Emergent Spatial Heterogeneity Structures the Assembly and Functioning of Ecological Communities: An Agroecological Perspective

by

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Dedication

To Ferdinand Joseph LaMothe

Acknowledgements

I am fortunate to have had several excellent mentors throughout my journey in science. Starting with Alan Rebertus and Mac Strand at Northern Michigan University, who both encouraged my interests in ecology, mycology, and freshwater entomology during my time up north. Upon arriving to the University of Michigan, I was lucky to find myself under the mentorship of David Gonthier and Linda Marín who both exercised astonishing patience with me while showing me the ropes of day to day life as a scientist in training. I want to especially thank David Gonthier for being not only a wonderful mentor but a great friend during the time we overlapped in Ann Arbor. His help and encouragement were instrumental in me deciding to continue down the path of pursing science. My summer at San Francisco State University under the mentorship under Ed Connor was extremely important in cultivating my interest in pursuing science. Ed demonstrated to me the importance of approaching one's ideas intensely and creatively but at the same time with a good dose of humility. He was also importantly the first person to sit down with me to show me what it looks like to write a line of code. Little did I know at that time the thousands of lines of code that would be written during this dissertation.

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Since this acknowledgment section has already gotten out of hand in terms of length, I think it is prudent to acknowledge the great creative minds that have inspired a lot of the work in this dissertation. First, my muse, Ferdinand LaMothe and the rest of the greats: Oscar Alemán, Henry Red Allen, Chet Baker, Bill Basie, Sidney Bechet, Bix Beiderbecke, Leon Chu Berry, John “Dizzy” Birks, Bob Brookmeyer, Teddy Bunn, Benny Carter, Paul Chambers, Charlie Christian, Eddie Costa, Tad Dameron, Johnny Dodds, Bob Dunn, Roy Eldridge, Duke Ellington, Slim Gaillard, Wardell Gray, Johnny Griffin, Edmond Hall, Coleman Hawkins, Fletcher Henderson, Johnny Hodges, Earl Hines, Illinois Jacquet, Jo Jones, James P. Johnson, Donald Lambet, Eddie Lang, Herbie Mann, William “Red Garland” McKinny, Jackie Mclean, Hank Mobley, Thelonious Monk, Benny Moten, Gerry Mulligan, Jimmie Noone, Charles Parker, Oscar Peterson, Bud Powell, Django Reinhardt, Adrian Rollini, Sonny Stitt, Willie “the Lion” Smith, Jabbo Smith, Willie Smith, Slam Stewart, Art Tatum, Clark Terry, Frank Teschemacher, Frankie Traumbauer, Craig Ventresco, Joe Venuti, Mal Waldron, Thomas Waller, Teddy Wilson, and Lester Young.

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Abstract

Heterogeneity is a ubiquitous feature of ecosystems and perhaps an important contributing factor to the oft noted difficulties associated with making generalizations in community ecology. Our answers to questions regarding the origins and consequences of various types of heterogeneity in ecological systems have long been met with contingencies and context dependency, highlighting the need to continually revisit our organizing metaphors. The work presented in this dissertation is concerned with these metaphors and especially those associated with the ecological processes that generate spatial heterogeneity in ecosystems. In eleven case studies, I attempt to understand the generation and subsequent implications of spatial heterogeneity for the assembly and functioning of ecological communities in agroecosystems.

I first address how ecological interactions create spatial pattern in Chapter 1 by presenting a novel demographic framework for understanding consumer-resource generated spatial patterns. I then explore how spatial heterogeneity influences ecological interactions in Chapter 2 and Chapter 3. Whereas in the former I ask how basic ecological interactions are influenced by dynamic patterns of heterogeneity in ecosystems, in the later I ask how changes in spatial structure influences pathogen epidemics. Chapter 4 then empirically explores how dispersal differentially alters community structure in leaf-litter metacommunities and Chapter 5 explores the use of coupled oscillators as a metaphor for ecological communities. These first five chapters represent an attempt to understand the feedbacks between ecological interactions that create spatial heterogeneity and how spatial heterogeneity structures ecological communities.

The dissertation then shifts focus to a fungal pathogen of coffee, the coffee leaf rust, and uses its community of consumers as a model system to understand how spatial heterogeneity influences community structure and how community structure influences biological control of the pathogen. Chapter 6 gives a brief overview of the history and ecology of the pathogen and its community, and Chapters 7-9 explore the assembly and organization of these communities, highlighting their interactions with the pathogen as well as among themselves. Finally, Chapters 10 and 11 are concerned with the structure of interaction networks associated with the coffee leaf rust and the provisioning of top-down control of the coffee leaf rust pathogen in both Mexico and Puerto Rico. Taken together, this dissertation contributes to our understanding of how ecological communities create and are impacted by the heterogeneous environments they occupy. Furthermore, this work attempts to highlight the importance of such concepts in an agroecological context where questions of community structure and population regulation have the potential for practical significance.

