

Qualitative Dynamics of the Coffee Rust Epidemic: Educating Intuition with Theoretical Ecology

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*The coffee rust disease (agent *Hemileia vastatrix*), a chronic and sometimes severe problem in Mesoamerica that burst dramatically onto the scene late in 2012, threatens the livelihoods of millions of farmers, and will potentially distort the economies of many of the world's most vulnerable nations. The immediate drivers of this particular epidemic are not known. Recent research, however, suggests that its source may be related to the simplification of a complex web of ecological interactions, a web that defies simple one-on-one attempts at management. Drawing on this research, we argue that the underlying ecological interrelationships in the system may make this particular agronomic problem intractable if conventional control methods are all that are implemented. It is reasonable to suggest that the situation calls for a revitalization of what pest control specialists have come to call autonomous pest control.*

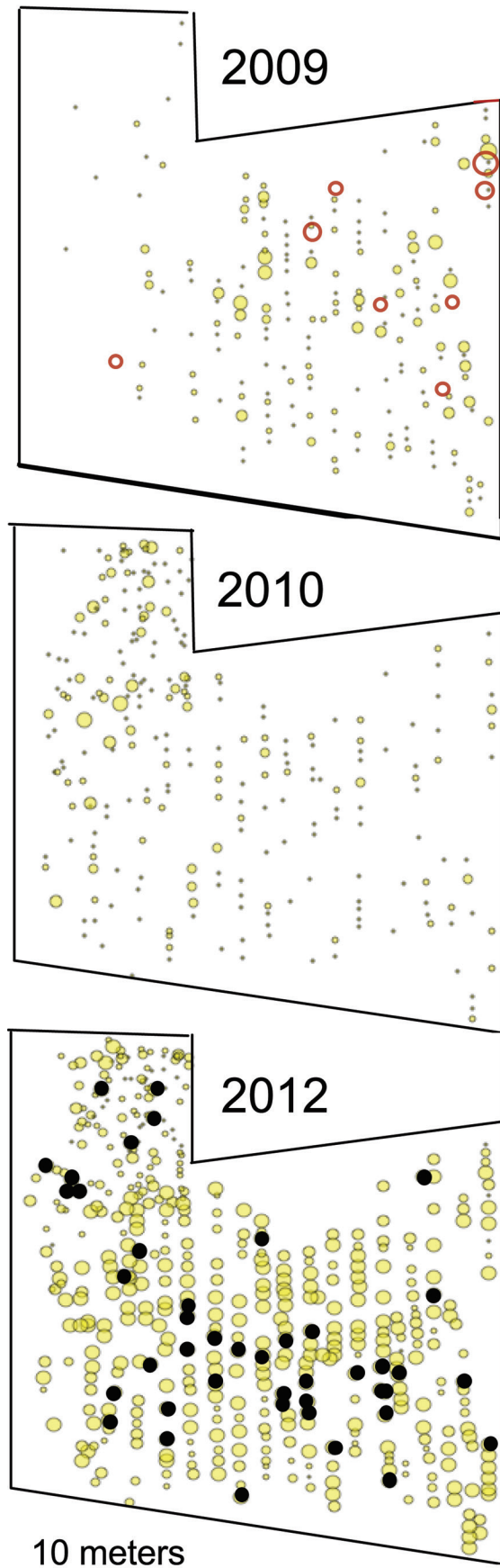
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Coffee is reported to be one of the most traded commodities in the world (Pendergast 1999), the base of economic support for millions of small farmers (Bacon 2004), and an important economic engine for many tropical countries—more than 20 in Latin America alone. The recent epidemic of the coffee rust disease from Mexico to Peru has been especially severe, with some reports anticipating as much as a 40%–50% reduction in yield over the entire region, which potentially affects many coffee-producing nations in Latin America (Cressey 2013). For example, our regular monitoring of a small plot in southern Mexico reflects the severity of the current epidemic (figure 1); over 60% of the plants in this plot experienced more than 80% defoliation, and almost 9% expired completely. Last year, the Costa Rican government signed an emergency decree allocating \$4 million to fight the spread of the disease (Inside Costa Rica 2013). Similar patterns have been reported anecdotally from Mexico to Peru (Cressey 2013). In all cases, the recommended measures include the application of fungicides—a strategy that may be counterproductive, as some recent research has suggested (Vandermeer et al. 2009, Jackson et al. 2012).

