

Novel community assembly and the control of a fungal pathogen in coffee agroecosystems

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HIGHLIGHTS

- The coffee leaf rust (CLR), *Hemileia vastatrix*, is the most devastating pathogen of coffee in the world.
- CLR has been maintained under control in Puerto Rico but not Mexico.
- Puerto Rico and Mexico have unique communities of CLR natural enemies.
- The mycoparasitic fungi, *Lecanicillium lecanii*, is more common on CLR in Puerto Rico than Mexico.
- Intercropping of citrus in coffee farms in Puerto Rico is associated with greater natural enemy attack of CLR.

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ABSTRACT

Ecological principles are frequently leveraged when considering the control of animal pests of crops. Still, pathogens have not generated similar research despite the current interest in the field of disease ecology. Here we use the most economically significant pathogen of coffee, the coffee leaf rust, *Hemileia vastatrix*, to understand the role of top-down control in its regulation. Large-scale sampling of the pathogen and its natural enemy community in Puerto Rico and Mexico reveal striking differences in the potential for biological control. Four main natural enemies are identified, a fungal parasite, a dipteran fungivore, a mite fungivore, and a snail generalist in Puerto Rico, with only two occurring frequently in Mexico. We suggest that the community of natural enemies is potentially an important mechanism contributing to the maintenance of the pathogen at relatively benign levels in Puerto Rico. We provide evidence that management is a contributing factor and is perhaps operative in part through its effect on the natural enemies of the pathogen. This work has applied significance not only for coffee production in Puerto Rico but also for understanding how this pathogen may be controlled in areas where it has been, and potentially will be, at epidemic status.

1. Introduction

Both pests and pathogens continue plaguing agriculture. Insect pests, especially, have generated a host of narratives concerning the complexity of their long-term control (Vandermeer et al., 2010; Vandermeer et al. 2019), frequently emphasizing the complex nature of their biology and the consequent need to develop control strategies that acknowledge ecological principles (Lewis et al., 1997). A rich history of biological control undergirds this position (Heimpel and Cock, 2018). Curiously, plant pathogens, likewise devastating for agriculture, have not generated such strong opinions regarding the importance of ecological principles, despite the currently intense interest in the field of

disease ecology. When dealing with insect pests, issues such as biological control are front and center in the minds of entomologists seeking control, while plant pathologists, on the other hand, seem quick to rely on developing resistant varieties of the crop. Basic ecological reasoning is not well-positioned to explain this distinction, apparently an anthropogenic vestige. Here we argue that ignoring higher trophic level potential (e.g., biological control) is a missed opportunity and may be counterproductive. We use the distribution of the coffee leaf rust (CLR) in the Americas as an example.

The CLR, caused by the fungus *Hemileia vastatrix*, has a history of devastation in the world's coffee production systems, from Sri Lanka in the nineteenth century to Mesoamerica in the twenty-first (McCook,

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2019; Avelino and Anzueto, 2020; Avelino et al., 2004; 2006; 2015; 2020). Yet, its effect on coffee production is variable, likely responding to local and regional contingencies. From the plant itself (coffee) to its “pest,” the CLR fungus, to the enemies of that pest, the system falls within the increasingly popular ecological topic of novel ecosystems (Hobbs et al., 2009; 2013; Perfecto and Vandermeer, 2015). It is, we propose, the ecological context in which the components of novel agricultural communities are embedded that will determine what makes a pathogen a minor nuisance in one region, but a crippling epidemic in another. The case of the 1869 CLR epidemic in Sri Lanka could ultimately have been the result of CLR escaping the natural enemies which presumably controlled it in its native region of Equatorial Africa, a pattern that is likely to repeat itself. Here, we provide evidence that suggests the difference between its recent catastrophic impact on coffee in Mexico and its relatively benign nature in Puerto Rico can be tied to the relative importance of distinct novel communities, and in particular, an assemblage of natural enemies that is more diverse and abundant in Puerto Rico than in Mexico.