Introduction

Heterogeneity is a ubiquitous feature of most, if not all ecosystems in one form another. Spatial heterogeneity is an omnipresent and scale dependent reality that has to be considered to understand ecosystem dynamics (O'Neil et al., 1987; Koltier and Wiens 1990; Levin 1992). An accounting of spatial heterogeneity has demonstrated its importance in structuring a variety of ecosystem processes, from primary production (Pringle et al., 2010) to nutrient cycling (Schlesinger et al., 2196). In a community ecological context, spatial heterogeneity has long been an acknowledged factor in influencing the structure and function of communities (Hanski 1998; Hanski and Ovaskainen 2000; Liebold and Chase 2018; Vandermeer and Jackson 2018). While there are countless experiments and studies, both empirical and theoretical, which highlight the importance of spatial heterogeneity in structuring ecological interactions and thus ecological communities, below we note some of historical importance for our field.

Some of the most foundational experiments in ecology have highlighted the inadequacy of a reductionist approach that separates the ecological communities under study from the realities of the spatial heterogeneity they typically face in their ecosystems. Gause's early experiments in 1934 on consumer-resource interactions highlighted this fact early on. Despite his success in reproducing the competitive dynamics predicted by the Lotka-Volterra competition equations, Gause found himself unable to at first reproduce, even qualitatively, the expected consumer-resource dynamics of oscillations experimentally (Gause 1934). He found consistently that *Didinium nasutum* over-exploited its resource *Paramecium caudatum*, resulting in the collapse of the system. It wasn't until Gause had the idea to introduce immigrants of both *D.*

nasutum and *P. caudatum* that he could get the system to persist with oscillations thus corresponding qualitatively with the basic theory (Gause 1934; Gause et al., 1936; Luckinbill 1973). This introduction of immigrants into his microcosm suggests the importance of an "outside" supply of organisms for the system to persist, something which was later verified for this same system (Luckinbill 1974). This necessity of immigration hinted at the fact that spatial structure and dispersal may be an important mechanism which structures even the most basic ecological interactions, a reality that is appreciated today by most all ecologists (Levin 1969; Leibold et al., 2004). Remarkably similar results were discovered approximately 25 years after Gause's foundational experiments, when Carl Huffaker studied the predator-prey dynamics of two mite species in the laboratory. Like Gause, Huffaker found that his system would not persist unless placed into a spatially extended environment with heterogeneity which consisted of an array of oranges. Huffaker's experiments highlighted the importance of heterogeneity in the environment, using various techniques to modify the dispersal capabilities of both predator and prey to demonstrate how spatial heterogeneity plays a role in stabilizing the ecological interaction.

An accounting of the impact that spatial heterogeneity has on community dynamics is essential and sets the stage for questions of how spatial heterogeneity emerges in ecosystems, given its importance in community ecology. While there are numerous frameworks to understand where spatial heterogeneity comes from, a useful first question may be to ask whether heterogeneity emerges from endogenous or exogenous factors. Exogenous explanations may include, for example, plants preferring particular soil-types, thus implicating the underlying geology of an area as a force determining the spatial distribution of a plant community. An endogenous driver of spatial heterogeneity may emerge from the network of competitive interactions among plants in the community (Vandermeer and Yitbarek 2012), facilitation between organisms (Stump et al., 2018), or even consumer-resource interactions (Comins et al., 1994). While it is likely the case that both exogenous and endogenous factors work in concert to determine the structure of spatial heterogeneity in ecological communities, understanding the relative contributions of these two classes of processes can be a useful way of understanding how they are structured (Yitbarek et al., 2011; Li et al., 2016).

In the early 1950's Alan Turing proposed a framework for understanding the dynamics of endogenously generated spatial heterogeneity which has laid a foundation for ecologists to build upon (Turing 1952; Segel and Jackson 1972). Central to his framing was the idea of activator-inhibitor systems, where activators grow by themselves and inhibitors emerge to control the activators, both diffusing in a spatial context. The key to pattern formation with this elegant insight is that activators and inhibitors need to be diffusing in space at different rates. When there is differential diffusion in space, typically with inhibitors diffusing faster than activators, pattern formation occurs. This process of unequal diffusion leading to pattern formation is sometimes referred to diffusive instability or Turing instability (Turing 1952). The qualitative elements of Turing's insight have provided a mechanistic framework that has been applied with great success in ecology (Alonso et al., 2002; Rietkerk and Van de Koppel 2008; Rietkerk et al., 2021)

Although Turing's mechanism for the generation of spatial heterogeneity is quite broad, it has largely been successful in terms of describing intraspecific species interactions in pattern formation, with what has been called scale-dependent feedbacks (Rietkerk and Van de Koppel 2008; Pringle and Tarnita 2017). The basic idea is that positive feedbacks within a population dominates locally in space and negative feedbacks take over at larger distances (Rietkerk and Van de Koppel 2008), resulting in self-organized spatial structure. While multiple ecological mechanisms may fit within the scale-dependent feedback framework, other interspecific ecological interactions which correspond to Turing's activator-inhibitor framework such as consumer-resource interactions, are known to create spatial patterns (Comins et al., 1992; Hassell et al., 1994; Alonso et al., 2002).

An appreciation that spatial heterogeneity emerges from ecological processes, as has been demonstrated in the Turing framework, in conjunction with an understanding that spatial heterogeneity influences ecological interactions, suggests the potential for feedbacks between these two dynamic processes of pattern formation and ecological interactions. My PhD dissertation is concerned with this dynamic feedback between pattern formation and ecological interactions and attempts to understand not only this feedback process, but how it structures ecological communities and how that community structure subsequently influences ecological processes in agroecosystems.