The history of the disease serves as an important backdrop to the current crisis. It was first reported in Sri Lanka (then Ceylon) in 1868 and, within 5 years, had spread across the entire island (Monaco 1977). It became so devastating in Sri Lanka, southern India, and Java that coffee agriculture

had to be effectively abandoned (McCook 2006). Such a seemingly apocalyptic event in history understandably generates fear that it could happen again. An outbreak in Angola in 1966 may have been the source of a trans-Atlantic dispersal to Bahia, Brazil (Bowden et al. 1971), and, within a few years, the disease was found throughout that state and, subsequently, throughout Brazil. Anticipation of its spread to the north caused considerable concern, and farmers throughout the region were extensively warned of the coming disaster (Fulton 1984, Schieber and Zentmyer 1984). However, the actions recommended for farmers were only partially based on evidence, and many farmers ignored the recommendations, anyway. In the end, worries that the disease would be as devastating in the Americas as it had been a century earlier in Asia were seemingly overblown, and the pathogen remained a troublesome but not devastating problem for coffee production. Even those farms forgoing the recommended phytosanitary or control methods were not subject to the devastation that had been feared. Why the dire predictions never materialized until now is not certain. It has been suggested, however, that the complexity of the coffee ecosystem, especially in its more traditional form, may have previously acted as a buffer against epidemics of the disease (Avelino et al. 2004, Jackson et al. 2009, 2012, Vandermeer et al. 2009, 2010).

Dealing with the problem is challenging, with current recommendations focused on fungicides and phytosanitation



procedures based on uncertain background information. Indeed, the complexity of this disease has been challenging for conventional disease control strategies (Kushalappa and Eskes 1989, Avelino et al. 2004). Rather, drawing on work by both ecologists (Soto-Pinto et al. 2002, Jackson et al. 2009, 2012, Vandermeer et al. 2009, 2010) and phytopathologists (Kushalappa and Eskes 1989, Avelino et al. 2004, 2012), it could be the larger ecological structure of the agroecosystem that needs to be considered, which echoes the many recent calls for a more nuanced approach to the management of ecosystem services, in general, (Perfecto and Vandermeer 2010, Tscharrntke et al. 2012, Vandermeer and Perfecto 2012) and to pest control, specifically (Lewis et al. 1997, Vandermeer et al. 2010). In the present article, we argue that specific well-known ecological complications form a complex, dynamic system that allows both the sustained maintenance of control and an occasional escape from control under the same ecological structures. However, we also suggest that small, seemingly trivial changes in environmental conditions could generate dramatic shifts in the underlying dynamics of the disease.

The coffee rust disease as an element of a larger ecosystem

The overall system includes, first, the agent of the coffee rust disease, the fungus *Hemileia vastatrix* (figure 2a). An important additional component of the general agroecosystem is a mutualistic association of the ant *Azteca instabilis* with the

Figure 1. Incidence of coffee leaf rust (*Hemileia vastatrix*) over a 4-year period in one permanent plot in a shaded coffee farm in Chiapas, Mexico. The farm is “Finca Irlanda,” a farm of approximately 300 hectares, managed as a typical shaded system, with a single owner, and basically representative of coffee production in the region. The plots for the years 2009 and 2010 show the relative number of leaves with rust lesions. The largest symbols represent the most leaves for that year; all of the other sizes are relative to that number (data unavailable for 2011). Also in year 2009, the position of concentrations of the white halo fungus (*Lecanicillium lecanii*) is shown with open and empty circles (colored red in the online version). The size of the circle is proportional to a qualitative estimate of the size of the infestation on the scale insect, *Coccus viridis* (no concentrations existed in 2010). Note the shift in concentration of the disease between 2009 and 2010, which was due to a local concentration of *L. lecanii* (see Jackson et al. 2012 for an interpretation). Year 2012 is an estimate of the percentage defoliation of the same bushes. The largest symbols are 100% defoliated. The black symbols represent trees judged to be dead (dead trees were encountered only in 2012). The odd shape of the sampling area is due to complicated local topographic features. All of the samples were taken in December and January, with the year being recorded as that of December.

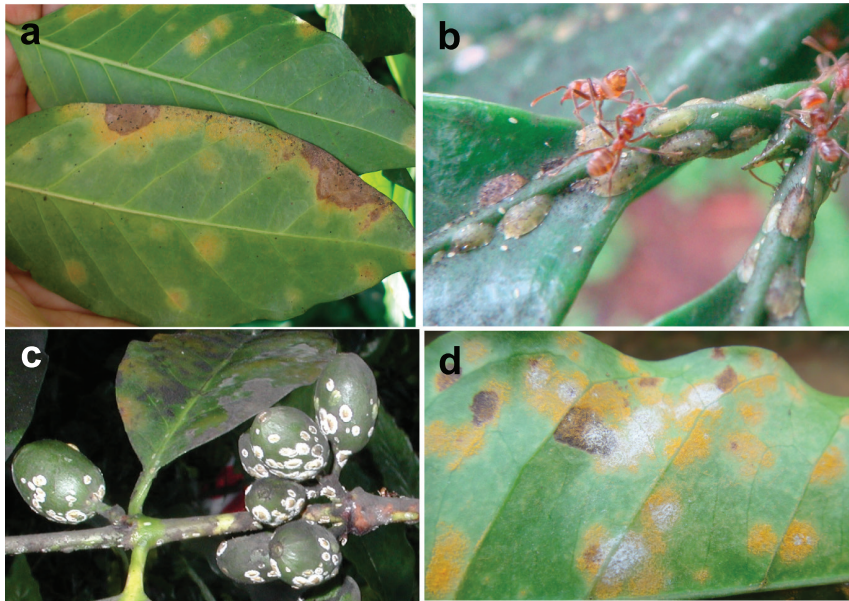


Figure 2. The four actors in the relevant subsystem. (a) Lesions of the coffee rust, *Hemileia vastatrix* (the light lesions and necrotic tissue). (b) The arboreal nesting ant, *Azteca instabilis*, tending the green coffee scale, *Coccus viridis*. (c) Infestation of white halo fungus, *Lecanicillium lecanii*, on a concentrated population of the green coffee scale. White mycelial tissue surrounds each individual scale insect. (d) Coffee rust being attacked by white halo fungus (the granules are rust spores; the white mycelial tissue is white halo fungus). Photographs: John Vandermeer.