The basic ecological principles involved in this interpretation are central in the extensive literature on invasive species, which suggest that the absence of natural enemies in a new location can sometimes explain the notable success of the invasive species (Roy et al., 2011; Yitbarek et al., 2017). When similar ecological reasoning is applied in an agricultural setting, the same forces should be at play. Corresponding to basic ecological/evolutionary principles, crop pests emerge from two sources: hitchhikers from the introduced species’ natural range (the crop), or as evolutionary adaptations or preadaptations from local fauna and flora (Strong et al., 1977). Such fundamental principles should also apply to higher trophic levels, which is to say, the natural enemies of the pests. And importantly, there is no scientific reason to expect that such fundamental ecological dynamics should be absent from host/pathogen systems, as evidenced by, for example, early enthusiasm for research on phage therapy in human disease systems (Chanishvili, 2012).

The CLR has been devastating Mesoamerica for nearly ten years, causing significant damage to the production of one of the world’s most important internationally traded agricultural commodities (Avelino et al., 2015). As for the crop itself, it is difficult to exaggerate the social and economic importance of coffee, not only for consumers worldwide, but also as the major export of many countries, and the basis of sustenance for millions of farmers worldwide (Pendergrast, 2010). The devastating losses due to CLR have understandably received widespread attention (McCook and Vandermeer, 2015). While solutions are imagined mainly in the form of resistant varieties and fungicides, relatively little attention has focused on the well-known fact that CLR has been “under control” for some time in most areas around the world. While the dynamics of CLR have been mainly studied in areas where the pathogen is epidemic, for a good reason, we suggest that insight can be gleaned from studying the dynamics of the pathogen in places where it remains at relatively low levels, as in Puerto Rico. In particular, we propose that focusing on the novel assembly of the pathogen’s natural enemy community can lend insight as to why the pathogen remains under control regionally.

Here we report on a series of long-term surveys in both Mexico and Puerto Rico regarding the CLR and its community of natural enemies. Our hypothesis (Hajian-Forooshani et al., 2016) is that the community of natural enemies, especially the mycoparasitic *Lecanicillium lecanii*, are the main factors that maintain the disease relatively benign in Puerto Rico and fail to do so in Mexico. We provide evidence that management, especially with respect to intercropped species, is also a factor and perhaps operative in part through its effect on the natural enemies of the pathogen.

2. Materials and methods

2.1. The study sites

The study was conducted in the Cordillera Central of Puerto Rico, the main coffee-growing region on the island, and in the Sierra Madre de Chiapas in Mexico, also a major coffee-growing region. Twenty-five locations were sampled in Puerto Rico ranging in elevations from 344 m AMSL to 887 m AMSL, while in the six sites in Mexico elevation ranges from 900 m AMSL to 1150 m AMSL. Management characteristics were variable with a sharp distinction between organic shade and non-organic sun production in Mexico, versus non-organic and highly variable management in Puerto Rico. Other background conditions are discussed elsewhere, for the Mexico site (Philpott and Foster, 2005) and the Puerto Rico site (Perfecto and Vandermeer, 2020).

The communities of natural enemies at both sites stem from a combination of the aforementioned processes of co-introduction and recruitment from the associated biodiversity in the agroecosystems and surrounding forests. In both regions, the dipteran larvae *Mycodiplosis hemileiae* has been presumably co-introduced from eastern Africa with coffee. The genus tends to contain species that are specialists on the various species of rust fungi and thus it is not likely to have any alternate hosts in Mexico or Puerto Rico (Nelsen, 2013). *M. hemileiae* larvae were first reported in the scientific literature in the Americas (Mexico and Puerto Rico) in 2014 although it remains unclear how long the species has been present (Hajian-Forooshani et al. 2016). A second natural enemy occurring in both regions is the fungus, *Lecanicillium lecanii*, whose biological control potential for the coffee leaf rust has been previously noted (Jackson et al., 2012a; 2012b; Vandermeer et al., 2009; 2014; Hajian-Forooshani et al., 2016; Gómez-De La Cruz et al., 2018), and is common in Ethiopia, the native range of *Coffea arabica* (Zewdie et al., 2021). The third natural enemy is a species of mite (*Ricoseius loxoches*) which is known to consume CLR spores and complete its lifecycle in patches of CLR spores (Oliveira et al., 2014). *R. loxoches* is present in both Mexico and Puerto Rico, but with distinct relative abundances, being very common in Puerto Rico but too rare in Mexico to collect any meaningful data (authors observations). Finally, *Bradybaena similis*, is a well-known invasive species around the globe which, along with other unidentified gastropods, has recently been identified as a consumer of CLR spores (Hajian-Forooshani et al., 2020). Notably, *B. similis* occurs throughout Puerto Rico and, although present in Mexico (Naranjo-Garcia and Castillo-Rodriguez, 2017) the authors have never seen it or the characteristic orange excrement left behind from gastropods consuming of CLR spores in the Mexican coffee farms sampled in this study.