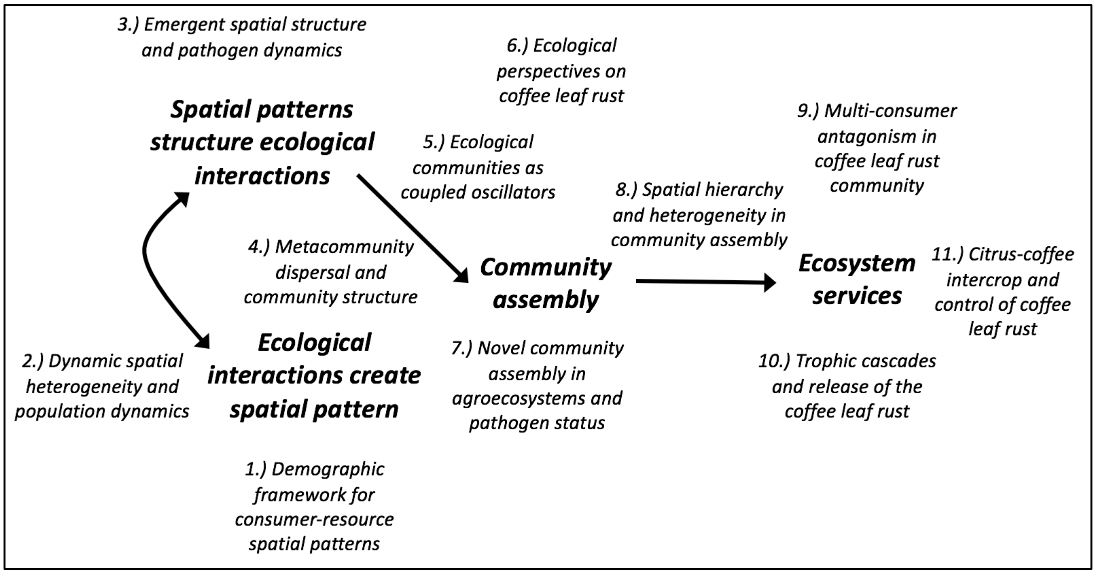

Figure I.1: Conceptual diagram of interrelated themes of my dissertation. Bold phrases connected by arrows represent core themes that tie together the various chapters. Chapters are in italics preceded by their number. The chapters are positioned close to the themes (or relationship between themes) that they correspond to.

Figure I.1 lays out the structure of the work contained in this dissertation, where there are four central themes of the work presented here. My first theme is how ecological interactions create spatial pattern and in Chapter 1 I present a framework for doing so with consumer-resource systems. I then turn to the theme of how spatial patterns structure ecological interactions, and ask about the feedbacks between these first two themes in Chapter 2 by exploring how dynamic spatial heterogeneity feeds into the dynamics of host-parasitoid systems. In Chapter 3, I focus exclusively on the issue of how spatial structure influences pathogen dynamics using a modeling approach. In Chapter 4 I take an empirical approach and link the first two themes to the third theme of community assembly to ask how dispersal alters community structure in empirical metacommunities. Staying with the theme of community assembly and organization, Chapter 5 puts forth an alternative way of viewing community organization, through the lens of coupled oscillators.

Chapter 6 introduces the final theme of the dissertation, ecosystem services in agroecosystems, and focuses on the coffee leaf rust, where we introduce the basic history and ecology of the pathogen. In Chapter 7 I address the community assembly of natural enemies of the coffee leaf rust in two regions where coffee is cultivated and the coffee leaf rust pathogen has had dramatically different histories. Chapter 8 and Chapter 9 bridge the two themes of community assembly and ecosystem services to understand the details of community assembly of the coffee leaf rust natural enemy community in Puerto Rico, where I explore interactions within the community and the impact of the community on the coffee leaf rust. In Chapter 10 the focus turns to the influence of trophic interactions in structuring the control of the coffee leaf rust and finally Chapter 11 explores how the management of an intercrop structures ecological interactions and biological control of the coffee leaf rust through a pathway of indirect and direct interactions.

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Chapter 1 The Population Dynamics of Consumer-Resource Induced Spatial Patterns: Insights from the Demographics of the Turing Mechanism

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Abstract

Alan Turning's proposed inhibitor-activator mechanism underlying spatial pattern formation has been successfully applied by many fields of science to explain a wide range of natural phenomena. In ecology, the inhibitor-activator mechanism is often abstracted as a consumer-resource system, one of the most fundamental ecological modules in nature, and has been shown to generate a wealth of spatial patterns. Here we propose the existence of a fine scale demographic spatial pattern (DSP) that should be universal among spatially clustered consume-resource pattern generating systems, and propose a series of hypotheses about how this DSP should structure ecological dynamics in space and time. Utilizing 13 years of large-scale spatially explicit data on the distributions of arboreal ants, we present an empirical method for detecting DSP in natural populations and confirm its existence. We then show how the DSP generates spatiotemporal patterns in consumer-resource dynamics as well as long term patterns

age-specific mortality rates that emerge from the spatial dynamics of the system. This work highlights how synthesizing the theoretical elegance of Turing's hypothesis with ecological dynamics allows us to not only understand how ecological patterns are formed but also provides a mechanistic framework for studying the Turing mechanism consumer-resource systems.

