect population increases, there is more food for the ant, and it will therefore make more nests and expand its territory, creating even more refuge area for the scale insect. However, as the ant expands its area of influence (because of an abundance of scale insects that are not eaten by the adult beetles that the ant chases away), an increasing fraction of the area becomes refuge and, therefore, not available to the adult beetles (assuming, for the sake of argument, that the phorids are unable to restrict this expansion). At the extreme, there must be some point at which the beetle is unable to find enough prey to continue its population expansion, because almost all of the area would now be a refuge for the scale insect. Therefore, theoretically, the inevitable expansion of the refuge would lead to the eventual local extinction of the beetle predator. It could, of course, be the case that this expected instability of the system does not express itself for diverse reasons or perhaps for an excessively long time. However, purely theoretically, it represents a potential problem for persistence of this control agent.

The theoretical problem (whether it represents a real problem is not the topic at this point) is resolved by some very simple natural history observations. A fungal disease, known as the white halo fungus (*Lecanicillium lecanii*), almost inevitably becomes epizootic (epidemic), especially when local population densities of the scale insect become large (figure 7; Jackson et al. 2009, 2014). The fungus can occasionally be found on isolated scale insects, but almost always is most evident when scale insects have built up a significant local population density, and such a buildup can only happen when they are under the protective custody of the *Azteca* ant.



Figure 7. Scale insects massively infected with the white halo fungus (*Lecanicillium lecanii*). Each scale is surrounded with the mycelium of the fungus, creating a halo around each individual scale insect. Photograph: John Vandermeer.

In the end, we see that the *Azteca* ant plays a key role in the control of this pest. On one hand it protects the scale insect from its adult beetle predator but only in the area of the refuge of the scale, which is defined by the ant itself (in combination with its key parasite, the phorid fly). On the other hand, it permits the scale insect to build up such large local populations that the white halo fungus frequently becomes epizootic and drives the scale insect to local extinction. It is a curious inverse application of Gause’s traditional competitive exclusion principle, which might be expected to apply between the fungus and the beetle because they share this same food source. It seems unlikely, however, that the scale could be controlled completely by either the beetle or the fungal disease, except in the context of a spatial pattern generated by the *Azteca* ant (and its phorid fly parasitoid). The massive expansion of the ants that might be expected theoretically never happens, partly because of the local effect of the fungal disease and the beetle larvae together reducing the scale insect population locally. Therefore, the dynamic nature of the ant cluster mosaic (e.g., figure 2), always provides a small set of refuges (areas surrounding *Azteca* nests) that allows the beetle predator to be maintained throughout the coffee farm. From the point of view of the beetle, it is perhaps ironic that the beetle itself may be involved in the organization of the spatial pattern that is required for its own persistence (Jha et al. 2012, Liere et al. 2012, 2014).

There is yet an additional complication. The fungal disease, once it arrives, multiplies extremely rapidly. But, as was noted above, it does not arrive in the first place (at least not all that regularly) unless the scale population is large and locally concentrated. Therefore, once the disease gets there, it increases to epidemic levels and wipes out the entire population of scale insects (in a local area), creating a

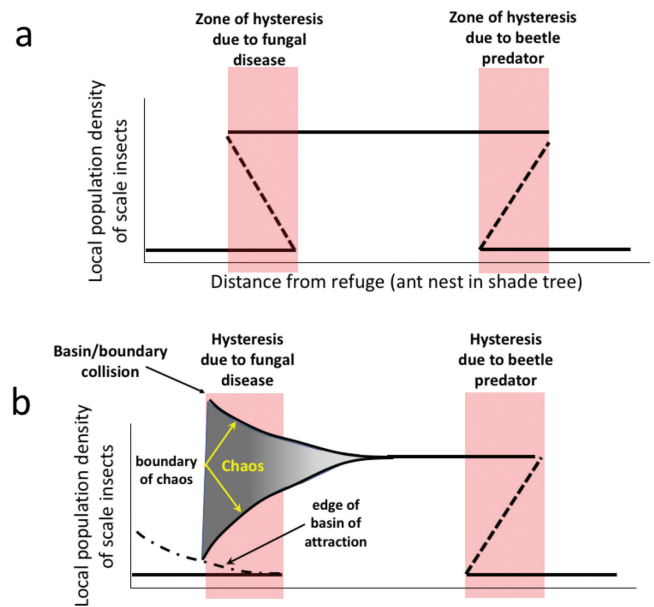


Figure 8. Conceptual diagrams of the overall expected dynamics of the control system for the green coffee scale, an expanded version of figure 4. (a) The prospects for two distinct hysteretic zones each associated with a distinct control element (Ong and Vandermeer 2018). (b) Because of the “boom, bust” nature of the white halo fungal disease, we have argued elsewhere that population trajectories are likely to be formally chaotic (Vandermeer and Perfecto 2019). The lower equilibrium point (i.e., zero scale insects) will exist within a basin of attraction (as will any attractor), and that basin will have an edge (frequently called a separatrix). The chaotic attractor will be constrained within some limits, and those limits are referred to as the boundary of the attractor. When the fluctuations of the chaotic attractor become especially large, its boundary will intersect the edge of the basin of attraction in what is normally referred to as a basin or boundary collision (Vandermeer and Yodzis 1999).

classical situation of boom and bust and hysteresis in space (figure 8a). Although it is a somewhat complicated argument that has been made in a couple of different ways elsewhere (Ong and Vandermeer 2015, Ong et al. 2018, Vandermeer and Perfecto 2019), the disease can clearly generate a locally chaotic dynamic trajectory. Its population dynamics over time are therefore expected to be both oscillatory and unpredictable. Furthermore, as the relevant population gets closer to the ant nest (its refuge from the beetle), the oscillations with its disease are expected to be more and more extreme. Eventually, they become so extreme that they transcend the boundaries of a critical value and both scales and disease completely disappear. Note that chaotic trajectories have boundaries (population densities that never go either higher or lower than some critical values), and the equilibrium point at zero is constrained within a basin of attraction. As the system gets closer to the refuge, the combination of a

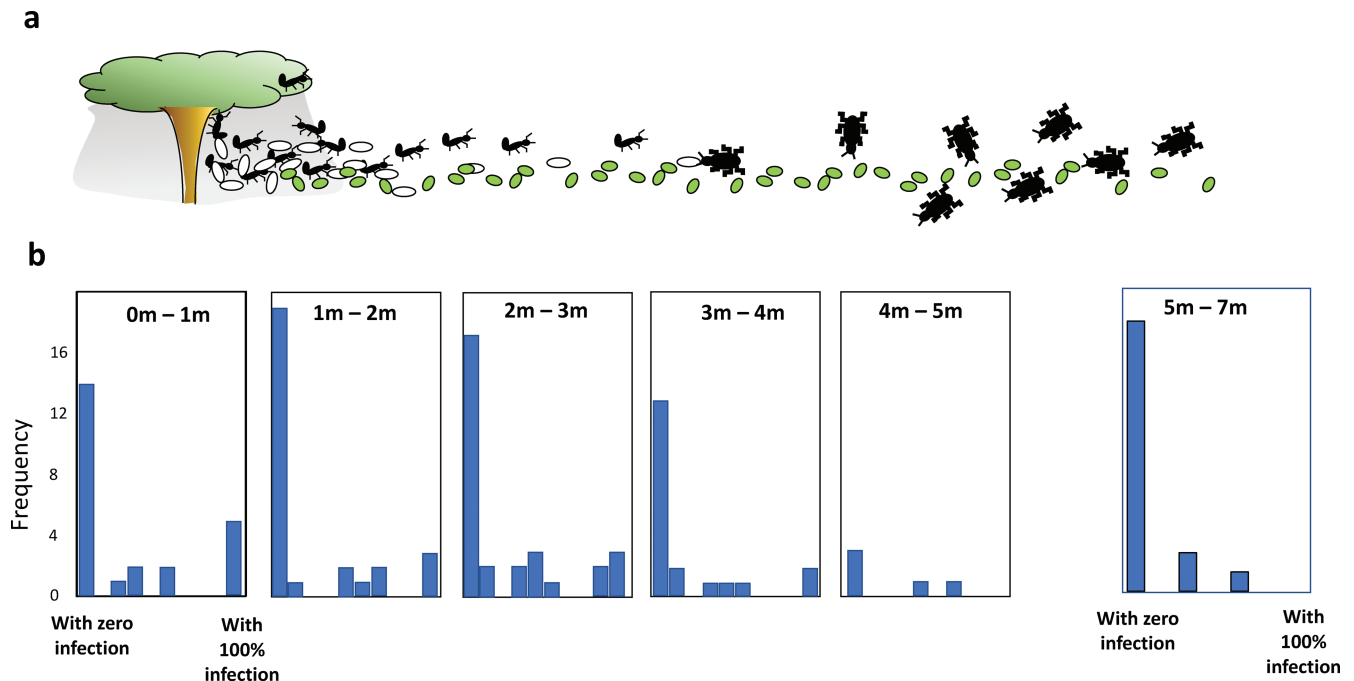


Figure 9. Distribution of the white halo fungus disease (caused by *Lecanicillium lecanii*) as a function of distance to the central nest. (a) A conceptual diagram of the spatial pattern expected from the dynamics, where the black figures represent the beetle predator to the right and the Azteca ants to the left, the green shaded ovals represent the healthy, uninfected scales, and the white ovals represent the scales infected with the white halo fungus. (b) Frequency distributions of coffee bushes with various levels of white halo fungus, each panel ranging from 0% (all scale insects on a bush healthy) to 100% (all scales insects on a bush completely covered with the disease). Only bushes with more than 50 scale insects are included (109 bushes from the total of 211 bushes sampled around 20 Azteca nests).

lower bound on the scale population and the rapidity with which it can increase when under protection from the ants combine to frequently produce chaotic oscillations, and the collision between the boundary of the chaos and the basin edge causes the population to crash, in a basin or boundary collision (Vandermeer and Yodzis 1999). The basic dynamics are illustrated in cartoon form in figure 8b.

To the extent there exists evidence to support the ideas of chaos and basin or boundary collision as represented in figure 8, we display some data in figure 9. The expectation from a chaotic approach to a basin boundary collision is complicated (Scheffer et al. 2012) and requires a far more dense data set than we currently have, but what is available certainly supports the idea that, as the system approaches the refuge, it undergoes complicated and relatively unpredictable behavior within a hysteretic zone. A complicating issue is the fact that the scale insect population density is the main determinant of the probability of infection, and that density increases as the refuge is approached. As the refuge is approached, we expect an increase in total scale population (including those infected) and an increase in the fungal infection rate. With the increase in total scale population we expect an increase in susceptible scales (i.e., uninfected) as the refuge is approached. Within the refuge, we expect the signal of flickering (Sheffer 2009), which, in

this case, would result in a bimodal distribution of bushes, many with no infection and many with high infection with few intermediates. That is precisely the pattern suggested by the data presented in figure 9. At the periphery of the refuge (the graph at 5–7 meters), we generally have very few scales and low levels of disease incidence. Moving further into the refuge area, we see a gradual buildup of disease incidence (labeled “with 100% infection” in figure 9b), culminating in bimodality when we arrive at a distance of 0–1 meters.