2.2. Surveys of the rust and natural enemies

In Puerto Rico, monthly surveys were done on 25 farms from Aug 2018 to July 2019. On each farm a central area 10x10 m was established in an area that qualitatively appeared much like the rest of the farm, and 20 coffee plants were selected randomly within each of the plots. Surveys recorded the number of leaves containing CLR on the whole plant, and the number of *M. hemileiae* larvae, the proportion of CLR lesions that had evident covering of the mycoparasite (*L. lecanii*), the number of CLR lesions that contained populations of the mite (*R. loxoches*), and the number of leaves containing gastropod feces with CLR spores (presumably from *B. similis* and other gastropods; see Hajian-Forooshani et al. 2020) on 25 of the leaves that had rust lesions.

Due to large amounts of variability in the amount of CLR on farms throughout Puerto Rico (see below), we chose a farm that had the highest incidence of CLR for a more detailed study which included a larger sampling area, more plants sampled, and a greater sampling frequency. On that farm (code UTUA2) we established three 20x20 m plots and marked and georeferenced each coffee bush on the plot. Every-two weeks the plots were sampled for CLR and all four natural enemies.

Comparative work in Mexico was concentrated in two large coffee farms, one with considerable shade and a second with much less shade, approaching what is popularly referred to as sun coffee (Philpott and Foster, 2005). In each of these landscapes we established three 20x20 m plots, using the same methodology as in Puerto Rico, including biweekly samples of the CLR and its natural enemies over a 12-month period.

The disparity in sampling schemes between Mexico and Puerto Rico, with 25 10 × 10m plots in Puerto Rico along with three 20 × 20 plots on a single farm, and six 20 × 20 plots on two farms (three plots on each farm) in Mexico is the result of a confluence of factors. First, personal observations from previous work in these regions (citation) have noted important regional differences in the complexity of the natural enemy communities, where they happen to be more diverse in Puerto Rico (4 commonly occurring natural enemies) than in Mexico (2 natural enemies, both only seasonable present). Consequently, a larger-scale sampling scheme seemed justified in Puerto Rico where relatively little is known about the CLR compared to the region of Mexico where the study took place. Second, personal observations suggested the variability in farm management is much greater in Puerto Rico than in the various large-scale plantations in the study sites in Mexico. In Puerto Rico, a variety of crops are grown in conjunction with coffee in several different shade management contexts, from coffee-citrus intercrops to sun coffee to rustic coffee. Capturing the extent of this farm-to-farm variability, although not directly quantified for this study, was a motivating factor for a more spatially extensive sampling scheme in Puerto Rico. The more restrictive sampling of six plots across two farms each in Mexico is in part due to the large scale of the farms (approximately 300 ha each in comparison to approximately 10 ha average in Puerto Rico) and the more restrictive range of management in the region which includes predominately sun coffee or shaded polyculture, which we captured with our sampling.

3. Results

In Puerto Rico, the dynamics of CLR as well as its natural enemy community have remained largely unknown due to the relatively benign

status of the pathogen as compared to other regions in the Americas (Rodriguez and Monroig, 1991; and personal observations). One of its most striking features is its geographic variability, with some sites being heavily impacted while others remain almost CLR-free, with no clear spatial signature (Fig. 1). Eight of the 25 sites had barely detectable rust and ten had significant quantities (Fig. 2). Furthermore, there was no evident geographic pattern for either CLR or any of the natural enemies (Fig. 1). The natural enemy community is clearly dominated by the presence of the mycoparasitic fungi *L. lecanii* (Figs. 1 & 2) invariably present across the whole coffee-producing region wherever CLR is present. In addition to *L. lecanii*, the dipteran larvae, *M. hemeliae*, is also a common feature, consistently the second most abundant natural enemy. The other two natural enemies, the CLR-mite and CLR-snail tend to be more sporadically distributed (Figs. 1 & 2).