Turing and consumer-resource spatial patterns

The Turing activator/inhibitor mechanism provides for a qualitative understanding of self-organization of spatial patterns (Turing 1952; Nijhout 2018), as applied to many areas of science from chemistry (Winfree & Strogatz 1984), to cosmology (Nozakura & Ikeuchi 1984), and in biology, from the cell to the ecosystem (Kondo & Miura 2010, Kefi et al. 2007). Particularly in ecology, consumer-resource motifs provide a useful analogy to Turning's conceptualization, with resources being activators, consumers inhibitors and both "diffusing" through space. As ecologists first began to explore spatially explicit consumer-resources models, it became clear that a variety of patterns, from traveling waves, stationary lattices, chaos and clustered distributions, were an inevitability of their spatial extension (Comins et al. 1992; Alonso et al. 2002; Baurmann et al. 2007; Bascompte et al. 1995). This theoretical inevitability of patterns emerging from such systems resulted in the frequent suggestion that this consumer-resource motif may be responsible for many observed large-scale spatial patterns in ecosystems (Maron & Harrison 1997). While evidence for Turing-like mechanisms has been found to be operative in several empirical systems it has been rarely attributed to consumer-resource interactions but rather often abstracted to function in single-species scenarios in the form of scale-dependent feedbacks (Rietkerrk & Van De Koppel 2008; Schoelynck et al. 2012; Pringle & Tarnita 2017).

We suggest that lack of empirical support for consumer-resource generated spatial patterns stems from a lack of clear hypotheses regarding the basic population dynamics of spatially explicit consumer-resource systems. Here we seek to develop an understanding of the critical features of such systems and propose several patterns that should be universal in their population dynamics to provide a framework that can be applied broadly to other systems. To explore such generality we distinguish between the large and fine scale structures of a spatial pattern, wherein the large-scale structure is the pattern across a landscape and the fine-scale structure is an inset of that large-scale pattern. Much attention has been paid to large-scale descriptions of spatial pattern (Klausmeier 1999; Pascual & Guichard 2005; Kefi et al 2014), and we propose that the fine-scale patterns in the constitutive elements of the larger scale spatial pattern may be informative in understanding the dynamics and mechanisms driving pattern formation, within the basic paradigm of the Turing process driven by a consumer-resource interaction.

Demographic spatial patterns and clustered populations

One of the most common spatial patterns that emerges in both nature and a plethora of different ecological models, including consumer-resource models, is the clustered distribution of organisms. Most frequently these patterns are quantified at larger scales, with a nearest neighbor measure (e.g. Ripley's K), analysis of power spectra (e.g. wavelet analysis) or a quantification of the cluster size frequency distribution (Pascual & Guichard 2005; Vandermeer et al. 2008; Kefi et al 2014). While studying spatial pattern at these larger scales have proven fruitful in developing our understanding of pattern formation, we propose to couple this large-scale approach with an interrogation of the fine-scale pattern embedded within these large-scale patterns. With clustered spatial patterns, this means "zooming in" to the scale of individual clusters to understand how processes taking place locally feed up to influence the large-scale spatial pattern. Furthermore, by focusing on the demographics of fine-scale structure we propose that signals of the precise mechanism of both activation and inhibition of the Turing mechanism can be understood in detail.

The dynamics of local demography (the resource clusters) is almost certainly related to the mechanism of the spatial pattern formation at the larger scale. The simple fact that resource populations diffuse (dispersing locally) spatially suggests the existence of a “demographic spatial pattern” (here by referred to as DSP) where the oldest resources occur in the center of a cluster and youngest on the edge. This DSP should be apparent in any resource that is at least semi-sessile and disperses locally (e.g. plants, bacteria, ant colonies, etc.), and provides a fine-scale spatial pattern embedded within the large-scale pattern that can be used to interrogate the spatial population dynamics of both resource (activator) and consumer (inhibitor).

Given the existence of DSP, inevitable from the spatial dynamics of the resource species alone, we expect that it will structure the larger scale spatial consumer-resource dynamics in two ways. First, while consumers diffuse through space between elements of the fine-scale structure they will first encounter the periphery of clusters where the youngest resources will be located, a basic feature of the DSP. Consequently, we expect the highest pressure from consumers to be usually found on these younger resources. Second, this pattern of consumers aggregating on younger resources should in turn result in higher age-specific mortality rates for younger resources, which again should be on the edges of clusters. Intuitively, the degree to which these two hypothesized patterns in the dynamics will be apparent should depend on the relative diffusion rates of both the resource and consumer populations, as the diffusion rates will structure the strength of the DSP in the resource clusters.

Diffusive instability and demographic patterns

In Turing's initial conceptualization of pattern forming systems, the idea of diffusive instability (sometimes called Turing instability) was central. Qualitatively, diffusive instability refers to mechanism that drives pattern formation these systems, where activators and inhibitors diffuse at unequal rates with inhibitors typically diffusing faster than activators. One way to quantify this is by looking at the ratio of the resource (DR) and consumer diffusion rates (DC). If we constrain the system so that, $\mathrm{DR} \leq \mathrm{DC}$, and define $\mathrm{DDI} = \frac{\mathrm{DR}}{\mathrm{DC}}$, we can glean a picture of how the relative diffusion rates influence dynamics of DSP formation in consumer-resource systems. Given that, $0 \leq \mathrm{DDI} \leq 1$, we can explore how pattern formation dynamics are influence by where DDI lies. We can see that when DDI is closer to 0, consumers are diffusing much faster than resources, which will result in a less pronounced DSP within resource clusters due to the inability of large resource clusters to form from arrival of highly mobile consumers and the subsequent elimination of the cluster. The closer DDI is to 1, the faster the resource populations diffuse relatively to the consumers which should create a more pronounced DSP in resource clusters. Thus, both the large-scale spatial pattern, as quantified by cluster size frequency distribution, and fine-scale spatial pattern, as quantified by the DSP, are influenced by the relative diffusion rates of consumers and resources. In a later section, we demonstrate how trends in demography which are structured by the DSP in resource clusters can be used to approximate the relative diffusion rates in consumer-resource systems