What is not immediately obvious from this analysis is that there are really three qualitatively distinct outcomes at a local level, which is to say on a particular coffee bush. If the bush is very close to the *Azteca* nest, the ants forage vigorously and, therefore, the scale insects are highly protected from the beetle predator. Consequently, they build up very high local populations, and are subjected, eventually, to the white halo fungus disease, effectively eliminating the entire population (and, of course, the fungus itself dies locally after its food source is eliminated). At the other extreme, when the coffee bush is far removed from the ant nest, the scale insect is constantly attacked by the adult beetles (as well as some other natural enemies such as hymenopteran parasitoids; Uno 2007) and never is able to build up a substantial population. Therefore, it would appear that either very close to an *Azteca* nest or very far away from an *Azteca* nest the

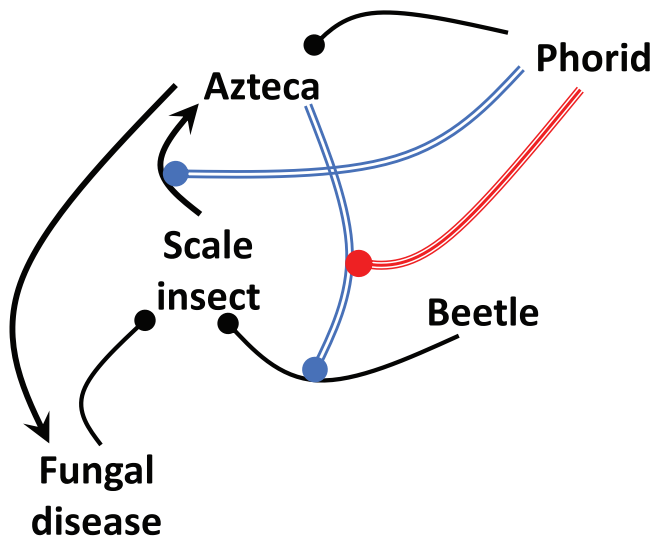


Figure 10. Basic elements of the system, illustrating some of the complexities involved in the natural regulation of this potential pest. The arrowheads indicate positive effects, and the filled circles indicate negative effects. The connections to connections (e.g., the *Azteca* connects to the curve connecting the beetle to the scale insect) represent trait-mediated indirect effects, which are higher order effects. Note the hypergraph-like structure wherein the phorid interferes with the ability of *Azteca* to interfere with the ability of the beetle to prey on the scale insect, what we refer to as a trophic cascade.

green coffee scale is kept under control. However, in the real world, there is no such thing as only far away or very near; many coffee bushes are neither.

The result is a complex system in which the *Azteca* ant forms a reaction or diffusion Turing-like pattern-forming complex that acts as a pilot structure, driving the spatially dependent direct control system. The ant exerts a behavioral restriction on the beetle (an indirect nonlinear effect), but the phorid exerts a behavioral restriction on the ant (another indirect nonlinear effect), causing what has been referred to as a trait-mediated cascade of effects and imposing a hypergraph-like structure on the system (Golubski et al. 2016). The concentration of ants creates refuges within which the adult beetle predator (*A. orbiger*) is restricted from active predation but within which the pest, the scale insect, builds up very dense local populations, the consequence of which is a high attack rate of the white halo fungus disease. Regulation of this herbivore is therefore effected through a complex system involving a Turing process, nonlinear indirect interactions, critical transitions, hysteresis, chaos, basin or boundary collisions, and a hypergraph, all elements of the burgeoning field of complex systems. The elements of the system are illustrated in figure 10. Note the central role of the *Azteca* ants. It is worth emphasizing that these ants are obligate tree nesters, which suggests that the trend to eliminate the shade trees in the system, thought to be a

modernizing effort, completely breaks down this complex system.

An interesting complication emerges as we understand the importance of these two obvious natural enemies of the scale insect (the coccinellid beetle and the pathogenic fungus). We began by proposing a predator–prey driven Turing mechanism to generate the clustered distribution of ant nests, a clear application of what has previously been noted; predator–prey systems distributed in space can generate Turing-like patterns. The predator was the phorid parasitoid, and the prey was the *Azteca* ant. However, the spirit of the Turing mechanism involves only generalized reaction and diffusion terms, wherein the reaction is thought to be a coupled positive or negative effect. And in the present example, there are two clear negative effects on the ant through the attack on its food. Both the predatory beetle *A. orbiger* and the white halo fungus are enemies of the scale insect, the main food of the *Azteca*, and therefore both constitute a negative effect. It has been independently suggested that either the beetle (Liere et al. 2012) or the fungus (Jackson et al. 2009, 2014, MacDonald et al. 2013) could be the repression agent that generates the Turing-like pattern. Evidence from a combination of modeling and empirical observations suggests that either could be true. If the beetle is the cause of the pattern formation, it is an especially interesting situation in that the beetle population itself is dependent on the existence of the spatial pattern for its own survival (it needs clusters of ant nests for its larvae to survive and areas free of ants for its adults to feed) but is the cause of the formation of that pattern in the first place (Liere et al. 2012, 2104).

The coffee berry borer: indirect nonlinearities

Perhaps the most directly obvious of the three pests is the infamous coffee berry borer, because of its habit of drilling directly into the seed, which is the basic commodity that goes to market. It emerged as a major pest in the 1980s and is regarded as far more important, on most farms, than the green coffee scale. The literature on the coffee berry borer is now enormous because of its sometimes devastating effect (Murphy and Moore 1990, Damon 2000). A variety of natural enemies have been reported, including the fungus *Beauveria bassiana* (De La Rosa et al. 2000), anole lizards (Monagan et al. 2017), birds (Kellerman et al. 2008, Johnson et al. 2010, Karp et al. 2013, Chain-Guadarrama et al. 2019), possibly bats (Williams-Guillen et al. 2008, Karp et al. 2013), and parasitic Hymenoptera (Howard and Infante 1996, Barrera et al. 1990, Gómez et al. 2005, Infante et al. 2005, Vega et al. 2009). But, by far, the most obvious natural enemies are ants.

There is now a substantial literature documenting the general category of ants as major predators on this seed-eating herbivore (Bustillo et al. 2002, Philpott and Armbrecht 2006, Armbrecht and Gallego 2007, Philpott et al. 2008, 2012, 2014, Larsen and Philpott 2010, Gonthier et al. 2013, De la Mora et al. 2015, Morris et al. 2015, 2018, Morris and Perfecto 2016). As in the case of the predacious beetle on the scale insect, some rather casual observations can easily

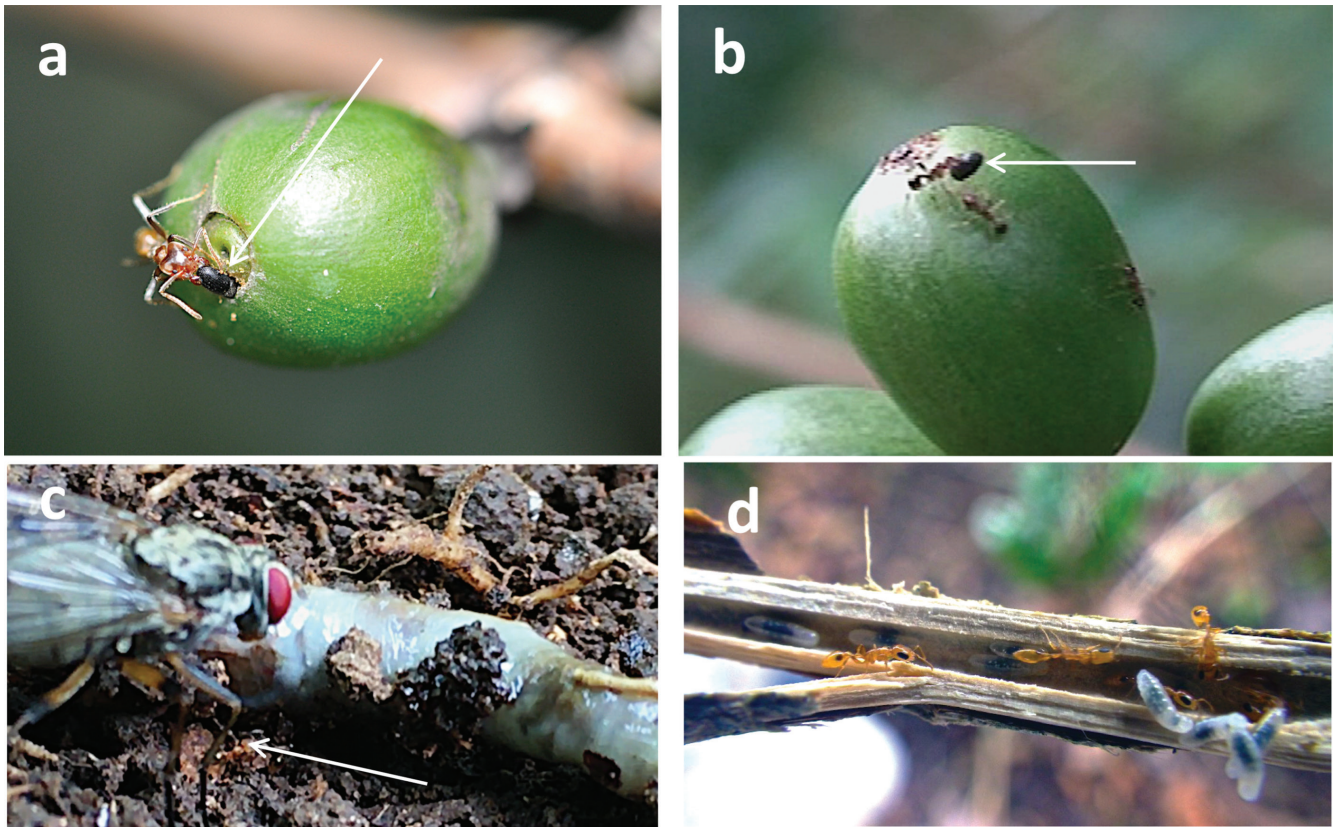


Figure 11. Four major ant predators of the coffee berry borer. (a) *Azteca sericeasur* grabbing an individual berry borer in the act of boring into the fruit (the arrow points to the borer). (b) *Pheidole synanthropica* individuals cooperating to bring a coffee berry borer (which they had just removed from the hole it was burrowing) back to the nest (the arrow points to the borer). (c) *Pheidole protensa*, a ground-nesting and foraging species, in the act of burying a worm. The foraging fly provides a size comparison; the white arrow points to an individual ant. (d) *Pseudomyrmex simplex*, an arboreally foraging and nesting species, in its nest in a hollow coffee twig. Photographs: (a, b) Estelí Jiménez-Soto. (c) John Vandermeer. (d) Stacy Philpott.