Time series from the 20x20 m plots illustrate the complex nature of the dynamics of CLR and the natural enemies in both Mexico and Puerto Rico (Fig. 3). Two patterns are of particular importance. First and most obviously, the occurrence and diversity of the natural enemy community is far more pronounced in Puerto Rico than in Mexico, with Puerto Rico having four natural enemies that are relatively common throughout the study period compared to only two in Mexico, *Mycodiplosis* and *L. lecanii*, both of which occur at lower densities than in Puerto Rico. Also of note are differences in the incidence of the natural enemies between regions: in Mexico there tends to be a single population burst, whereas in Puerto Rico there is a sustained incidence of all four natural enemies. In Puerto Rico, at least 30 % of all plants that have CLR have *L. lecanii* throughout the whole growing cycle (Fig. 3). For one plot, the percentage of plants with *L. lecanii* is above 65 % all year long (Fig. 3), in contrast to Mexico where the incidence of the natural enemies never surpasses 40 % even at the peak of CLR.

An additional pattern is evident from the time series on the 20 × 20 m plots (Fig. 3). Within the plots in Mexico, it is evident that the two management styles (sun versus shade) are strongly correlated with the infection rate of CLR. In the shade coffee system, CLR never surpasses 60 % and is usually below 40 %, whereas in the sun coffee system it never falls below 60 %. Making the same comparison in Puerto Rico is difficult

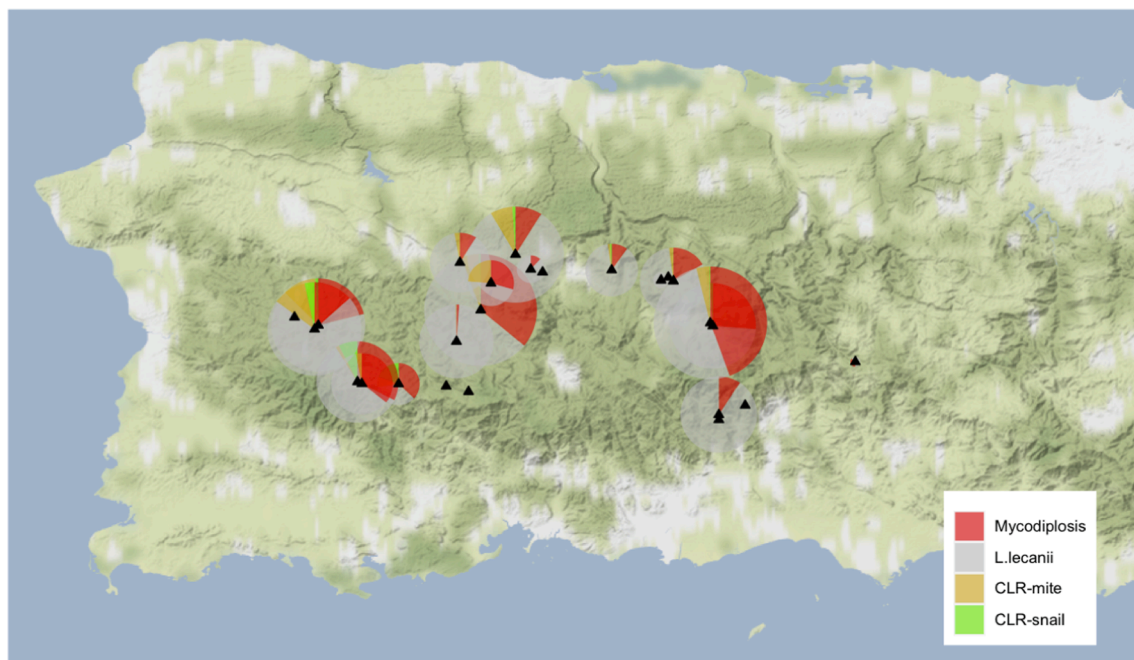


Fig. 1. Abundance of coffee leaf rust (CLR) and the community of its main natural enemies, across the region in Puerto Rico, where the size of the circles is proportional to the average amount of CLR from a 12-month cycle of collected data. The fills of the circles represent the average composition of natural enemy communities throughout the 12-month cycles. Red – *Mycodiplosis* (*M. hemeliae*); grey – *L. lecanii*; gold – CLR-mite (*R. loxochelae*) and green – CLR-snail (*B. similis* and other CLR consuming gastropods). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