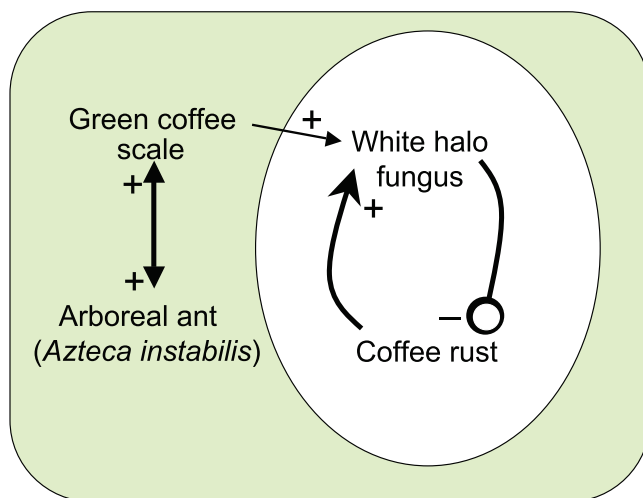


Figure 3. Diagram of the basic formulation. The white oval is the dynamic part (i.e., the part specifically modeled), and the shaded background represents the constant background (the constant parameters in the model). Although, in nature, it is all dynamic, the qualitative dynamics of the general system can be envisioned with this simplification. The arrowheads indicate positive effects, and the open circle indicates a negative effect.

green coffee scale (*Coccus viridis*), another potential pest of coffee (figure 2b; Vandermeer and Perfecto 2006). The

key element connecting the insect pest (green coffee scale) with the pathogen (coffee rust disease) is the white halo fungus (*Lecanicillium lecanii*), a well-known pathogen of the green coffee scale (figure 2c; Easwaramoorthy 1978, Reddy and Bhat 1989). It is mostly known as an entomopathogen occasionally promoted as biological control for various insect pests (Roditakis et al. 2000), but it is also known to attack other fungi—in particular, the coffee rust (figure 2d; Shaw 1988, Eskes 1989, Jackson et al. 2009, 2012). These four components (figure 2) are embedded in a much larger system of ecological interactions (Vandermeer et al. 2010), but some insight can be gained by considering only this small component of the larger system.

It is likely that the complexity of the larger system will preclude precise prediction of either the timing or the extent of an outbreak (Vandermeer et al. 2010). Nevertheless, the dynamics of these two fungi can be qualitatively envisioned within the key features of that larger system, a formulation that leads to the model developed below.

The formulation assumes, first, that the green coffee scale acts as if it were a refuge for the white halo fungus and, second, that the rust fungus (the agent of the rust disease in the coffee) is attacked by the white halo fungus, the latter of which gains energy from the attack. The generalized qualitative structure is illustrated in figure 3. The ant–scale mutualism (with all other associated elements; Vandermeer et al. 2010) provides an environmental backdrop within which the dynamics between the two fungi operate.

A qualitative theoretical model based on elementary ecological forces

The basic framework (figure 3) leads to a simple model with some important but unexpected qualitative consequences. The mycoparasitic fungus, *L. lecanii*, becomes dramatically epizootic as an entomopathogen whenever the scale insects, *C. viridis*, are at high local density (figure 2c; Jackson et al. 2012). The scale insects reach such densities only when they are tended by the ants (figure 2b; Vandermeer and Perfecto 2006). Once they have established, however, a given density of scale insects acts as if it were a fixed resource (Vandermeer and King 2010) from the point of view of the entomopathogenic and mycoparasitic fungus, *L. lecanii*. Therefore, the scale insect, as host to the *L. lecanii* fungus, provides a fundamental base that supplies spores of the latter to the general environment—which is to say that the scale insect density is partly responsible for setting the carrying capacity of the

Box 1. The relative abundance of *Lecanicillium lecanii* and *Hemileia vastatrix* over time.