To demonstrate this hypothesized fine-scale demographic structure, we leverage the well-studied consumer-resource system of a tree-nesting ant *Azteca sericeasur*, and its parasitoid predator, the phorid fly *Pseudacteon spp*. This empirical system's dynamics contain the two features which correspond to the classic activator and repressor elements of Turing's basic equations. Frist, the activation occurs through the budding of ant colonies – individual queens move with a group of workers to a neighboring tree, effectively a low "diffusion" rate, and the second element, repression, occurs via the parasitic fly consuming and destroying ant-nests. Thus, the budding of ant nests is the activator, which has a low diffusion rate (mainly from tree to nearby tree) while the attack of the fly is the repressor, which has a high diffusion rate (mainly from wind dispersal), setting up the appropriate conditions for diffusive instability (Segel & Jackson 1972; Segel and Levin 1976).

The data used to explore the hypothesized DSP and its implications come from a 45 Ha plot that was surveyed annually for the presence of *Azteca* ant nests from 2004-2016, providing an extensive spatially explicit time series for 13 years of resource distributions (Figure 1.). We use this empirical dataset to demonstrate our framework for detecting the DSP in nature and to quantify long-term patterns of age-specific mortality. This analysis is coupled with extensive field surveys that aim to quantify the strength of the consumer-resource interaction across the demography of the resource (*Azteca* ant nest ages). Finally, we present an individually based spatially explicit consumer-resource model to compare with our empirical system and understand how the feedbacks between spatial pattern and consumer-resource interactions structure observed dynamics of the system.

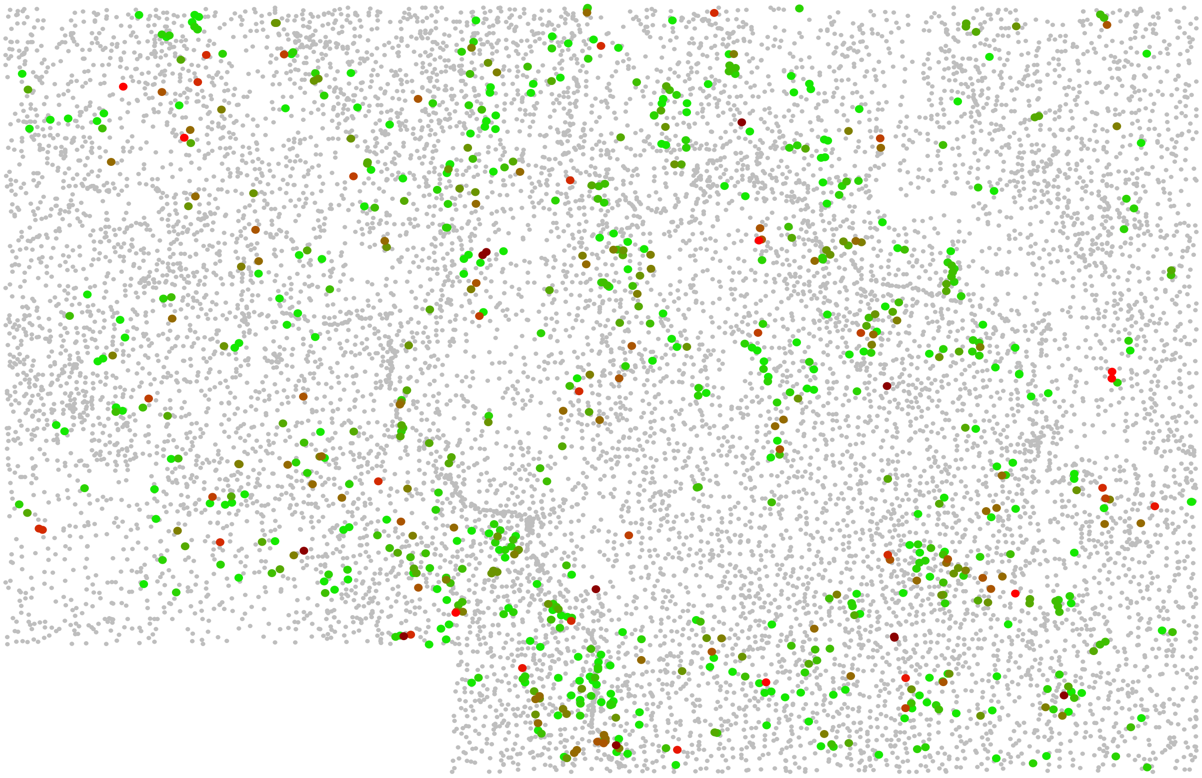

Figure 1.1: Map of the 45 hectare plot in Chiapas Mexico for year 2016. Grey points are trees that do not contain ant nests. All colored points are trees with Azteca sericeasur nests. The colors range from dark red (oldest nests) to light green (youngest nests).