convince one that, in particular, the *Azteca* ants are major predators (or at least antagonists) to the coffee berry borer, and a variety of detailed studies support that conviction (Perfecto and Vandermeer 2006, Pardee and Philpott 2011, Gonthier et al. 2013). However, further examination reveals another major ant predator, *Pheidole synanthropica*, a rather large-body species (about the same size as *Azteca*) that nests in the ground but forages vigorously both on the ground and in the coffee bushes. Detailed observations (Jiménez-Soto et al. 2013) established that this species is a major predator of the berry borer. It takes the berry borer approximately 1–2 hours to completely burrow into the fruit (although Spongel 1994 reported that it took up to 8 hours), which means it is unprotected and unable to escape the predacious activity of the ants for that period of time. Both *Azteca* and *P. synanthropica*, if they encounter a berry borer trying to burrow into a seed, grab the borer by its posterior end and pull it out of the fruit. *Azteca* tends to simply throw the borer off the tree (although some small percentage seems to be taken back to the nest and therefore predated on), whereas *P. synanthropica* almost inevitably takes the borer back to its

nest. Therefore, we might say that *Azteca* is mainly a general antagonist to the berry borer, whereas *P. synanthropica* is definitely a predator (figure 11).

The consequences of this difference are quite important. Although *Azteca* provides some protection to the coffee from the ravages of the berry borer, when the borer is simply thrown to the ground it can easily climb (or fly) back up and try again to bore into the seed. Indeed, there is some reason to suspect that the borer actually prefers to burrow in seeds that are protected by ants, presumably taking advantage of the ant's mutualistic behavior toward the scale insects and protecting it from other predators that may attempt to enter the seed in which it is eating endosperm and creating the new generation of berry borers. However, this strategy is compromised by other species of predators (especially ground-foraging ants) that can directly prey on the borers when they are thrown to the ground, one of which is *P. synanthropica*. And this species (among others) is highly aggressive, limiting the activity of the smaller species (Perfecto and Vandermeer 2013).

A number of these smaller species of ants (e.g., figure 11c, d) are also known predators of the coffee berry

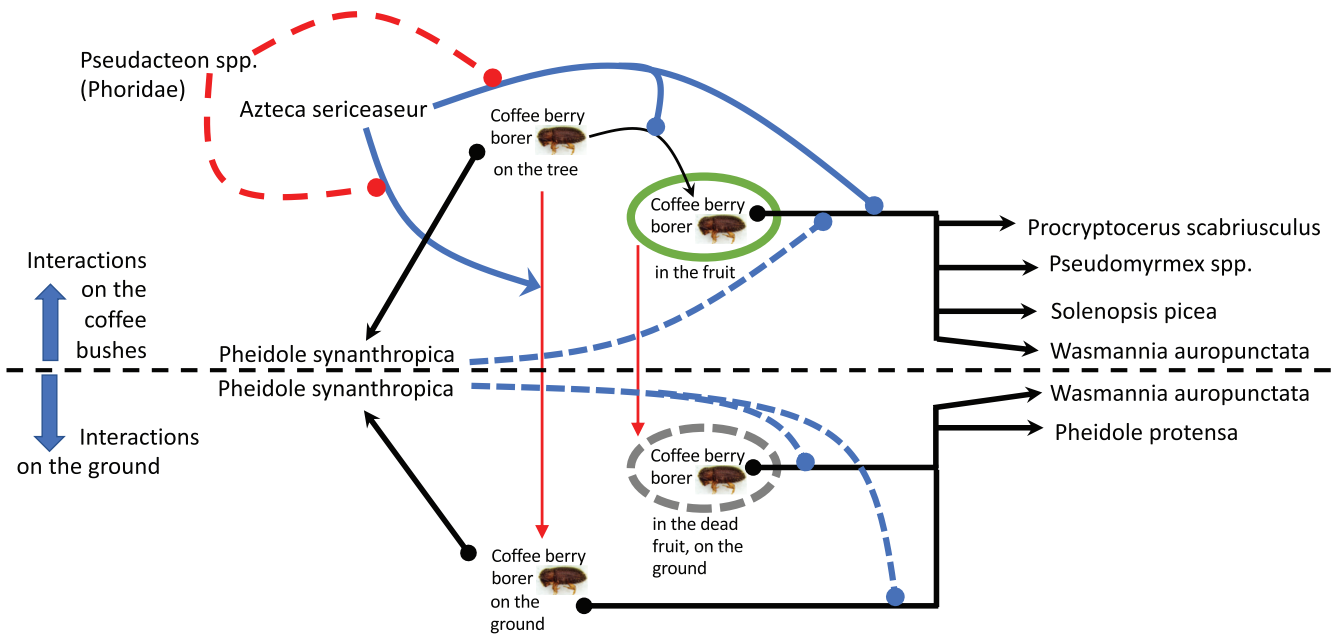


Figure 12. Summary diagram of part of the ant community associated with the regulation of the coffee berry borer. As in figure 10, the arrowheads indicate positive effects, the filled circles indicate negative effects, and the connections to connections represent trait-mediated higher-order indirect effects. The five smaller-body species, *P. scabriusculus*, *Pseudomyrmex* spp., *S. picea*, *W. auropunctata*, and *P. protensa* prey on the berry borer within the coffee berries, as well as on the ground. The two larger-body species, *A. sericeaseur* and *P. synanthropica* attack the borer adults before they enter the berries but also have an indirect effect on the smaller species, interfering with their predatory activity. The horizontal dashed line represents the division between interactions that occur on the coffee bushes (above) and those that occur on the ground (below). The solid black connections indicate direct predatory effects. The bold blue curved lines (both solid and dashed) indicate indirect effects. The dashed blue lines (the indirect effects imposed by *P. synanthropica*) indicate the connections that were eliminated in 2012 (see the text), and the dashed red lines are the negative trait-mediated effects of the phorids on the Azteca ants.

borer (Gonthier et al. 2013, Morris and Perfecto 2016, Morris et al. 2018). These species offer considerable regulatory potential because they are capable of entering the coffee seed through the hole that the borer makes (Larsen and Philpott 2010). One group is the twig-nesting complex, including the genus *Pseudomyrmex* (at least three species are common), and *Procryptocerus scabriusculus*, all adept at entering hollow arboreal structures because they normally nest in hollow twigs (figure 12d; Larsen and Philpott 2010). Other small arboreal ants capable of entering the hole made by the berry borer include the arboreally nesting *Solenopsis picea*, which nests in superficial structures, such as moss, surrounding the branches of the coffee bushes (Morris and Perfecto 2016). On the ground, a variety of ground foraging ants, including *Pheidole protensa* (figure 11c), and a variety of other species in that same genus are small enough to enter the borer's hole. Of particular interest is the well-known *Wasmannia auropunctata* (the electric ant, or the little fire ant), which nests and forages on both the ground and arboreally (Morris and Perfecto 2016, Yitbarek et al. 2017). There are many other potential ant predators in the system, but these are the ones we have studied in particular.

Azteca clearly dominates over *P. synanthropica*, and both of them dominate over the smaller species in the system,

reducing their nest density (i.e., overall population density, because, in ants, the nest is the variable of interest) significantly (Perfecto and Vandermeer 2013). In summary, there are at least six species of ants that are predators on the coffee berry borer, suggesting that ants represent an excellent natural enemy to regulate the coffee berry borer. However, the foregoing natural history suggests that the system is not so simple. Although several of the smaller arboreal species (*Pseudomyrmex* spp., *S. picea*, *P. scabriusculus*, and *W. auropunctata*) could be effective predators on adults, larvae and pupae of the berry borer within the fruit on the bush, they are effectively unable to engage in such predation if *Azteca* or *P. synanthropica* ants are around. Fruits that are not harvested tend to dry out and fall to the ground, providing a refuge for the beetles during the dry season but also being exposed to the potential predation from the smaller ants (*W. auropunctata* and *P. protensa*). However, those smaller ants have dramatically reduced populations if they are forced to compete with *P. synanthropica*, which, because of its larger size, is unable to penetrate the borer hole in the fruit. In other words, the whole system seems to be operating in a complicated fashion with potential predators interfering with one another but perhaps acting in an emergent fashion to at least partially regulate this key herbivore, the coffee berry borer.

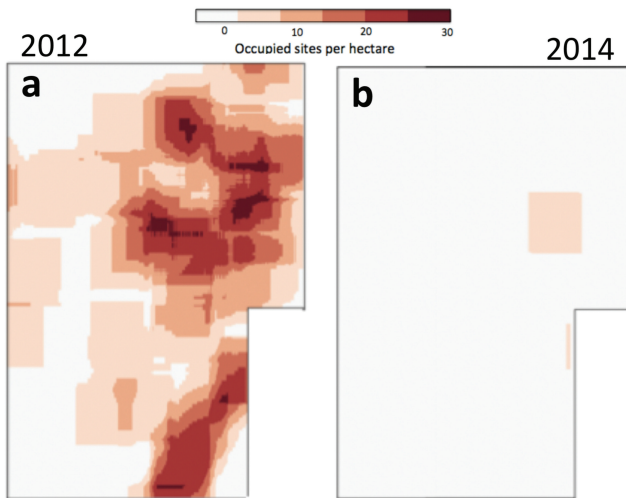


Figure 13. Heat maps of occurrence of *P. synanthropica* in 2012 and 2014, illustrating the dramatic collapse of this population of this species.