We begin by assuming that the dynamics of *Lecanicillium lecanii* follow the simple logistic form

$$\frac{dL}{dt} = \lambda L \left[\frac{K_c - L}{K_c} \right],$$

where K_c is the carrying capacity of *L. lecanii* conditioned by the abundance of scale insects, which, for this simple model, we presume to be constant, and L is the abundance of *L. lecanii* in the system. The parameter λ is the intrinsic rate of natural increase of the white halo fungus. Assuming that λ is proportional to the abundance of *Hemileia vastatrix* in the system, H , we have $\lambda = aH$, and assuming that *H. vastatrix* in the absence of its controlling agent, *L. lecanii*, is logistic, we take the normal Lotka–Volterra assumptions for a predator and prey to obtain the following basic model:

$$\frac{dL}{dt} = caHL \left[\frac{K_c - L}{K_c} \right] - mL$$

and

$$\frac{dH}{dt} = rH[1 - H] - aHL \left[\frac{K_c - L}{K_c} \right],$$

where m is the independent mortality rate of *L. lecanii*, r is the intrinsic growth rate of *H. vastatrix*, and c is the conversion efficiency of *H. vastatrix* to *L. lecanii*. The equilibria can be found by setting the derivatives equal to zero and solving, and stability conditions can be determined by extracting eigenvalues for each equilibrium point, thus resulting in the four qualitatively distinct outcomes depicted in figure 4. Mathematical details can be found in Vandermeer and King (2010).

L. lecanii fungus. The basics of the model are illustrated in diagrammatic form in figure 3, and the mathematical detail is in box 1. Further analytical details can be found elsewhere (Vandermeer and King 2010). Here, we simply note the model's qualitatively distinct outcomes (figure 4).

In general, there are two possible stable equilibrium points—one a stable focus (damped oscillations; figure 4a), the other a node (asymptotic approach to a fixed point; figure 4d)—the existence of which depends on particular parameter values. At some parameter values (figure 4b, 4c), these two basic stable forms occur simultaneously, with a saddle point between them. Two simultaneous stable singularities at some parameter values reflect the well-known ecological form of alternative regimes: Regime 1, with a high carrying capacity of *L. lecanii*, maintains *H. vastatrix* under control (i.e., at a low density); regime 2, with a low carrying capacity of *L. lecanii*, results in an outbreak of *H. vastatrix* (i.e., at a high density).

Beginning with a high carrying capacity of *L. lecanii* (figure 4a), as the carrying capacity is reduced, the system undergoes a *blue-sky* bifurcation (in which two new singularities, a node and a saddle, appear “out of the blue”; figure 4b). The result is a system of two alternative attractors (figure 4b), with two basins of attraction separated by a *separatrix*, on which the saddle is located. In this case

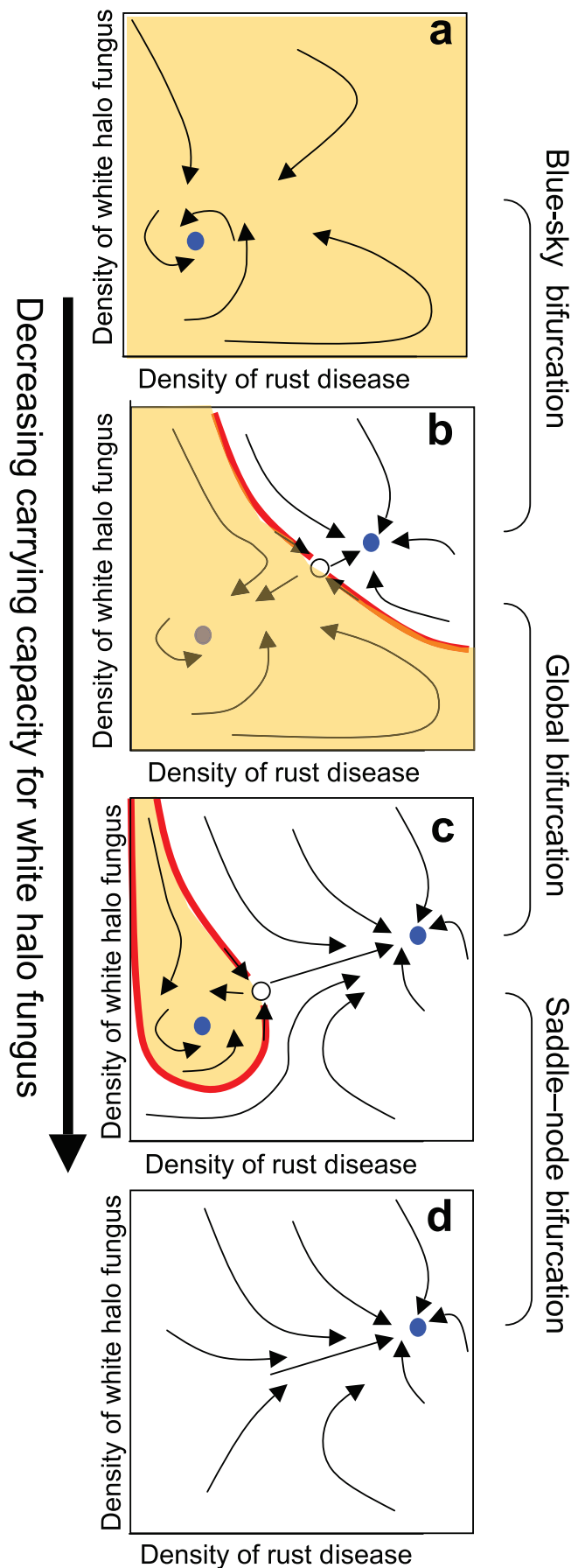
(figure 4b), it is evident that the disease might very well be maintained under control (i.e., at the focal point, which is a low density of *H. vastatrix*) for long periods of time. Indeed, if the densities of both fungi begin the growing season at low densities, the lower equilibrium point will be approached every year. However, as is always the case with alternative attractors, stochastic perturbations may result in occasional jumps over the separatrix separating the two ecological regimes, such that the *H. vastatrix* suddenly surges out of control (i.e., approaches the upper stable equilibrium point). This sort of outbreak would be expected to be non-recurring if indeed the system begins near zero every growing season.