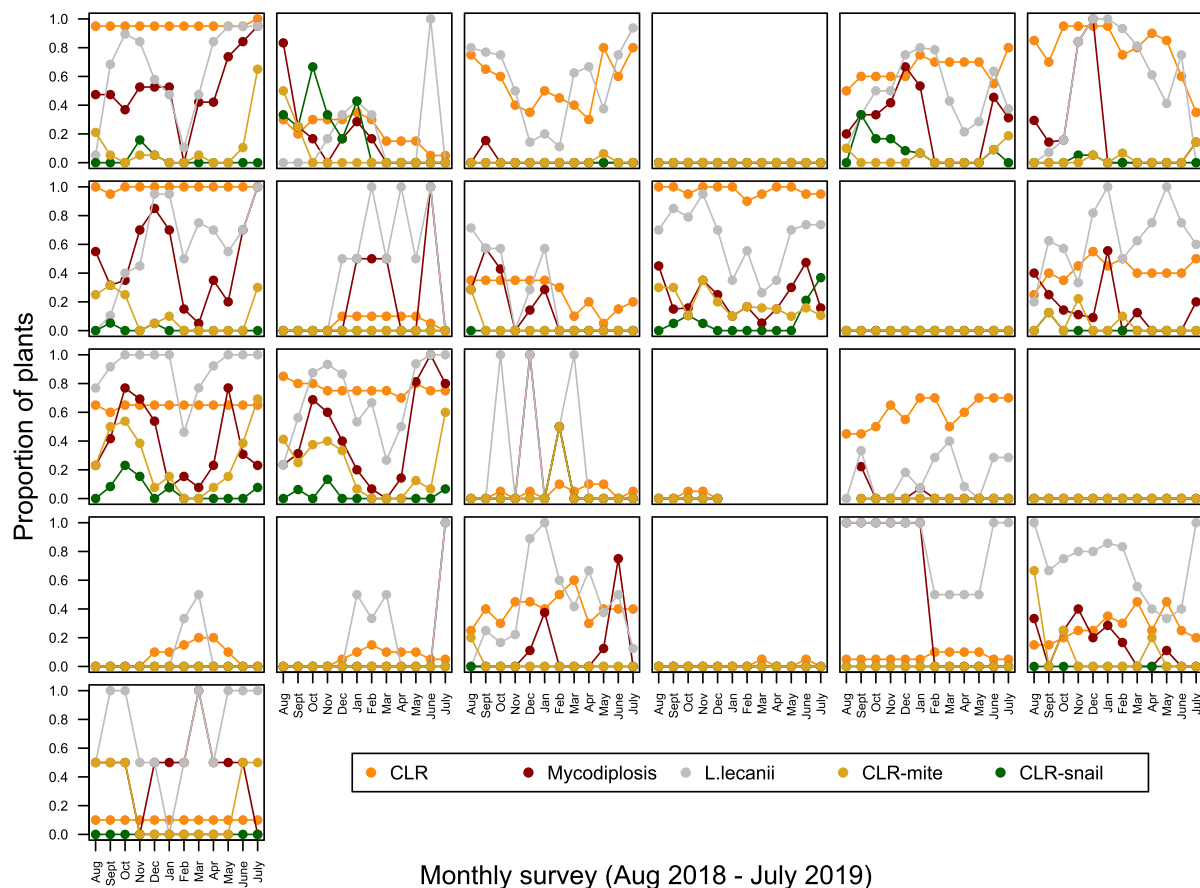


Fig. 2. Distribution of the coffee leaf rust (CLR) and its community of natural enemies across 25 farms in Puerto Rico. On each of the 25 farms surveyed, 20 individual plants were monitored for a year. Each plot shows the proportion of the 20 plants infected with CLR and the proportion of CLR-infected plants with natural enemies present. The y-axis ranges from 0 to 1 and the x-axis represents each of the 12 months from the survey ranging from August 2018–July 2019.

since the shade management there is far more complex than in the Mexico site and measurements of shade from farm to farm do not suggest any relationship at all with respect to the rust (see [supplementary material](#)). Recall that the particular farm this fine-scaled study was accomplished was chosen because it was the farm with the highest incidence of coffee rust of the 25 sampled farms.