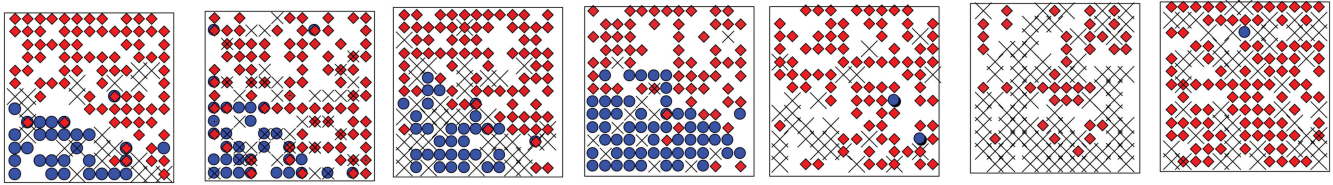
Adding to this complication is the phorid fly. As was noted earlier, this fly has an important trait-mediated effect on the *Azteca* ants, the foundation of the Turing patterns we seem to see at a large scale and effectively contributes to the maintenance of the major predator of the green coffee scale (see figure 10). However, because, as all evidence suggests, the *Azteca* ants so dominate the coffee bushes where they forage that the smaller ants are unable to persist there, we might expect the same sort of trait-mediated cascade we saw with the control of the green coffee scale. Indeed, in controlled laboratory settings, the coffee berry borer has its success rate of penetrating coffee fruits reduced in the presence of the phorid flies. The importance of this effect is in the addition of what has been referred to as *vertical biodiversity* to the system (Philpott et al. 2012), the smaller ants who had been effecting control over the berry borer were restricted from doing so by the action of the *Azteca*, but when the phorids were introduced, the smaller ants again became effective predators. Although the *Azteca* ants reduced the effectiveness of berry borer predation from these smaller ants (specifically *P. simplex*, *P. scabriusculus*), the phorids reduced the effectiveness of the *Azteca* in reducing the effectiveness of the smaller ants in their effectiveness in controlling the berry borers, a similar trait-mediated cascade that we saw for the green scale control. All of this is summarized in figure 12.

It is tempting to conclude something like “the more ants the better.” However, cascading indirect effects sometimes can have unexpected consequences, meaning that such a conclusion ought to be tempered with more careful analysis. Although we acknowledge this system as complex, it makes some sense to try and simplify it a little to perhaps gain some deeper insight into its operation. A glance at figure 12 suggests that there are two generalized groups of ant predators on the berry borer: the big ants (*Azteca* and *P. synanthropica*) and the small ants (*Pseudomyrmex* spp., *S. picea*, *W. auropunctata*,

P. scabriusculus, and *P. protensa*). So we can think of it as a two-predator, one-prey system. But there is an obvious indirect effect because the bigger ants negatively affect the ability of the smaller ants to be predators, as was discussed above. Depending on nest densities, it would seem that because the smaller ants prey on all three life stages of the borer and throughout the year for those that forage in infected berries on the ground, they might, in the end, be more efficient predators than the larger ants. Furthermore, the larger ants have an indirect trait-mediated effect on the smaller ants, reducing their effectiveness. One might argue that it is the existence of the smaller ants that potentially regulates the borers over the long run. Unpublished evidence even supports the idea that the berry borer actually seeks areas that are under protection from the ants, supporting the speculation of Gonthier and colleagues (2013) that the berry borer gains protection from smaller (more effective?) predators by preferring to attack berries under the protection of larger ants.

This basic speculation was put to an unintended test in 2012. Because of a major outbreak of the coffee rust disease (as will be discussed in the following section), the coffee landscape where we work was heavily sprayed with a combination of calcium carbonate and copper sulfate, a permitted activity for organic agriculture. In figure 13, we show the distribution of *P. synanthropica* as a heat map based on how many tuna fish baits placed in coffee bushes had swarms of *P. synanthropica* after about 30 minutes. It is clear that in a single year, a population of thousands of nests of *P. synanthropica* simply disappeared. Surveys in subsequent years indicated that the smaller ants in the system began to recuperate from the reduced state they had been in, apparently because of the indirect effects of *P. synanthropica* (Ennis and Philpott 2017, Philpott 2010). Those small ants that attack the borer within the seed, both on the tree and on the ground, especially increased over the next few years. In figure 14, we show the distribution of several of the species in a 50 × 50 meter subplot within the 45-hectare plot. Note how, during the years 2009–2012, the distribution of *P. synanthropica* remained relatively constant, perhaps slowly increasing in its area of dominance, at the expense of *P. protensa* on the ground and *S. picea* arboreally. Then, after the collapse of *P. synanthropica* between 2012 and 2013, both of those smaller species (*P. protensa* on the ground and *S. picea* in the trees) began to move into the area previously dominated by *P. synanthropica*. If the above speculations about how the ant community affects the borer are true, we might expect that the elimination of one of the borer’s predators (*P. synanthropica*) would result in better overall control of the berry borer. In surveys of the berry borer in 2005 and then repeated in approximately the same area in 2018, the attack rate of the borer went from an average of about 15% of berries infected with borers to less than 1%. Insect populations are notoriously variable and respond to many cues in the environment by increasing and decreasing population numbers, frequently in unpredictable ways. Therefore, although this dramatic decline in borer numbers cannot be

Terrestrial foragers



Arboreal foragers

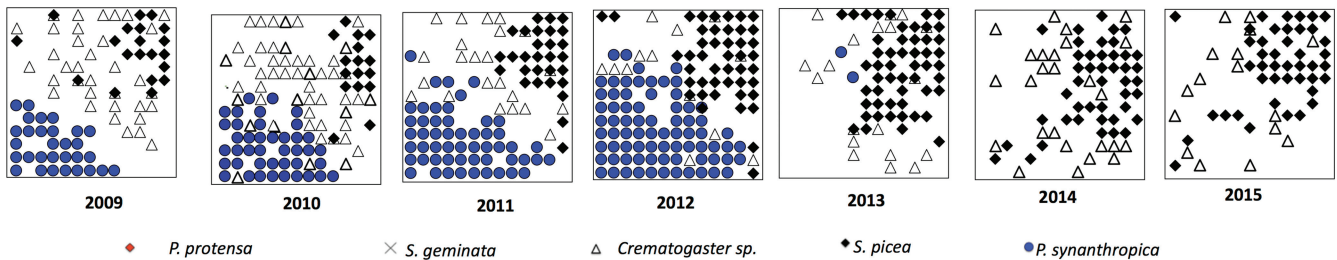


Figure 14. Changes in the presence of five species of ants over a 7-year period, showing the disappearance of the species *P. synanthropica* in year 2013. Each symbol represents the occupation of tuna baits, either on the ground or in the nearest coffee bush to the census point. The census points were spaced 4 meters from each other, and the whole plot is 50 × 50 meters.

directly linked to the change in the ant community structure, it is nevertheless worth noting that the underlying narrative of how that community functions as a system of biological control concords perfectly with the changes observed.

The coffee rust disease: Historical devastation and the inevitability of surprise

In the early 1980s, a specter haunted the coffee growing regions of Central America. The infamous coffee rust disease (figure 15a; caused by the rust fungus *Hemelia vastatrix*) had arrived in Brazil, and its eventual spread all the way to Mexico was expected, causing extreme worry among farmers and technical advisors. This worry was certainly justified on the basis of the history of the coffee rust disease in Asia (McCook and Vandermeer 2015). Great Britain's expansion in what was then called Ceylon (today's Sri Lanka) was qualitatively distinct from many of its previous imperial adventures. Planting what was effectively a monoculture of coffee, along with a great deal of infrastructure (roads and railroads) for the time, it was a remarkable centrally planned agricultural development plan. However, the plan effectively created ideal conditions for any disease that could get a foothold, with its virtually shadeless monoculture and networks of roads and railroads that could help distribute the fungal spores widely. When the disease arrived, it took hold and spread throughout the entire island, eventually causing a complete loss of coffee production (which is why Ceylon tea is a well-known commodity but Ceylon coffee became nonexistent in the late nineteenth century).

However, the rust scare of the 1980s Mesoamerica turned out to be a bit of a false alarm, at least until 2012. Before that year, the rust was always an irksome constraint on production, but the complete devastation that had been

feared when it was discovered in the early 1980s never came to pass; it was a problem, to be sure, but not one to get overly agitated about. But then, without much warning, there was an explosion of coffee rust in the 2012–2013 cycle. Countries in the zone declared emergencies as one of their main sources of income (sometimes the major one) seemed to be threatened with severe disruption. Local governments throughout the affected area provided emergency support to coffee producers and both the United Kingdom and the United States came up with significant international aid, specifically for what rapidly came to be called the most devastating emergency in the history of coffee production throughout the region (Avelino et al. 2015).

There are two ecological questions associated with this episode. First, why did the disease not become rampant for approximately 30 years after its introduction, and, second, what caused the very sudden explosion? Although the answers to either of these questions remain enigmatic, using tools from complexity science provides us with some ideas.

The relevant biology of the rust disease is well known. A windblown spore adheres to the undersurface of a leaf and encounters a small amount of moisture, causing germination directly into a stoma. The mycelia grow intercellularly and produce haustoria, which penetrate into the plant cell and absorb nutrients, effectively killing the cell. As the fungus grows within the leaf tissue it eventually forms uridia that contain new spores, exiting the leaf from other stomata, causing the characteristic yellow spots on the undersurface of the leaves (figure 15). The transmission dynamics of the disease are dual (Vandermeer and Rohani 2014), with some close plant-to-plant dispersion of spores (Vandermeer et al. 2017), especially when plants are close enough to touch one another, along with propagule rain from the general spore load that

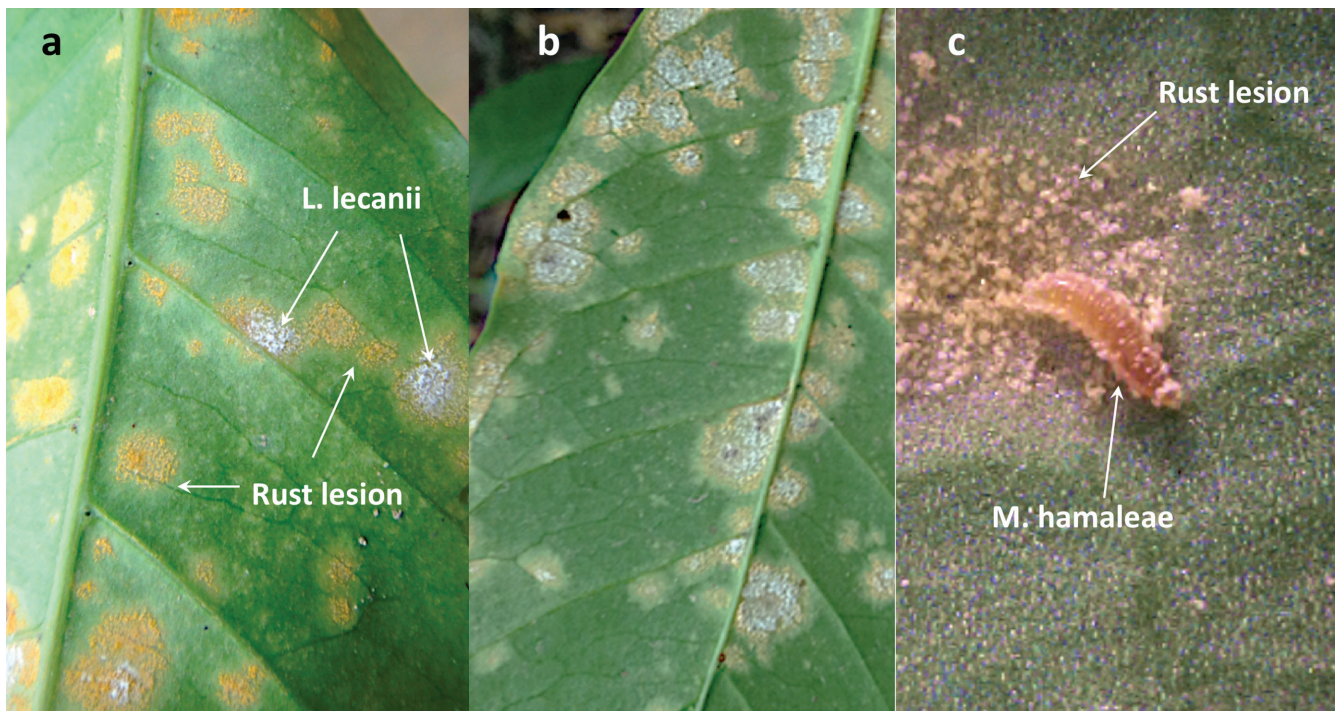


Figure 15. Elements of the coffee rust disease. (a) Rust lesion on the bottom of a leaf, along with the attack of the antagonistic mycoparasite, *Lecanicillium lecanii*. (b) Epidemic of *L. lecanii* on the rust lesions (photo from Puerto Rico). (c) Larva of the fly spore predator, *Mycodiplosis hamaleae*.