With further reduction in the carrying capacity of *L. lecanii*, a rather more subtle bifurcation will occur. In this bifurcation (from figure 4b to figure 4c), the general organization of the vector field, itself, is transformed in a global bifurcation (Vandermeer and King 2010). This bifurcation (figure 4c) is curious in that the overall system appears not to have changed, because there remain two stable equilibria separated by a saddle point. However, even though there is an

equilibrium point for which *H. vastatrix* remains under control (the lower focal point), if the initial densities at the beginning of the growing season are always near zero, the system will always wind up at the upper equilibrium point—which is to say, with *H. vastatrix* at outbreak levels. This sort of outbreak would therefore be expected to recur every year.

Finally, further decreases in the carrying capacity generate a saddle–node bifurcation, such that the stable point representing control of the disease completely disappears (figure 4d). In this case, there is no opportunity at all for control.

Therefore, we see that, with a slow change in the carrying capacity of *L. lecanii*, it is possible to engender three sorts of bifurcations: first, a *blue-sky* bifurcation, in which a pair of equilibrium points—one a saddle the other a node—emerges; second, a global bifurcation, in which the underlying dynamical rules, themselves (the vector field), change; and third, a saddle–node bifurcation, in which a pair of equilibrium points, one a saddle and the other a focus, merge (at the point of bifurcation, the eigenvalues have zero complex parts, and, therefore, the focal point is formally a node at that point). Therefore, a system situated in the state shown in figure 4a may gradually transform, then suddenly switch to the state shown in figure 4b. What had been a highly robust and resilient control of the disease now becomes one that at least entertains the possibility of the pest's escaping control,



thus making the control potentially sensitive to stochastic perturbations. With further reduction in the carrying capacity of *L. lecanii*, conditions will change to present us with the arrangement in figure 4c. In this case, if the system begins near the origin every growing season, the disease will remain permanently out of control. So we go from a situation of complete control (figure 4a) to a system usually under control with an occasional outbreak if a stochastic perturbation pushes the system to cross the separatrix (figure 4b) and then to a system of recurring outbreaks (figure 4c, 4d).

Empirical support for the basic model framework

It is clear that this single fungus, the white halo fungus, is not likely to control the rust disease completely. However, even with only partial control, it should be possible to detect signals, albeit subtle ones, of the basic dynamics. In a series of field studies, we have indeed seen such subtle effects on several occasions (Vandermeer et al. 2009, Jackson et al. 2012). For example (see Jackson et al. 2012 for details), in figure 1, the switch from higher infections in the right-hand part of the plot in 2009 to higher infections in the left-hand part of the plot in 2010 was correlated with pockets of relatively high density of the white halo fungus in 2009 and virtually no white halo fungus at all in 2010. The visual effect is, we think, convincing, and a more detailed analysis shows it to be statistically significant (Jackson et al. 2012).

An additional expectation is that the disease incidence should be negatively correlated with the presence of ant nests (under the assumption that the green coffee scale reaches densities that attract the epizootics of the white halo fungus only when it is under protection of the ants), one of the first correlations reported theoretically linking the white halo fungus to the rust disease in the field (Vandermeer et al. 2009). We repeated this correlation study, with similar expectations, at the end of the growing season in 2013 (in

Figure 4. The relevant bifurcation types in the basic system. The bold curves indicate the separatrix between the basin of attraction for control of the rust disease (shaded) from the basin of attraction for the escape of the rust from control (unshaded), the solid points represent stable equilibria, the open points indicate unstable (saddle) points, and the thin arrows illustrate the structure of the vector field. (a) With complete control of the rust disease under all circumstances. (b) After the saddle-node bifurcation that resulted in a new pair of equilibrium points, one a stable node and the other a saddle, which generates the possibility of escape from control for the rust disease. (c) After the global bifurcation, which rearranged the entire vector field, ensuring the almost inevitable escape of the rust from control, especially if the system starts near the origin each growing season. (d) After the second saddle-node bifurcation, leaving a single node of rust as a major pest.