Uncovering DSP and its impact on empirical consumer-resource dynamics

To characterize the DSP, we first isolate all the ant nests that fall within a given radius (*r*) around nests of a given age class. For each focal nest age class, we performed a linear regression of the ages of satellite nests as a function of distance to focal nest (from the focal nest in the center to the maximum of *r*) (Figure 2a). The regression coefficient of the i^{th} age class (b_i) is calculated across all the different nest age classes (Figure 2b). The qualitative pattern that is hypothesized given the existence of a DSP in the resource clusters is clear -- as we move away from older nests in any direction, the age of neighboring nests should decrease resulting in negative regression coefficients (b_i) for older nests. The opposite is true for younger nests where we would expect a more positive regression coefficients to emerge due to nest ages increasing as we move away from the focal nest (see Figure 2b).

If a DSP exists in our system, then we expect a systematic trend in the aforementioned regression coefficients (b_i), such that they transition from negative for old nests to positive for young nests. This will result in a negative relationship between the focal age of nests and their corresponding regression coefficients (b_i) (Figure 2c). This negative relationship between nest age classes their regression coefficients (b_i) which describe nest ages of their neighborhood in space, can be used as a metric of the strength of the DSP in resource clusters. Here we take the existence (as defined here by a significant regression) of such a pattern in nest ages and regression coefficients as evidence of DSP. An overview of the quantification of the DSP in resource clusters is laid out in Figure 2.

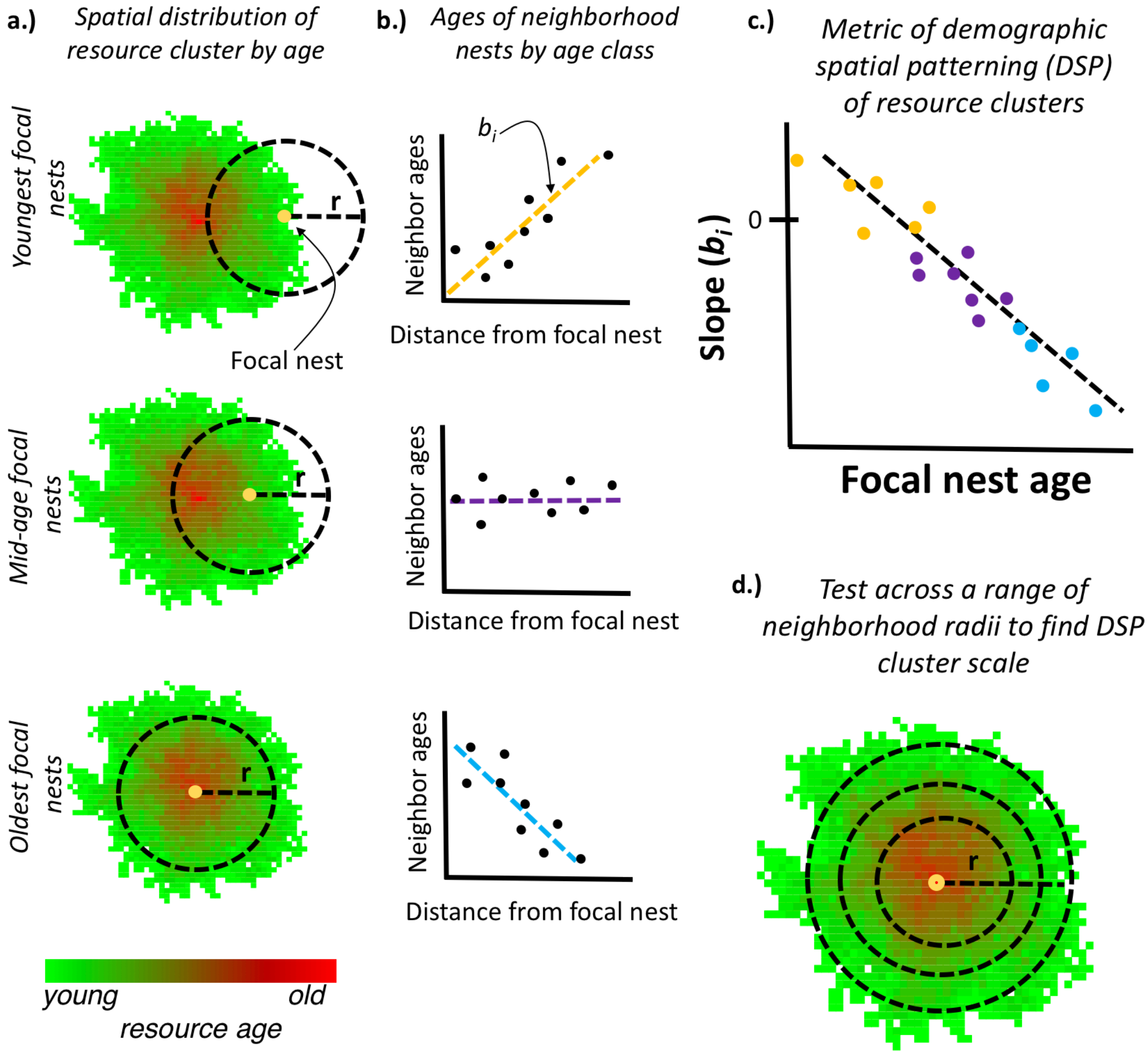

Figure 1.2: Illustrating the calculation of the Demographic Spatial Pattern (DSP). ***a.)*** *Clustered nest age distribution in space with older nests shaded black and less shade for younger and younger nests.* ***b.)*** *Relationship between nest age class and distance from centralized nest for old and young nest.* ***c.)*** *Linear regression coefficient (b_i) as a function of the age of the focal nest. The coefficient from the regression in c.) is used to quantify the spatial demographic pattern of the nests (resources) in space. We refer to this regression coefficient as the Demographic Spatial Pattern (DSP).* ***d.)*** *illustrates how the same test was conducted across a range of spatial scales (r) to detect the scale of DSP in our system.*