exists in the atmosphere, especially in areas of high concentration of coffee production, when that coffee is attacked by the rust. From the perspective of an individual coffee plant, there are two sources of rust spores: its local neighbors and the general accumulation of spores in its region—that is, from the overall spore load in the atmosphere. But it is also the case that this coffee plant and all others over a very large region contribute to the spores in the overall spore rain from the atmosphere. Coffee plants generally both receive spores from the general spore pool and contribute to that pool. Given this narrative, it is easy to imagine a situation in which a generally traditional shade coffee landscape would receive a particular rate of spore rain each year and would contribute a bit to the general pool, but because the shade trees act as windbreaks, much of the spore load is never delivered to the coffee plants. One could imagine an equilibrium in which the rust disease would be endemic but not severe, partly because the wind-borne spores have limited access to the coffee trees, meaning that the increment of spore load in the general atmosphere would be limited.

Focusing on the large landscape level, if the abundance of spores in the atmosphere is low, it is likely that the incidence of the disease (the fraction of farms with an epidemic) will also be low. But each epidemic will increase the spore density in the atmosphere. The probability that a given farm will become epidemic is a function of both the spore density in the atmosphere and the dispersion rate from the atmosphere to the farm. Changing focus to the local level, the rate of spread

of spores from coffee bush to coffee bush on an average individual farm will partially determine whether the rust within that farm will become epidemic. From the point of view of an individual coffee bush, the danger of being infected by a spore comes from two sources: the atmosphere and neighboring infected plants—a regional source and a local source.

Imagine that a forested ecosystem is gradually deforested of both shade trees in the coffee farms and the trees in the natural forest around them, and ask what proportion of the farms could be susceptible to an epidemic of coffee rust? According to a simple model that incorporates both regional and local dispersal (Vandermeer and Rohani 2014, Vandermeer et al. 2017), the initial deforestation (which we presume increases the general, long distance dispersion of the spores, because of increasing wind dispersal) will generate an increase in the number of farms experiencing an epidemic. That increase is likely to be slow and steady at first, but there will be a specific point at which a critical transition will occur and a large number of farms will suddenly become highly infected. This will happen in the complete absence of any other environmental driver, such as climate change or a new more virulent strain of the disease. Indeed, one study in Costa Rica (Avelino et al. 2012) showed that the incidence of rust disease was correlated with the amount of sun coffee and pasture in the surrounding landscape. It could very well be that the sudden outbreak of coffee rust in 2012 is an example of the inevitability of surprise arising from the formality of a critical transition that we have

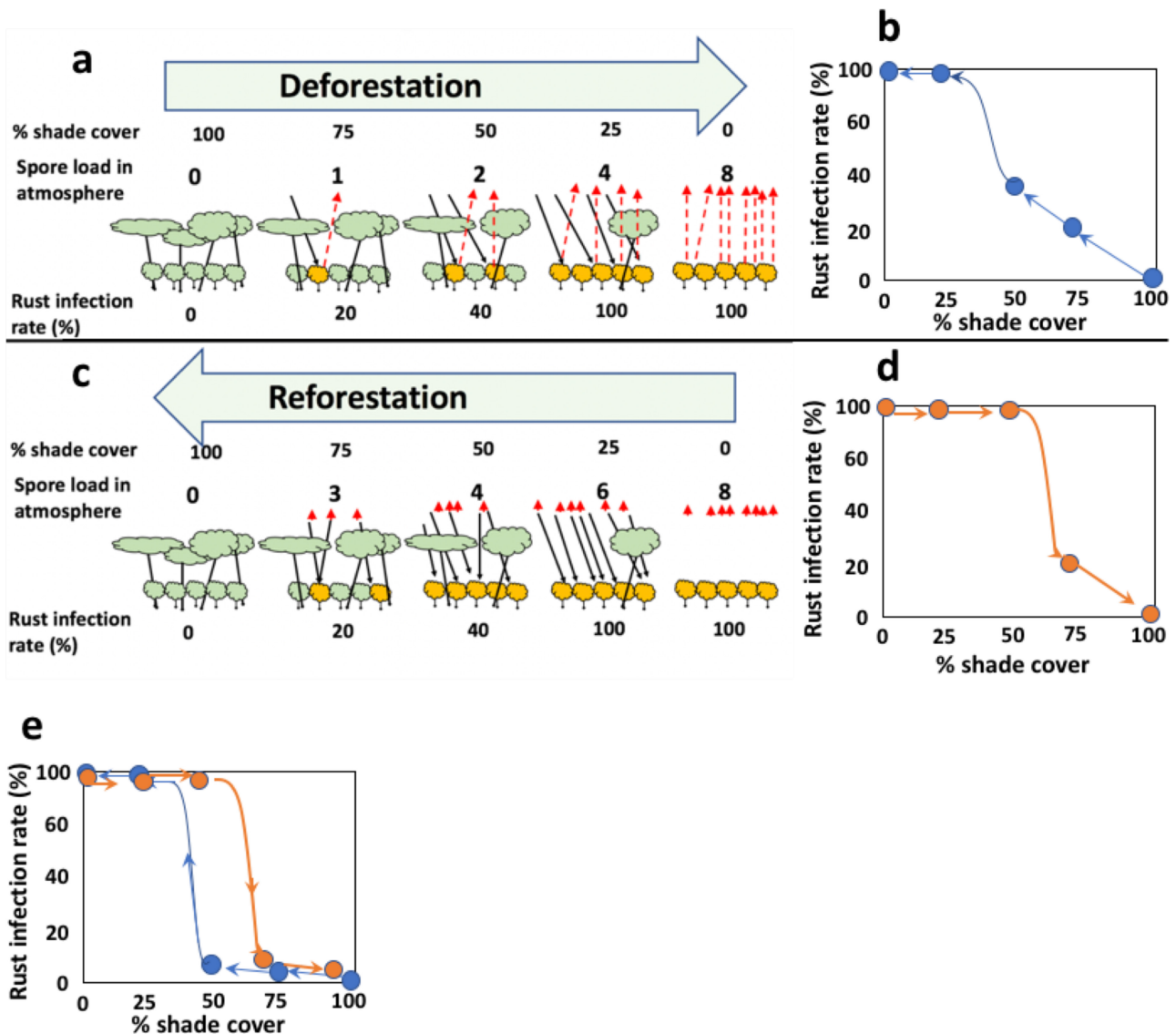


Figure 16. Conceptual diagram of the coffee rust disease as it relates to the problem of deforestation (including the removal of shade trees from the coffee farms themselves), pictured in the present figure as the shade in coffee, but representative of deforestation more generally in the overall region. (a) As deforestation proceeds, the fallout of spores from the environment increases (because of less wind break), and the resultant increased rust infection rate contributes more spores to the general spore population in the atmosphere, indicated by the arrows pointing upward. (b) The combined effect of increased penetration of spores from the atmosphere because of deforestation and the increased contribution of spores into the atmosphere from higher infection rates creates a critical transition (from 40% infection, suddenly jumping to 100% infection as deforestation goes from 50% to 25%). (c) Reversing the deforestation trend begins with the problem that there is an extremely high spore density in the atmosphere, indicated by the small arrowheads at the lowest shade cover. For heuristic purposes, in this cartoon version, we ignore the contribution of new spores and presume that the atmospheric spore load gradually decreases because of the gradual decrease in the rust infection rate, as the reforestation procedure continues. (d) The combined effect of decreased penetration of spores from the atmosphere because of reforestation and the slow reduction of spores in the atmosphere resulting from reduced input from lower infection intensities. (e) Combining the ideas of the deforestation–reforestation cycle into a single critical transition or hysteresis graph. The drawing is based on the analytic model of Vandermeer and colleagues (2015).

come to associate with highly nonlinear complex systems (Vandermeer 2011). A cartoon version of this theoretical process is presented in figure 16.

An important component of the rust disease system, not yet completely understood, is the existence of several natural

enemies of the rust (Jackson et al. 2012a, 2012b, Hajian-Forooshani et al. 2016, Vandermeer et al. 2014). Providing an example of the sorts of ecological complexity of popular literature, the fungal disease of the first pest we discussed, the green coffee scale (figure 7), is caused by the same species of

fungus that, when given the chance, attacks the coffee rust fungus. That same white halo fungus (*L. lecanii*) that attacks the green coffee scale, now acts as a mycoparasite (figures 7, 15a, 15b). Because this natural enemy is also a natural enemy of the green coffee scale, the connection to the *Azteca* ant became obvious early on (Vandermeer et al. 2009, Jackson et al. 2012a, Hajian-Forooshani et al. 2016); *Azteca* creates conditions under which the scale insect becomes highly concentrated locally, which attracts the infestation of the white halo fungus and creates local hot spots of spores that disperse locally and attack the rust. Correlative evidence for this hypothesis, prior to the 2012 epidemic of rust, comes from multiple sources (Vandermeer et al. 2009, 2014, Jackson et al. 2012a). Indeed, there has been considerable discussion at international conferences on the potential of *L. lecanii* as a spray for the rust disease. Our work suggests that partial control of the rust may naturally occur through this and other agents (Jackson et al. 2012a, 2012b, Vandermeer et al. 2014, Hajian-Forooshani et al. 2016), although the epidemic throughout Mesoamerica in the 2012–2013 growing season shows the potential for the disease to escape such control, if, in fact, it did exist before that.