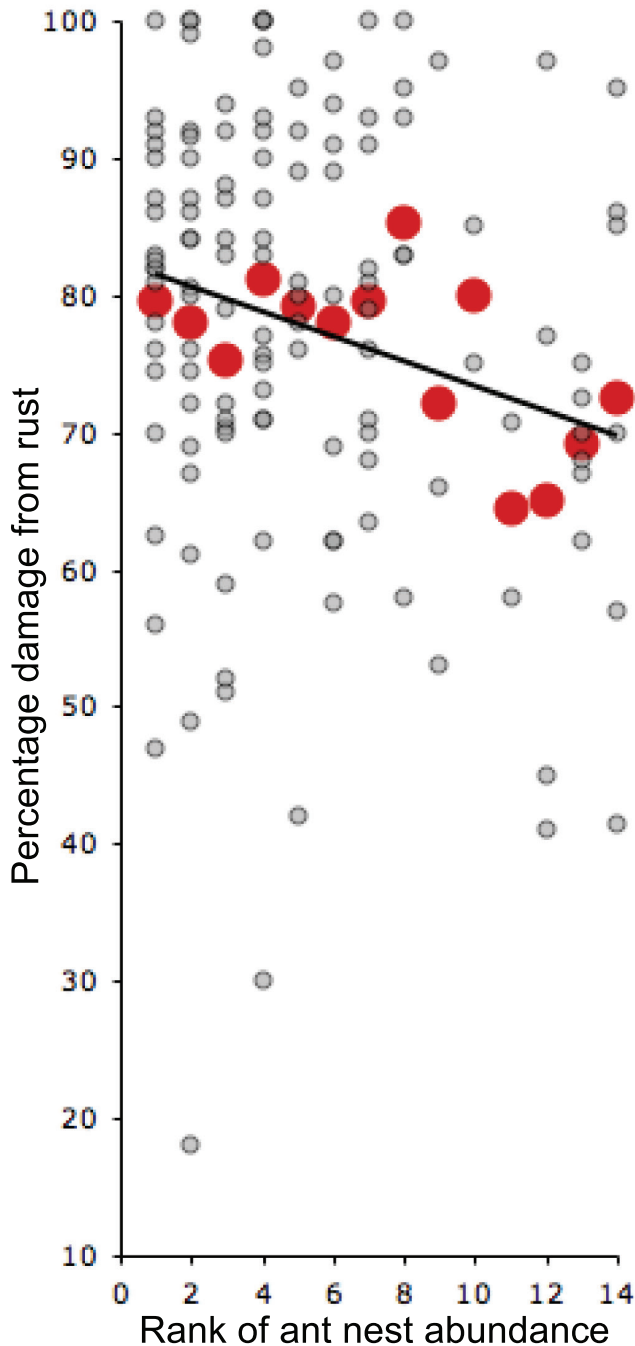


Figure 5. Results of surveys in March 2013 (damage from rust) and April–June 2012 (ant nests), showing the relationship between ant nest abundance and the percentage of damage from the rust. The large circles are means for a particular rank, and the small circles are values for each of the 128 50 × 50 meter plots. The line is a linear regression through the mean values ($p = .022$).

March, immediately after the massive epizootics of the rust disease), in the same 45-hectare plot that had originally been studied. We evaluated the impact of the coffee rust in a series of 128 small plots (50 × 50 meters) within the 45 hectares

and compared that data set with a previous census (from April–May of 2012) of nests of *A. instabilis* in those same small plots. The idea is that the locations of the ant nests are more likely to correspond to concentrations of *L. lecanii*, which will create locally abundant spores, which will then attack *H. vastatrix*. This leads to the expectation that the effect of the rust should be negatively correlated with ant nest density. The main results are illustrated in figure 5. It is evident that there is a small but detectable effect, as would be expected from the basic structure of the system (figure 5).

Given that the qualitative state of the system in our model depends on the carrying capacity of *L. lecanii*, it is important to ask what background conditions will generate a large or small carrying capacity. The general tendency for the past 20 years has been the reduction of shade cover in coffee. Traditionally, in northern South America, Central America, and Mexico (the Brazilian style of coffee production is quite distinct), coffee has been grown under a canopy of shade trees, much as it grew in its original habitat in Ethiopia (Perfecto et al. 1996). Beginning in the late 1980s, there has been a tendency throughout the region to reduce the amount of shade in pursuit of higher yields (Perfecto et al. 2005). Along with this reduction in shade, there may have been a concomitant reduction in the background entomofauna (especially *C. viridis*), partly because of the reduction in nesting sites of arboreal ants (the mutualists of the scale insects) and partly because of increased insecticide spraying. This gradual decrease in shade cover generated, we hypothesize, a change from the disease system under continual control (as in figure 4a) to the system made vulnerable to stochastic jumps (as in figure 4b). If this is the case, it would be expected that, in subsequent years, the disease would revert to a state of control (i.e., the lower equilibrium point in figure 4b). However, if the gradual decrease in shade cover has generated the situation presented in figure 4c, we can expect the disease to maintain its epidemic status year after year. Currently, it is not possible to tell which of these two alternatives will present itself.