4. Discussion

Both large-scale sampling of CLR and its natural enemy community in Puerto Rico as well as the fine-scale detailed bi-weekly sampling at nine 20x20m coffee plots at both sites, illustrate some striking distinctions between a region where the pathogen is in epidemic proportions versus a region where the pathogen is relatively benign. Most notable is the abundance of natural enemies in both regions. The widespread distribution and frequent occurrence of the natural enemies in Puerto Rico, even when CLR is relatively rare, is in stark contrast to the dynamics of the natural enemies in Mexico where they exhibit a seemingly strong seasonal dynamic. We suggest that the widespread distribution and high incidence of these natural enemies in Puerto Rico may contribute to the benign nature of the rust there. Furthermore, we propose that *L. lecanii* is likely the main controlling factor in Puerto Rico. Both the island-wide surveys as well as the finer-scale data show *L. lecanii* occurring at high rates even when CLR is at low densities. Its high occurrence in addition to the apparent consumer-resource oscillations that emerge island-wide ([Fig. 4.](#)) suggests that *L. lecanii* may be a controlling agent of the CLR in Puerto Rico but is likely not so in Mexico. The question then arises, if the same natural enemy is present in both

Mexico and Puerto Rico, why does it seemingly control the pathogen in Puerto Rico and not Mexico?

Specifically in Puerto Rico, CLR appears to present itself in two categories, sites where CLR is persistent throughout the year and sites where the rust never gains enough momentum to take hold ([Fig. 2](#)). The same pattern is seen in the natural enemy community to some extent as well, although the dynamics are notably different, where evident fluctuations occur irrespective of the abundance of CLR ([Fig. 2](#)). While there is variability across the landscape, a clear pattern emerges of the densities of CLR and its natural enemies co-varying through time, especially obvious in the case of *L. lecanii* with apparent consumer-resource oscillations ([Fig. 4a](#)), and importantly this oscillatory pattern is absent from the other natural enemies of the CLR ([Fig. 4b–d](#)).

Prior work conducted with *L. lecanii* and CLR suggests a potential mechanism for the importance of *L. lecanii* in Puerto Rico compared to Mexico ([Hajian-Forooshani et al., 2016](#)). *L. lecanii* is both a mycoparasite as well as an entomopathogenic fungus that attacks a wide range of insects, but notably sap-feeding hemipterans such as scale insects. It has been demonstrated that *L. lecanii*'s attack on CLR can be facilitated by large population densities of scale insects in coffee agroecosystems, where the mycoparasite spills over to CLR ([Vandermeer et al., 2009; Jackson et al., 2012a; Vandermeer et al., 2014](#)). Throughout the coffee-producing region of Puerto Rico, scale insects, and in particular the green coffee scale (*Coccus viridis*), is a widespread and sometimes nuisance pest. The green coffee scale occurs not only on coffee plants but is also a common and potentially damaging pest of citrus which is widely cultivated, and often intercropped with coffee. Given that the green coffee scale is an intermediary that allows *L. lecanii* to attack coffee rust