It is quite a remarkable qualitative impression one gets when examining the rust and its control comparatively. It is endemic but rarely epidemic in Puerto Rico but has maintained a relatively severe status in much of Mesoamerica since 2012 (Hajian-Forooshani et al. 2016). Examining coffee leaves in Mexico easily reveals the presence of *L. lecanii* but only after considerable searching effort, whereas in Puerto Rico, it is almost inevitable that, if one encounters the rust on a leaf, it is almost certain that one encounters *L. lecanii* also. What seems epidemic in Puerto Rico is the *L. lecanii* that seems to keep the rust under control.

In addition to the white halo fungus, the larval form of a small fly, *Mycodiplosis hamaelae*, preys on the spores directly on the coffee leaf (figure 15c; Hajian-Forooshani et al. 2016) but probably also acts as a dispersal agent, at least locally (on an individual leaf). Several species of mites are also involved in the consumption or local dispersal of spores.

The coffee leaf rust continues to plague Latin American coffee farmers. Our studies suggest a combination of its transmission dynamics and how they are affected by management issues, such as the quantity of shade and the density of planting, plus a variety of control from above elements (the mycoparasitic fungus, *L. lecanii*; the fly larvae, *M. hamaelae*; and, possibly, fungivorous mites) represent a source of control, which sometimes fails (Vandermeer et al. 2014).

Conclusions

Understanding the general structure of ecological communities has long been a central goal of ecology, from Haeckel to us. Empiricists commonly, and probably necessarily, focus on the community of X, which is to say an assemblage of species defined by some set of criteria: the fungal community of Lake Wobegon, the community of gall-forming insects of oak trees, the microbial community of the human

gut, the community of four ciliate species, and so on. Theoreticians perhaps feel less constraint. In the present article, we have defined the community as the herbivores of the coffee plant and their associates, in which top-down control is the goal of management (bottom-up control implies overuse of the basic resource—i.e., a pest problem). The framing of regulation from above from theoretical ecology translates directly into biological control from agroecology. Indeed, in agroecology regulation from above is elementary, in that the top-down agents are frequently obvious (e.g., ants eat the berry borer, a beetle and a fungal disease control the scale insect, and a mycoparasitic fungus attacks the coffee rust disease). However, stopping at that level of understanding may obscure more than clarify, much as the simple phrase *controlled from above* may indeed obscure (Ehrlich and Birch 1967, Murdoch 1969). Precisely how that control is affected may involve many complicated interactions and contingencies, making, we argue, the framing of complex systems a necessary one. The fungus that attacks the scale is most efficient when the scale is hyper dense at a local level, something that cannot happen unless it is under the protection of a mutualistic ant, which deters the other predator (the beetle), which, however, is able to take advantage of a spatial pattern that is self-organized through a Turing-like process, and so forth. Indeed, we argue that the understanding we claim to have of this system so far comes from detailed study, both empirical and theoretical, and, most importantly is dramatically enriched through the application of some of the concepts newly developed in the distinct field of complex systems. Almost 10 years ago, some of us published a summary of this overall system (Vandermeer et al. 2010), suggesting that understanding it required more than just an identification of who eats whom. This update emphasizes that point.

Our narrative in the present article is perhaps a bit heterodox. We study a very complicated system (see figure 17), and we seek to understand it through theoretical ecology. To some, at least in the recent past, this might imply a large-scale computer model or sophisticated data manipulation. Our approach is distinct, recalling the wisdom of Levins' (1966) paper on the strategy of model building. We seek to understand, at a deep level, how this system works, not necessarily for the purpose of predicting its future state. We offer theoretical propositions, many of which are stimulated by mathematical arguments, but we do not seek what postmodern thinkers would have called a “totalizing discourse” with a large-scale model. Rather, we seek to use recent advances in complex systems as a way of stimulating thought, with the mathematical models that go along with them as “educating our intuition,” as Levins urged frequently. The models themselves (all of which can be extracted from the individual studies cited in the references) represent approximate metaphors for this complex reality, all fitting into a hierarchy of understanding (Levins 1966), which is mainly qualitative even though originally formulated through mathematical reasoning.

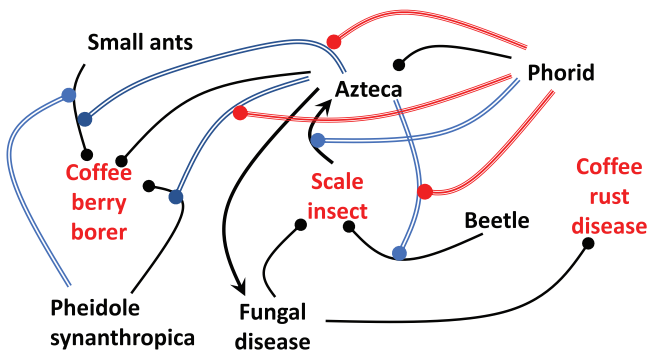


Figure 17. Extending the diagram of figure 10 to include all three pests and emphasizing how the three subcomponents are interconnected. The black connectors represent direct connections, the blue connectors (double lines) represent second-order effects, and the red connectors (triple lines) represent third-order connectors. The small filled circles represent negative effects, and the arrowheads represent positive effects.

Furthermore, our claim that this is a complex reality is meant to imply something deeper than the obvious claim that it is complicated. It is a complex system. Systems can be complicated but not complex and complex but not complicated. For example, if the only players in the system were *Azteca*, *C. viridis*, and *A. orbigera*, the system wouldn't be exceptionally complicated (only three players), but it would be a complex system, because it would have a clear emergent property (self-organization). Even adding the phorid would mean two predators and two prey, but the spatial pattern that emerges and the dependence of one system on a second system operative at a completely distinct time scale is an essential structural component of the system as a whole. The emergence would defy understanding if only the separate component parts were studied, which is to say if it were approached from a purely reductionist perspective. If the only players were the ants and the coffee berry borer, but the ants did not exhibit trait-mediated indirect interactions, the system would be complicated (many species of ants) but not necessarily complex. This distinction between complicated and complex is important for our narrative. Because it is a complex system, it requires a more holistic approach to understand and manage, and there's more potential for surprise (e.g., regime shifts, nonlinearities, chaos). A merely complicated system would not have these characteristics.

That our model system is coffee is significant in several ways. First, traditional coffee management, with its characteristic shade trees, helps to create landscapes that are friendly to biodiversity conservation (Perfecto et al. 1996, Perfecto and Vandermeer 2015). It is a classic high-quality matrix for all sorts of animals and plants. Second, it involves a commodity that is of extremely high value, sometimes the main source of wealth for entire countries. Third, it is the basis of livelihood for millions of small farmers the world over. Fourth, when properly cultivated with shade, it joins

other agroforestry systems in the worldwide struggle against climate change. Given all that, understanding the details of its operation would seem worthwhile, and marshaling recent insights from complex systems to anchor that narrative brings one of the classical questions of community ecology (control from above) into focus as a practical issue. Consequently, besides being of potential importance for ecology, it makes ecology important for some practical aspects of this important crop. It is, for example, evident from only a qualitative understanding of the control from above system that a key element is the species of ant that nests in the shade trees and that, if those shade trees are eliminated (as some advisories suggest), the whole control structure will be dramatically interrupted.

Questions also arise about generality. Does this model system reflect something more general about the structure of control from above, or does it simply reflect interactions of this one particular system? First, most terrestrial systems have a spatial component involved, and framing the spatial component as one in which a subsystem operates to effectively create a spatial pattern in which other subsystems may operate is likely to apply frequently. Indeed, the idea of a predator-prey system generating a Turing pattern may be increasingly appreciated as more research programs interrogate the idea (e.g., Alonso et al. 2002, Baurmann et al. 2007). Second, population dynamics unfolding on this space are likely to be nonlinear, and this nonlinearity will frequently be of the form that critical transitions lead to an alternative equilibrium within hysteretic zones, which may be multiple and constrain the herbivores above which control is being exerted (Ong and Vandermeer 2018, Vandermeer and Perfecto 2019). Third, the idea that multiple herbivores have their own suite of controlling factors is almost certainly true, but the idea that there will be connections, even if weak, with other subcomponents of the control from above, is likely to be characteristic. These three generalities encompass the complex systems topics of Turing pattern formation, critical transitions, hysteresis, chaos, basin boundary collisions, trait-mediated indirect interactions, and scale-dependent spatial processes, all of which are exemplified in our model system, and certainly may be embedded in other systems of control from above. The message is not that these particular topics are essential but, rather, that control from above is not the one-dimensional process frequently imagined of a predator guild preying on a prey guild but, instead, a complex community of predators and parasites and diseases that interact with one another in complicated ways to eventually generate a self-organized system that exerts effective control over the herbivory.

Much as one might say that the vertebrate circulatory system is responsible for bringing oxygen to each cell in the body, one might similarly simplify and say that natural enemies in the coffee agroecosystem are responsible for the regulation of potential pests. However, it is the heart, the veins, the arteries, exchanges across membranes, and so forth that tell the real story of how the delivery of oxygen

to our tissues actually happens. It is a complex system, the details of which are certainly of interest to health and healing. Similarly, in our agroecosystem example, the subsystem that creates large-scale pattern sets the stage for a subsystem involving a predator and a disease that affect regulation of one pest, whereas the community structure of ants determines the efficiency of their predacious activities on a second pest and the disease that helps regulate the first pest is an antagonist to the third pest. This is all to say that yes, it is control from above, but that control is delivered through the ecological complexity of the community of natural enemies. It is misleading to suggest that listing the natural enemies and merely identifying them as such is sufficient. It is only through the lens of the reality of its state as a complex system that we may gain full appreciation of the ecological principle of top-down control, which then can be fully exploited in attempts to aid the management of this important agroecosystem.

There is something of a conundrum in this narrative. Although it is clear that knowledge of all the ecological complexity could inform practical decisions that producers might want to make, is such detailed knowledge really necessary to provide useful advice to the farmer? If ecological knowledge of the particular system is primitive, could well-meaning agroecological advisors give advice that will have unintended negative consequences? Post-WWII industrial agriculture enthusiasts embraced DDT and other pesticides creating the well-known pesticide treadmill that haunts us still today. Indeed, that is one of the issues that caused many environmentally conscious analysts to call for the science of ecology to be more actively embraced by agricultural planners. However, ecology is complicated. Secondary consequences cannot necessarily be predicted short of detailed study and the normal rules of thumb extrapolated from a few experiments or extralocal traditions could backfire. Perhaps the famous medical practitioner's oath *primum non nocere* (first do no harm) makes sense in agriculture as well.