However, other aspects of the disease dynamics, themselves, are also likely to be important. In particular, the fact that the spores of the fungus are dispersed by wind—and, indeed, dispersed potentially vast distances (Bowden et al. 1971)—suggest that larger landscape effects, such as deforestation to create pastures or conversion from shade to sun coffee, could have a major effect, independent of the control from above of parasitic fungi. In a very important study (Avelino et al. 2012), researchers in Costa Rica demonstrated that one of the major factors correlated with the incidence and severity of the disease was the amount of open area—especially pastures—in the neighboring landscape. In addition to our proposed mechanism of reducing the mycoparasites in the system through the increased fungicides inevitably involved in “modernization” of the production system, the straightforward increase in the dispersal of spores resulting from the reduced windbreak function of trees in the landscape could be operative.

Table 1. The known mycoparasites of the coffee rust disease.

Species	Reference
<i>Lecanicillium lecanii</i>	Kushalappa and Estes 1989
<i>Verticillium leptobactrum</i>	Kushalappa and Estes 1989
<i>Lecanicillium psalliotae</i>	Silveira and Rodrigues 1972
<i>Verticillium hemileiae</i>	Silveira and Rodrigues 1972
<i>Lecanicillium</i> sp.	Del Carmen de Arriola et al. 1998
<i>Aphanocladium melirolae</i>	Del Carmen de Arriola et al. 1998
<i>Paecilomyces liliacinus</i>	Del Carmen de Arriola et al. 1998
<i>Cladosporium hemileiae</i>	Kushalappa and Estes 1989
<i>Paranectriella hemiliae</i>	Kushalappa and Estes 1989

Adding to the hard empirical evidence, casual observations on a variety of farms in both Mexico and Puerto Rico lead us to believe that the mycoparasitic community (including but not exclusively *L. lecanii*) might very well represent local control, and the techniques of so-called modernization (e.g., cutting shade, applying fungicides) may gradually eliminate what has been effectively autonomous biological control (Lewis 1997, Vandermeer et al. 2010). On the island of Puerto Rico, for example, the disease is known but not common (at least not yet). Frequently, it is actually quite difficult to even find examples of it. However, at every farm on which we have found it, we have also encountered evidence of mycoparasitic activity, sometimes extremely active and frequently involving what appear to be distinct morphotypes. In Mexico, by contrast, although we have encountered evidence of mycoparasitic activity, it is not nearly as easy to find as it is in Puerto Rico. It might be that the Puerto Rican situation, with small farms nestled within natural and regenerating forests, provides a more conducive set of conditions for the development of a mycoparasitic microenvironment. Unfortunately, with the ongoing tendency to cut shade from coffee farms, we may see this situation change in the near future.

There are other species of mycoparasites known to attack the coffee rust fungus, although their effectiveness in the field cannot be judged at the present time. Combing the literature, we found nine different species that attack *H. vastatrix* in the laboratory (table 1). The unique aspect of *L. lecanii*'s being concentrated where the ant-plant mutualism occurs enabled us to obtain a small-scale local signal. It could be that any of these other species (or, undoubtedly, the many other species remaining to be studied) might have the same effect, but finding that signal could be impossible, because they may simply occur randomly around any particular coffee farm. Clearly, further study is warranted.

There is another issue regarding the qualitative state of the system, as it was revealed in our model. The exact value of carrying capacity for which the results of any of the bifurcations will occur depends on the point of initiation, as was

noted above. For example, if almost all spores are destroyed during the off season (the dry season), the system begins every growing season (the wet season) at a very low value. Alternatively, the reserve of spores may be set at the end of the wet season, such that the initiation point will be either at the point at which the rust is under control (the oscillatory point; the lowest point in figure 4a–4c) or at the point at which the rust is epidemic (the stable node; the upper point in figure 4b–d). Depending on this background for the seasonal holdover, the pattern of change in abundance due to a reduction in carrying capacity is expected to be distinct. For example, if the seasonal holdover of spores of the white halo fungus is low, the initiation point will be very low on the ordinate of figure 4 and will therefore be pushed either to the lower oscillating point under the conditions of figure 4a or 4b or to the upper stable node under the conditions of figure 4c or 4d. Using three scenarios of initiation points (near the stable node, near the zero values for both fungi, and near the oscillatory point), in figure 6, we illustrate the expected pattern of rust density as the carrying capacity is reduced. There are three distinct values of white halo fungus carrying capacity at which the regimes switch (i.e., switch from the state of rust at low values—under control—to rust at high values—epidemic) on the basis of the state of the system at the start of each growing season.

Furthermore, as the system changes regimes (equilibrium points), it is of interest to ask whether there might be, theoretically, a discernible statistical signal suggesting that a change is imminent (Scheffer et al. 2012). Because the calculations presented in figure 6 exclude the first 300 transient steps, recording only the subsequent 100 steps for each value of the carrying capacity of *L. lecanii*, the approach to the equilibrium point can be seen as the range of values plotted for any given value of carrying capacity. This system, as do many other dynamical systems, exhibits a critical slowing down near the point of bifurcation (Scheffer et al. 2012). It remains to be seen whether systematic data in any given locality might be adequate in quantity and quality to test the hypothesis of critical slowing down. To our knowledge, no such data currently exist.