By implementing the procedure illustrated in Figure 2 to detect the DSP across various spatial scales (Figure 3d) for the nest distributions in 2016, we find a consistent signature of this fine-scale DSP structure in the ant nests at the 12-25m scale (Figure 3). The slopes that result from of our measure of the DSP (Figure 3a) show that the DSP is apparent across a range of scales, which most likely a result of the range of cluster sizes observed in the resource population. Both the R^2 value and p-values of our measure of the DSP illustrate the 12-25m range where the signature of the DSP is strongest and differs greatly from the randomized allocation of the resource ages (Figure 3 panels b and c). These results suggest that the ant nests (i.e. resource/activator) leaves a historical trail of its diffusion, where by older resources are in the center and expand out radially forming the DSP.

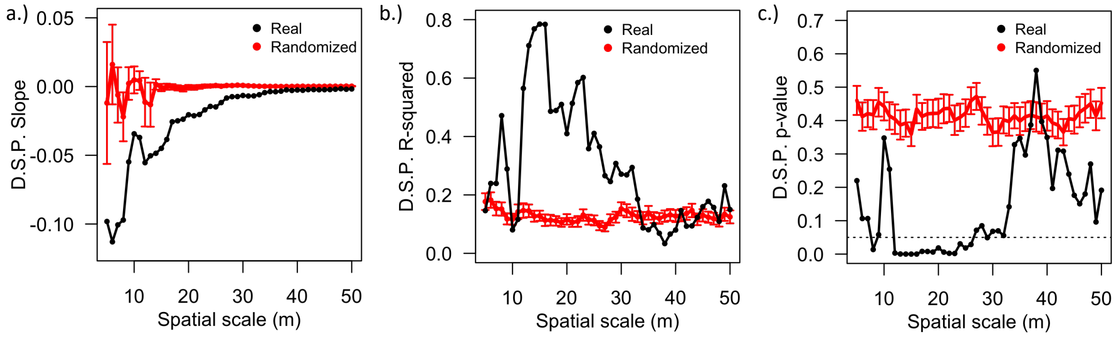

Figure 1.3: Statistical results from 2016 data, showing the Demographic Spatial Pattern as a function of d_{max}, as described in Figure 2. At each spatial scale nests were randomly assigned to trees and the procedure for calculating DSP was performed on the randomized data, repeating the randomization 100 times. The test was performed across various scales (d) ranging from 0-50m to estimate the scale at which pattern in nest age distribution emerges. ***a.)*** *Shows the estimate from the DSP test, b.) the coefficient of determination, R^2 and c.) the corresponding p-value (dotted red line at 0.05). All three graphs suggest that at about 20 m the DSP is most apparent. This tells us the hypothesized pattern is observed and it also gives us a biologically relevant scale at which self-organized pattern formation is acting.*

Given the existence of the DSP in the ant population, the second component of the Turing analogy is the repressor -- the parasitoid flies. Due to the DSP in the ant nest clusters, we expect to see diffusing parasitoids exerting higher pressure on the periphery of clusters (i.e. youngest *Azteca* nests). We surveyed the parasitic flies by disturbing *Azteca* nests of different ages and measuring: 1) the time to appearance of the first fly, 2) the number of flies that arrived during a 5-minute interval, and 3) the duration of the fly's attack after disturbance. As nest age increases, the time until the first fly arrives increases (p = 0.019; Figure 4a.), the number of flies decreases (p=0.03; Figure 4b), and the duration of the fly attack decreases with the nest age (p= 0.02; Figure 4c). Thus, via three different measures of consumer pressure our surveys support the hypothesis that consumers should be concentrated on younger resources. Again, we suggest that this higher consumer pressure from consumers is an emergent pattern that results from a combination of the DSP in the resource population and the diffusion of consumers through space searching for resources.