As farmers seek solutions to perceived problems on their farms, agroecologists rightly wish to use the science of ecology to help. However, frequently (most of the time), ecological knowledge of the particular system is not very well understood because it is only recently that agroecological advocates have begun to break into the mainstream, and the basic research required to understand some of the vexing problems the farmers face has yet to be done. It is therefore common to use a few rules of thumb: avoid monocultures, don't poison your natural enemies, maintain healthy soil, and so on. Such rules of thumb, on the basis of perceived ecological rules, for the most part make sense and probably conform well to the admonition *primum non nocere*. However, it is worth remembering the dust bowl, pest resurgence following pesticides, ocean dead zones, and other consequences that we live with today because a previous generation of farm advocates, equally sincere in their desires to help farmers, were prematurely confident in the ability of their tools to help the farmer.

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References cited

- Abrams PA, Walters CJ. 1996. Invulnerable prey and the paradox of enrichment. *Ecology* 77: 1125–1133.
- Alonso D, Bartumeus F, Catalan J. 2002. Mutual interference between predators can give rise to Turing spatial patterns. *Ecology* 83: 28–34.
- Armbrecht I, Gallego MC. 2007. Testing ant predation on the coffee berry borer in shaded and sun coffee plantations in Colombia. *Entomologia Experimentalis et Applicata* 124: 261–267.
- Avelino J, Romero-Gurdián A, Cruz-Cuellar HF, Declerck FA. 2012. Landscape context and scale differentially impact coffee leaf rust, coffee berry borer, and coffee root-knot nematodes. *Ecological Applications* 22: 584–596.
- Avelino J, Cristancho M, Georgiou S, Imbach P, Aguilar L, Bornemann G, Läderach P, Anzueto F, Hruska AJ, Morales C. 2015. The coffee rust crises in Colombia and Central America 2008–2013: Impacts, plausible causes and proposed solutions. *Food Security* 7: 303–321.
- Barrera JF, Baker PS, Schwarz A, Valenzuela J. 1990. Introducción de dos especies de parasitoides africanos a México para el control biológico de la broca del caféto *Hypothenemus hampei* Ferr. (Coleoptera: Scolytidae). *Folia Entomologica Mexicana* 70: 245–247.
- Baurmann M, Gross T, Feudel U. 2007. Instabilities in spatially extended predator–prey systems: Spatio-temporal patterns in the neighborhood of Turing–Hopf bifurcations. *Journal of Theoretical Biology* 245: 220–229.
- Bustillo AE, Cardenas R, Posada FJ. 2002. Natural enemies and competitors of *Hypothenemus hampei* Ferrari (Coleoptera: Scolytidae) in Colombia. *Neotropical Entomology* 31: 635–639.
- Chain-Guadarrama A, Martínez-Salinas A, Aristizábal N, Ricketts TH. 2019. Ecosystem services by birds and bees to coffee in a changing climate: A review of coffee berry borer control and pollination. *Agriculture, Ecosystems and Environment* 280: 53–67.
- 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, García-Ballinas JA, Philpott SM. 2015. Local, landscape, and diversity drivers of predation services provided by ants in a coffee landscape in Chiapas, Mexico. *Agriculture, Ecosystems and Environment* 201: 83–91.
- De La Rosa W, Alatorre R, Barrera JF, Toriello C. 2000. Effect of *Beauveria bassiana* and *Metarhizium anisopliae* (Deuteromycetes) on the coffee berry borer (Coleoptera: Scolytidae) under field conditions. *Journal of Economic Entomology* 93: 1409–1414.
- Ehrlich PR, Birch LC. 1967. The “balance of nature” and “population control.” *American Naturalist* 101: 97–107.
- Ennis KK, Philpott SM. 2017. Strong influences of a dominant, ground-nesting ant on recruitment, and establishment of ant colonies and communities. *Biotropica* 49: 521–530.
- Golubski AJ, Westlund EE, Vandermeer J, Pascual M. 2016. Ecological networks over the edge: Hypergraph trait-mediated indirect interaction (TMII) structure. *Trends in Ecology and Evolution* 31: 344–354.
- Gómez J, Barrera JF, Rojas JC, Macias-Samano J, Liedo JP, Cruz-Lopez L, Badii MH. 2005. Volatile compounds released by disturbed females of *Cephalonomia stephanoderis* (Hymenoptera: Bethyilidae): A parasitoid of the coffee berry borer *Hypothenemus hampei* (Coleoptera: Scolytidae). *Florida Entomologist* 88: 180–187.
- Gonthier DJ, Ennis KK, Philpott SM, Vandermeer J, Perfecto I. 2013. Ants defend coffee from berry borer colonization. *BioControl* 58: 815–820.
- Haeckel E. 1866. *Generelle Morphologie der Organismen. Allgemeine Grundzüge der organischen Formen- Wissenschaft, mechanisch*

- begründet durch die von Charles Darwin reformierte Descendenz-Theorie. Reimer.
- Hairston NG, Smith FE, Slobodkin LB. 1960. Community structure, population control, and competition. *American Naturalist* 94: 421–425.
- Hajian-Forooshani Z, Rivera Salinas IS, Jiménez-Soto E, Perfecto I, Vandermeer J. 2016. Impact of regionally distinct agroecosystem communities on the potential for autonomous control of the coffee leaf rust. *Environmental Entomology* 2016: 1–6.
- Haydon DT, Lloyd AL. 1999. On the origins of the Lotka-Volterra equations. *Bulletin of the Ecological Society of America* 80: 205–206.
- Howard RW, Infante F. 1996. Cuticular hydrocarbons of the host-specific ectoparasitoid *Cephalonomia stephanoderis* (Hymenoptera: Bethylinidae) and its host the coffee berry borer (Coleoptera: Scolytidae). *Annals of the Entomological Society of America* 89: 700–709.
- Hsieh HY, Perfecto I. 2012. Trait-mediated indirect effects of phorid flies on ants. *Psyche: A Journal of Entomology* 2012: 11.
- Hsieh HY, Liere H, Soto EJ, Perfecto I. 2012. Cascading trait-mediated interactions induced by ant pheromones. *Ecology and Evolution* 2: 2181–2191.
- Huffaker CB. 1958. Experimental studies on predation: Dispersion factors and predator–prey oscillations. *Hilgardia* 27: 343–383.
- Hunter MD, Price PW. 1992. Playing chutes and ladders: Heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology* 73: 724–732.
- Hunter MD. 2016. *The Phytochemical Landscape: Linking Trophic Interactions and Nutrient Dynamics*, vol. 74. Princeton University Press.
- Infante F, Mumford J, Baker P. 2005. Life history studies of *Prorops nasuta*, a parasitoid of the coffee berry borer. *BioControl* 50: 259–270.
- Iverson A, Jackson D, Burnham R, Perfecto I, Vandenberg N, Vandermeer J. 2018. Species complementarity in two myrmecophilous lady beetle species in a coffee agroecosystem: Implications for biological control. *BioControl* 63: 253–264.
- Jackson D, Skillman J, Vandermeer J. 2012. Indirect biological control of the coffee leaf rust, *Hemileia vastatrix*, by the entomogenous fungus *Lecanicillium lecanii* in a complex coffee agroecosystem. *Biological Control* 61: 89–97.
- Jackson DW, Zemenick K, Huerta G. 2012a. Occurrence in the soil and dispersal of *Lecanicillium lecanii*, a fungal pathogen of the green coffee scale (*Coccus viridis*) and coffee rust (*Hemileia vastatrix*). *Tropical and Subtropical Agroecosystems* 15: 389–401.
- Jackson D, Vandermeer J, Allen D, Perfecto I. 2014. Self-organization of background habitat determines the nature of population spatial structure. *Oikos* 123: 751–761.
- 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.
- Jackson D, Vandermeer J, Perfecto I, Philpott SM. 2014. Population responses to environmental change in a tropical ant: The interaction of spatial and temporal dynamics. *PLOS ONE* 9 (art. e97809).
- Jha S, Allen D, Liere H, Perfecto I, Vandermeer J. 2012. Mutualisms and population regulation: Mechanism matters. *PLOS ONE* 7 (art. e43510).
- Jiménez-Soto E, Cruz-Rodríguez J, Vandermeer J, Perfecto I. 2013. *Hypothenemus hampei* (Coleoptera: Curculionidae) and its interactions with *Azteca instabilis* and *Pheidole synanthropica* (Hymenoptera: Formicidae) in a shade coffee agroecosystem. *Environmental Entomology* 42: 915–924.
- Johnson MD, Kellermann JL, Stercho AM. 2010. Pest reduction services by birds in shade and sun coffee in Jamaica. *Animal Conservation* 13: 140–147.
- Karp DS, Mendenhall CD, Sandí RF, Chaumont N, Ehrlich PR, Hadly EA, Daily GC. 2013. Forest bolsters bird abundance, pest control, and coffee yield. *Ecology Letters* 16: 1339–1347.
- Kellermann JL, Johnson MD, Stercho AM, Hackett SC. 2008. Ecological and economic services provided by birds on Jamaican Blue Mountain coffee farms. *Conservation Biology* 22: 1177–1185.
- Lane PA. 2018. The road before us: Have we come to a “fork in the road” in defining complexity?. *Ecological Complexity* 35: 1–5.
- Larsen A, Philpott SM. 2010. Twig-nesting ants: The hidden predators of the coffee berry borer in Chiapas, Mexico. *Biotropica* 42: 342–347.
- Levins R. 1966. The strategy of model building in population biology. *American Scientist* 54: 421–431.
- Levins R. 1998. Qualitative mathematics for understanding, prediction, and intervention in complex ecosystems. Pages 178–204 in Rapport D, Contanza R, Epstein P, Gaudet C, Levins R, eds. *Ecosystem Health*. Blackwell Science.
- Li K, Vandermeer JH, Perfecto I. 2016. Disentangling endogenous versus exogenous pattern formation in spatial ecology: A case study of the ant *Azteca sericeasur* in southern Mexico. *Royal Society Open Science* 3: 160073.
- Liere H, Larsen A. 2010. Cascading trait-mediation: Disruption of a trait-mediated mutualism by parasite-induced behavioral modification. *Oikos* 119: 1394–1400.
- Liere H, Perfecto I. 2014. Cheating on a mutualism: Indirect benefits of ant attendance to a coccidiphagous coccinellid. *Environmental Entomology* 37: 143–149.
- Liere H, Perfecto I, Vandermeer J. 2014. Stage-dependent responses to emergent habitat heterogeneity: Consequences for a predatory insect population in a coffee agroecosystem. *Ecology and Evolution* 4: 3201–3209.
- Liere H, Jackson D, Vandermeer J. 2012. Ecological complexity in a coffee agroecosystem: Spatial heterogeneity, population persistence and biological control. *PLOS ONE* 7 (art. e45508).
- Lindeman RL. 1942. The trophic-dynamic aspect of ecology. *Ecology* 23: 399–417.
- MacDonald AJ, Jackson D, Zemenick K. 2013. Indirect effects of a fungal entomopathogen, *Lecanicillium lecanii* (Hypocreales: Clavicipitaceae), on a coffee agroecosystem ant community. *Environmental Entomology* 42: 658–667.
- Mathis KA, Philpott SM. 2012. Current understanding and future prospects of host selection, acceptance, discrimination, and regulation of phorid fly parasitoids that attack ants. *Psyche: A Journal of Entomology* 2012: 9.
- Mathis KA, Tsutsui ND. 2016. Cuticular hydrocarbon cues are used for host acceptance by *Pseudacteon* spp. phorid flies that attack *Azteca sericeasur* ants. *Journal of Chemical Ecology* 42: 286–293.
- Mathis KA, Philpott SM, Moreira RF. 2011. Parasite lost: Chemical and visual cues used by *Pseudacteon* in search of *Azteca instabilis*. *Journal of Insect Behavior* 24: 186–199.
- McCook S, Vandermeer J. 2015. The big rust and the red queen: Long-term perspectives on coffee rust research. *Phytopathology* 105: 1164–1173.
- Méndez VE, Castro-Tanzi S, Goodall K, Morris KS, Bacon CM, Läderach P, Morris WB, Georgeglou-Laxalde MU. 2011. Livelihood and Environmental Trade-Offs of Climate Mitigation in Smallholder Coffee Agroforestry Systems. Routledge.
- Moguel P, Toledo VM. 1999. Biodiversity conservation in traditional coffee systems of Mexico. *Conservation Biology* 13: 11–21.
- Monagan IV, Morris JR, Davis Rabosky AR, Perfecto I, Vandermeer J. 2017. Anolis lizards as biocontrol agents in mainland and island agroecosystems. *Ecology and Evolution* 7: 2193–2203.
- Morris JR, Perfecto I. 2016. Testing the potential for ant predation of immature coffee berry borer (*Hypothenemus hampei*) life stages. *Agriculture, Ecosystems, and Environment* 233: 224–228.
- Morris JR, Jimenez-Soto E, Philpott SM, Perfecto I. 2018. Ant-mediated (Hymenoptera: Formicidae) biological control of the coffee berry borer: Diversity, ecological complexity, and conservation biocontrol. *Myrmecological News* 26: 1–17.
- Morris JR, Vandermeer J, Perfecto I. 2015. A keystone ant species provides robust biological control of the coffee berry borer under varying pest densities. *PLOS ONE* 10 (art. e0142850).
- Murdoch WW. 1969. Switching in general predators: Experiments on predator specificity and stability of prey populations. *Ecological Monographs* 39: 335–354.