Conclusions

The model developed here is meant as an education of our intuition about the potential regime change, from a low-level persistence regime to an epidemic regime, emphasizing the need to go beyond a simple query about the pest agent and immediate control strategies. In this context, it is evident that a knowledge of more than simply the pest and its natural enemies is important, because the qualitative structure of the model depends on an understanding of some of the more complex aspects of the overall system (in this case, the mutualistic ants and their scale insects, which set the stage for the carrying capacity of the white halo fungus). Other mycoparasitic fungi are also known to attack the coffee rust, which suggests yet further complications of the ecosystem involving antagonistic fungi. Detecting effects at the field

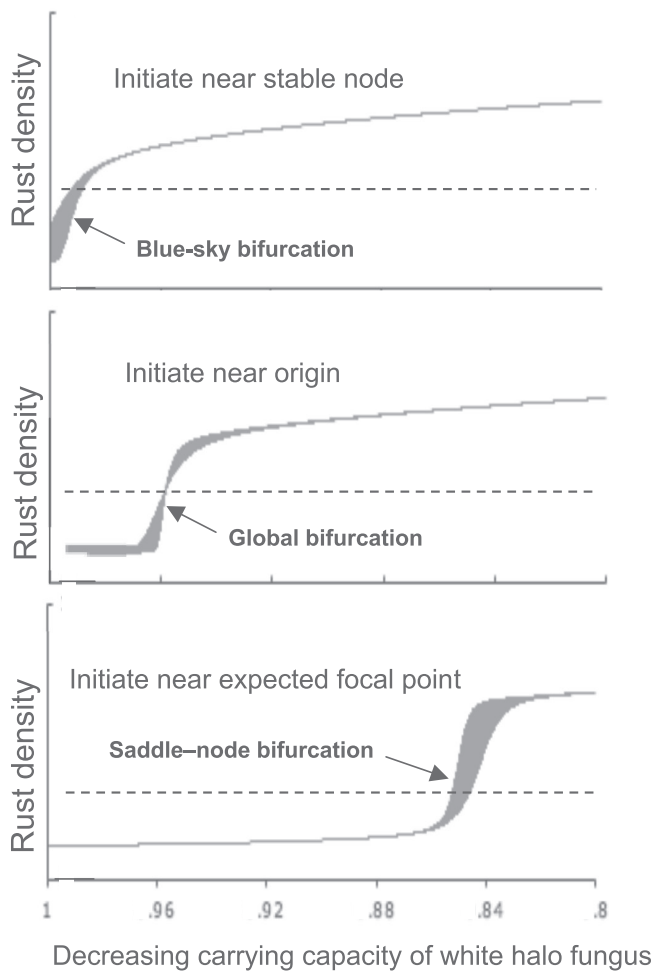


Figure 6. Changes in equilibrium values (for a slowly decreasing carrying capacity of the white halo fungus, decreasing in .003 increments of the proportional value; i.e., the maximum value is 1.0) for three different sets of initial conditions. Plotted are the values of rust density, including late transient approaches—i.e., values plotted for 100 iterations of the model after discarding the first 300 transients (see the text for the logic of the three scenarios). The dashed horizontal lines are included to facilitate comparison among the three scenarios (it is positioned at the value of the saddle point at the global bifurcation).

level is aided by the particular structure known to exist for the particular species *L. lecanii* (its spatial structure and association with the ant *A. instabilis*; figures 2 and 3), a situation that may not be replicable in other species. However, those other species may also function as important biocontrol agents. Consequently, a simple magic bullet approach of applying fungicide, which is one of the main methods currently being promoted in the affected countries, is doomed to failure in the long run. Instead, management practices that are focused on the maintenance of the complex web of ecological interactions should be promoted.

Precisely how to maintain that complex web is difficult to specify with precision because of the complexity of the system and the relatively meager background of ecology-oriented research in the system, which is a more general problem for sustainable agriculture. Perhaps, when as many resources are devoted to the more ecological aspects of agriculture as have been provided to chemistry-oriented productionist goals since World War II, recommendations for ecological management will be forthcoming. Nevertheless, certain management practices are clearly detrimental to the sort of complex biodiversity that harbors the control elements identified in the present work. Chief among them is the spraying of agrochemicals in general and the drastic reduction of shade, both of which have been steadily increasing throughout the region for the past several decades. Opening up the canopy to the winds that are evident to anyone walking through a sun coffee farm can only increase the efficiency of rust spore delivery, and high-population-density planting (typical in most sun management systems) encourages the spread of rust spores by contact from tree to tree along a row. And if, as we suggest, there are fungal natural enemies of the coffee rust in the system, spraying generalized fungicides may kill the controls of the disease. A general encouragement to “reforest” coffee farms has been repeatedly suggested as a treatment to increase biodiversity (Guharay et al. 1999, Staver et al. 2001) and, by implication, the sorts of complex ecological interactions that provide opportunities for autonomous pest control (Lewis et al. 1997, Vandermeer et al. 2010). The intuition that we claim to provide in this article is that a movement toward more shaded systems with minimal application of agrochemicals might be an appropriate recommendation for coffee farmers in the region.

Acknowledgments

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