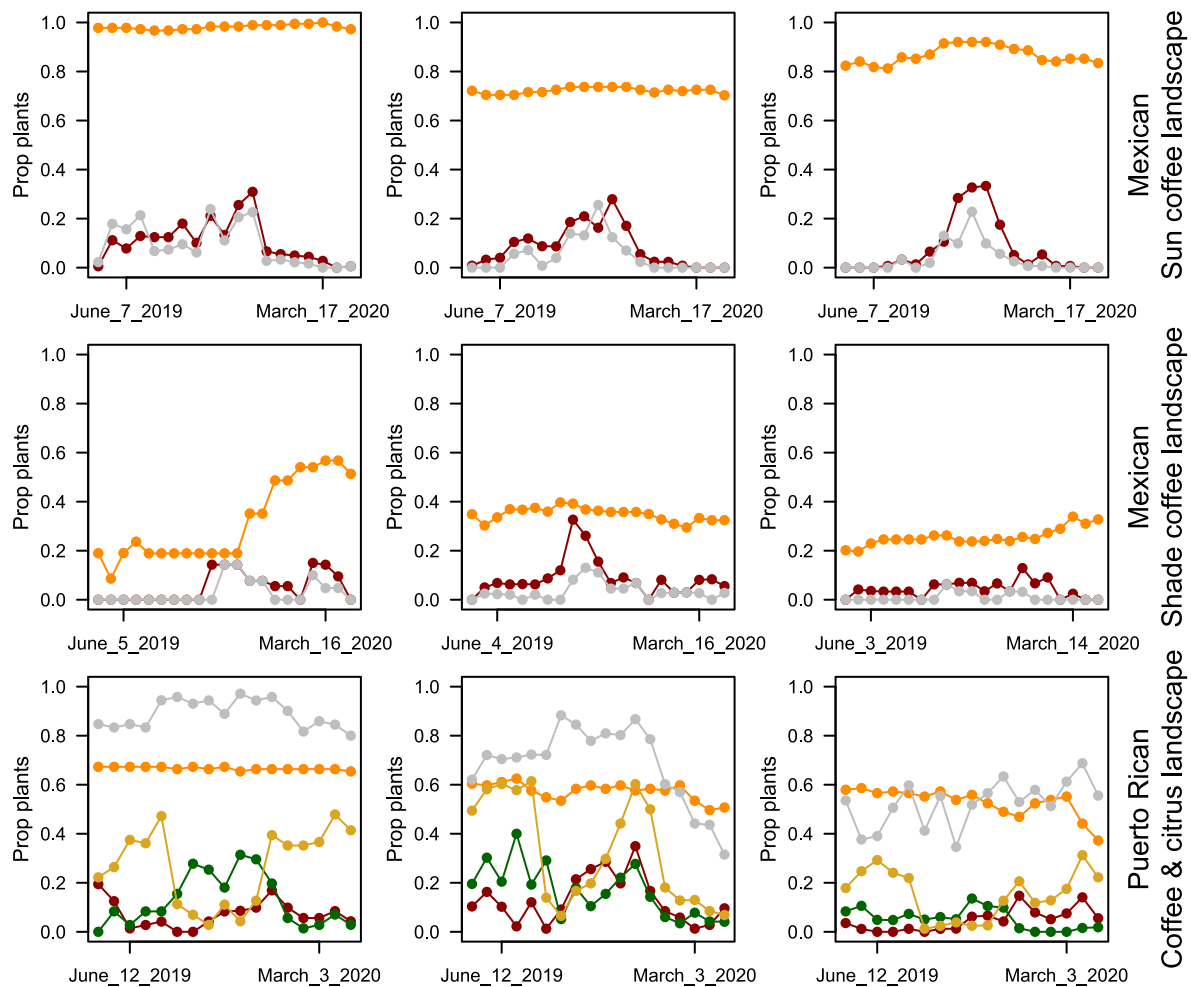


Fig. 3. Data from fine scale surveys (20x20m plots surveyed biweekly) in Mexico and Puerto Rico. Each point represents the proportion of plants that have CLR (orange), *Mycodiplosis hemileia* (red), CLR-snail (*B. similis*) (green), the CLR-mites (gold), and *L. lecanii* (grey). Note that the farm in Puerto Rico was chosen (out of the 25 sampled) for this detailed study because it was the farm with the highest incidence of CLR. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(Vandermeer et al., 2009; 2014), we surveyed populations of green coffee scale on coffee plants throughout the yearly cycle across the 25 sites where the rust was surveyed in Puerto Rico. We found that sites that have low coffee rust, as defined by having 20 % or fewer of the plants infected with coffee rust for most of the year, have higher densities of green coffee scale and green coffee scale infected with *L. lecanii* (High rust: mean GCS = 0.5875 ± 0.0314 , N = 14; Low rust: mean GCS = 0.9568 ± 0.04831 , N = 11. High rust: mean *L. lecanii* GCS = 1.086 ± 0.0419 , N = 14; Low rust mean *L. lecanii* GCS mean = 1.41 ± 0.0543 , N = 11). Thus, a higher density of green coffee scale is associated with low CLR sites throughout the coffee-producing region of Puerto Rico suggesting a similar spillover effect may be taking place in which the attack of *L. lecanii* on CLR is facilitated through its attack on the green coffee scale, which is especially abundant where citrus trees are present.