- Murphy ST, Moore D. 1990. Biological control of the coffee berry borer, *Hypothenemus hampei* Ferrari (Coleoptera, Scolytidae): Previous programmes and possibilities for the future. *Biocontrol News and Information* 11: 107–117.
- Nair PR, Nair VD, Kumar BM, Showalter JM. 2010. Carbon sequestration in agroforestry systems. Pages 237–307 in Sparks DL, ed. *Advances in Agronomy*, vol. 108. Academic Press.
- Odum HT. 1956. Primary production in flowing waters. *Limnology and Oceanography* 1: 102–117.
- Odum EP. 1959. *Fundamentals of Ecology*. Saunders.
- Odling-Smee FJ, Laland KN, Feldman MW. 1996. Niche construction. *American Naturalist* 147: 641–648.
- Ong TW, Vandermeer J. 2014. Antagonism between two natural enemies improves biological control of a coffee pest: The importance of dominance hierarchies. *Bio Control* 76: 107–113.
- Ong TWY, Vandermeer J. 2015. Coupling unstable agents in biological control. *Nature Communications* 6: 5991.
- Ong TWY, Allen D, Vandermeer J. 2018. Huffaker revisited: Spatial heterogeneity and the coupling of ineffective agents in biological control. *Ecosphere* 9: e02299.
- Ong TWY, Vandermeer J. 2018. Multiple hysteretic patterns from elementary population models. *Theoretical Ecology* 11: 433–439.
- Pardee GL, Philpott SM. 2011. Cascading indirect effects in a coffee agroecosystem: Effects of parasitic phorid flies on ants and the coffee berry borer in a high-shade and low-shade habitat. *Environmental Entomology* 40: 581–588.
- Pascual M, Guichard F. 2005. Criticality and disturbance in spatial ecological systems. *Trends in Ecology and Evolution* 20: 88–95.
- Pendergrast M. 2010. *Uncommon Grounds: The History of Coffee and How it Transformed Our World*. Basic Books.
- Perfecto I, Rice RA, Greenberg R, Van der Voort ME. 1996. Shade coffee: A disappearing refuge for biodiversity. *BioScience* 46: 598–608.
- Perfecto I, Vandermeer J. 2006. The effect of an ant/scale mutualism on the management of the coffee berry borer (*Hypothenemus hampei*) in southern Mexico. *Agriculture, Ecosystems and Environment* 117: 218–221.
- Perfecto I, Vandermeer J. 2008. Spatial pattern and ecological process in the coffee agroecosystem. *Ecology* 89: 915–920.
- Perfecto I, Vandermeer J. 2013. Ant assemblage on a coffee farm in southern Mexico: Spatial mosaic versus shifting patchwork. *Environmental Entomology* 42: 38–48.
- Perfecto I, Vandermeer J. 2015. *Coffee Agroecology: A New Approach to Understanding Agricultural Biodiversity, Ecosystem Services and Sustainable Development*. Routledge.
- Philpott SM. 2010. A canopy dominant ant affects twig-nesting ant assembly in coffee agroecosystems. *Oikos* 119: 1954–1960.
- Philpott SM, Perfecto I, Vandermeer J. 2008. Effects of predatory ants on lower trophic levels across a gradient of coffee management complexity. *Journal of Animal Ecology* 77: 505–511.
- Philpott SM, Perfecto I, Vandermeer J. 2014. Behavioral diversity of predatory arboreal ants in coffee agroecosystems. *Environmental Entomology*, 37: 181–191.
- Philpott SM, Armbrrecht I. 2006. Biodiversity in tropical agroforests and the ecological role of ants and ant diversity in predatory function. *Ecological Entomology* 31: 369–377.
- Philpott SM, Pardee GL, Gonthier DJ. 2012. Cryptic biodiversity effects: Importance of functional redundancy revealed through addition of food web complexity. *Ecology* 93: 992–1001.
- 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.
- Power ME. 1992. Top-down and bottom-up forces in food webs: Do plants have primacy. *Ecology* 73: 733–746.
- Rivera-Salinas IS, Hajian-Forooshani Z, Jiménez-Soto E, Cruz-Rodríguez JA, Philpott SM. 2018. High intermediary mutualist density provides consistent biological control in a tripartite mutualism. *Biological Control* 118: 26–31.
- Scheffer M. 2009. *Critical Transitions in Nature and Society*, vol. 16. Princeton University Press.
- Scheffer M et al. 2012. Anticipating critical transitions. *Science* 338: 344–348.
- Sponagel KW. 1994. La Broca del Café *Hypothenemus hampei* en Plantaciones de Café Robusta en la Amazonía Ecuatoriana. *Fachverlag*.
- Stauffer RC. 1957. Haeckel, Darwin, and Ecology. *Quarterly Review of Biology* 32: 138–144.
- Tansley AG. 1920. The classification of vegetation and the concept of development. *Journal of Ecology* 8: 118–149.
- Tilley H. 2011. *Africa as a Living Laboratory: Empire, Development, and the Problem of Scientific Knowledge, 1870–1950*. University of Chicago Press.
- Turing AM. 1952. The chemical basis of morphogenesis. *Philosophical Transactions of the Royal Society B* 237: 37–72.
- Uno S. 2007. *Effects of Management Intensification on Coccids and Parasitic Hymenoptera in Coffee Agroecosystems in Mexico*. PhD dissertation, University of Michigan.
- Vandermeer J, Perfecto I, Philpott S. 2010. Ecological complexity and pest control in organic coffee production: uncovering an autonomous ecosystem service. *BioScience*, 60: 527–537.
- Vandermeer J. 2011. Inevitability of surprise in agroecosystems. *Ecological Complexity* 8: 377–382.
- Vandermeer J. 2008. The niche construction paradigm in ecological time. *Ecological Modelling* 214: 385–390.
- Vandermeer J, Perfecto I. 2006. A keystone mutualism drives pattern in a power function. *Science* 311: 1000–1002.
- Vandermeer J, Rohani P. 2014. The interaction of regional and local in the dynamics of the coffee rust disease. *arXiv at: http://arxiv.org/abs/1407.8247*.
- Vandermeer J, Jackson D. 2018. Stabilizing intransitive loops: Self-organized spatial structure and disjoint time frames in the coffee agroecosystem. *Ecosphere*, 9: e02489.
- Vandermeer J, Perfecto I. 2017. *Ecological Complexity and Agroecology*. Routledge.
- Vandermeer J, Perfecto I. 2018. Ecological complexity in the Rosennean framework. *Ecological Complexity* 35: 45–50.
- Vandermeer J, Perfecto I. 2019. Hysteresis and critical transitions in a coffee agroecosystem. *Proceedings of the National Academy of Sciences* 116: 15074–15079.
- Vandermeer J, Jackson D, Perfecto I. 2014. Qualitative dynamics of the coffee rust epidemic: Educating the intuition with theoretical ecology. *BioScience* 64: 210–218.
- Vandermeer J, Hajian-Forooshani Z, Perfecto I. 2017. The dynamics of the coffee rust disease: An epidemiological approach using network theory. *European Journal of Plant Pathology* 150: 1001–1010.
- 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.
- Vandermeer J, Perfecto I, Philpott SM. 2008. Clusters of ant colonies and robust criticality in a tropical agroecosystem. *Nature* 451: 457–459.
- Vandermeer J, Yodzis P. 1999. Basin boundary collision as a model of discontinuous change in ecosystems. *Ecology* 80: 1817–1827.
- Vandermeer J, Rohani P, Perfecto I. 2015. Local dynamics of the coffee rust disease and the potential effect of shade. *arXiv preprint arXiv:1510.05849*.
- Vega FE, Infante F, Castillo A, Jaramillo J. 2009. The coffee berry borer, *Hypothenemus hampei* Ferrari (Coleoptera: Curculionidae): A short review, with recent findings and future research directions. *Terrestrial Arthropod Reviews* 2: 129.
- Werner EE, Peacor SD. 2003. A review of trait-mediated indirect interactions in ecological communities. *Ecology* 84: 1083–1100.
- Williams-Guillen K, Perfecto I, Vandermeer J. 2008. Bats limit insects in a neotropical agroforestry system. *Science* 320: 70.

Yitbarek S, Vandermeer JH, Perfecto I. 2017. Competitive release from native range does not predict invasive success of a globally dominant exotic ant species. *bioRxiv* (239277).

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