Given the clear importance of natural enemies in Puerto Rico and the evident relationship to shade in Mexico, hypotheses involving shade management and its effect on natural enemies may be warranted. While most investigations on shade's impact on CLR have mainly emphasized the effect of shade on physical factors, like wind and humidity, that may affect the transmission and germination of the fungus itself (Vandermeer et al., 2019), we find that qualitative observations on the relationship between CLR, the green coffee scale, the *L. lecanii* fungus, and citrus as an intercrop, suggest a complex of management style and natural enemy

dynamics that ultimately contributes to the management of this important pathogen. While follow-up work will be necessary to elucidate the mechanisms that explain the patterns reported here, we propose that shifting focus to the forces that shape the assembly of the ecological communities in these agroecosystems may help explain regional differences observed in agroecosystems around the globe.

CRedit authorship contribution statement

Zachary Hajian-Forooshani: Conceptualization, Methodology, Software, Data curation, Formal analysis, Writing – original draft, Writing – review & editing. **Ivette Perfecto:** Conceptualization, Data curation, Funding acquisition, Project administration, Writing – review & editing. **John Vandermeer:** Conceptualization, Data curation, Funding acquisition, Project administration, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

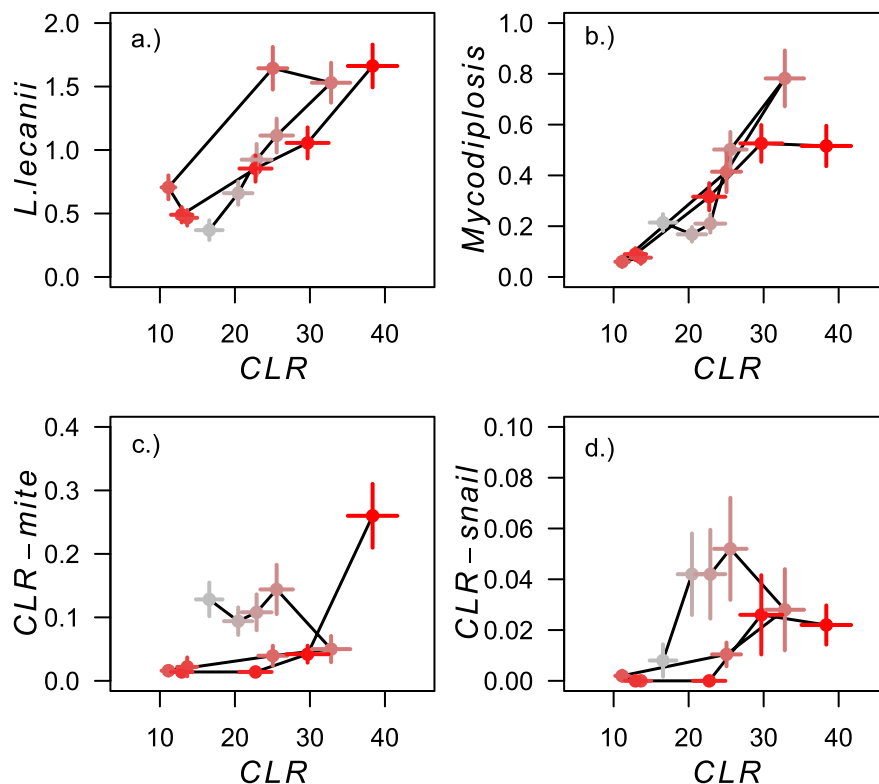


Fig. 4. Consumer-resource phase diagrams of the coffee leaf rust (CLR) and its natural enemies throughout Puerto Rico. Each point represents a monthly mean across the 25 sampled farms and colors represent the progression of time, with grey being August 2018 and bright red July 2019. a.) is the mean number of leaves with *L. lecanii*, b.) the mean number of leaves with *Mycodiplosis* larvae, c.) the mean number of leaves with CLR-mites (*R. loxochelae*), and d.) the mean number of leaves with CLR-snail (*B. similis*) excrement. Note that panel a.) with CLR-*L. lecanii* exhibits a counter-clockwise oscillation as expected from a consumer-resource interaction. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Data availability

Data and code can be found at: <https://github.com/ZHAJIANF/Hajian-Forooshani-Biological-Control-2022-code-and-data>

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocontrol.2022.105099>.

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