<u>Demographics of resource clusters structure consumer dynamics</u>

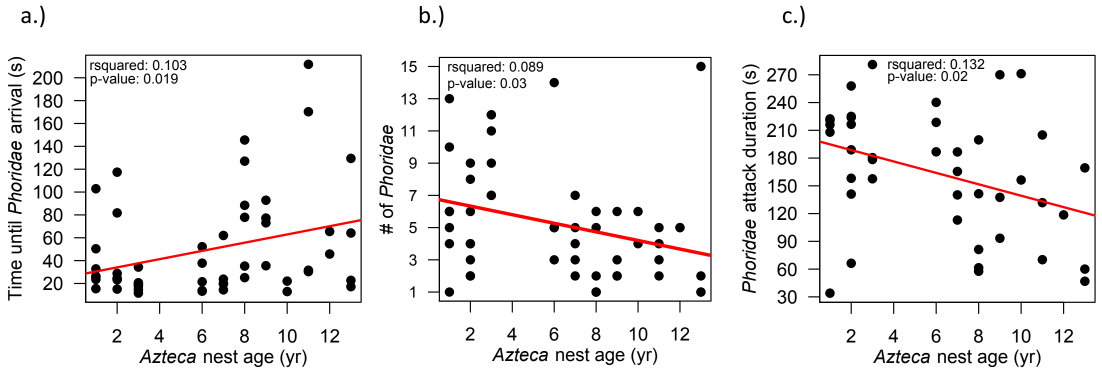

Figure 1.4: Three related lines of evidence of that parasitism (via parasitic flies) is less intense for old nests (which are in the center of clusters) than young nests (which are on the edges of clusters). ***a.)*** *shows the time until arrival, where at young nests flies arrive sooner than at older nests.* ***b.)*** *shows that more flies arrive at younger nests than older nests.* ***c.)*** *shows that as nests get older the duration of parasitoid attack decreases*

Given that consumer pressure is structured by the DSP, we ask whether this pattern emerges in the average age-specific mortality in the long-term data set of *Azteca* nests. The data show a clear signal of decreasing age-specific mortality as nest age increases (Fig 5), consistent with the expectation from the DSP. However, there is also a sharp deviation from that trend starting on six-year-old nests, where its age-specific mortality begins to increase. This pattern of age-specific mortality emerges likely emerges from the dynamics of both the fine-scale and large-scale spatial structures of the system. We see that the DSP structures age-specific mortality for nests 1-5 years old where youngest nests buffer older nests on the periphery of clusters (Figure 5a) but there is a critical point for 6-year-old nests where the trend reveres with a greater likelihood of older nests dying (Figure 5b). This change in mortality dynamics for older nests potentially results from density-dependent dynamics of parasitoids on clusters. A pattern previously seen from field surveys is that larger clusters of ant nests are associated with higher pressure from parasitoids (Vandermeer et al. 2006), thus making it more likely for larger clusters to attract to parasitoids and become eliminated.

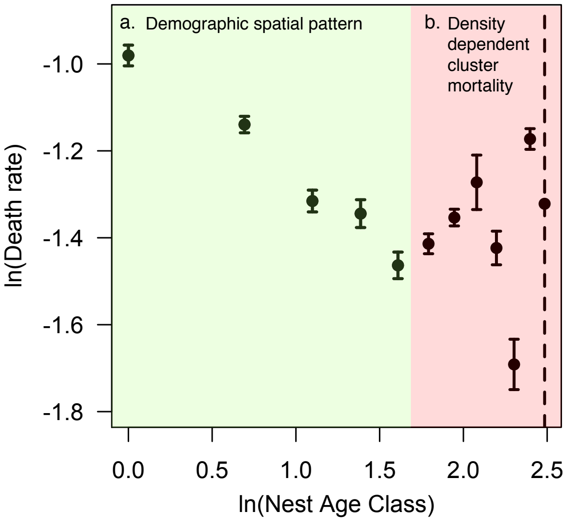

Figure 1.5: Shows the average age-specific mortality for the empirical ant nest data plotted on a log-log plot. a.) (green) shows the contribution of the demographic spatial patterning (DSP) in the resource clusters to the age specific mortality of nests aged 1-5 years. b.) shows the deviation from this pattern that represents the density dependent attack of clusters.

Diffusive instability, spatial pattern, and population dynamics

Given our hypothesis that the signal from the DSP should vary with the relative diffusion rates of the consumers and resources, we used a spatially extended consumer-resource model to explored a range of parameters that correspond to the diffusion (i.e. average distance moved) of the consumers to understand how it structures the spatial pattern of the resource and how that subsequently leads to tends in age-specific mortality of resources (Details of the model can be found in the methods section below). Recall that we can conceptualize diffusion in the system as the ratio of diffusion between the resources and consumers $\frac{D_R}{D_C} = D_{DI}$. For our simulations, the resource population stochastically diffuses to empty cells in their Moore-neighborhoods, effectively making $D_R = 1$. By keeping D_R constant, we can vary $D_C$to change the value of D_{DI} and understand how it impacts the population dynamics of the system.

Our model could qualitatively recreate the previously reported clustered spatial distribution of similar systems (Vandermeer et al., 2008; Jackson et al., 2014; Li et al., 2016) as quantified by the frequency distribution of cluster sizes approximating a power-function. Figure 6 shows characteristic snapshots after 1000 time steps of the model for increasing predator diffusion, and demonstrates how consumer diffusion impacts the DSP in the resource clusters. In short, relatively low consumer diffusion allows for larger clusters to build, note clear demographic structuring within clusters, while higher consumer diffusion rates reduce the overall size of the resource clusters and increase the frequency of small clusters (Figure 6 bottom row of panels). A analysis of exactly how those frequency distributions change with consumer diffusion is presented in the supplementary material (Figure S3). This scale free distribution of cluster size frequencies has been an essential feature of prior modeling attempts and our model corroborates previous qualitative assertions in that the explicit incorporation of the parasitic fly (repressor) into the model framework recreates the essence of these previous results. Again, we want to highlight how the extent to which we see the DSP in our model depends on the degree to which resources have clustered distribution, which is associated with dispersal limitation (relatively low diffusion compared to the resource) of consumers.

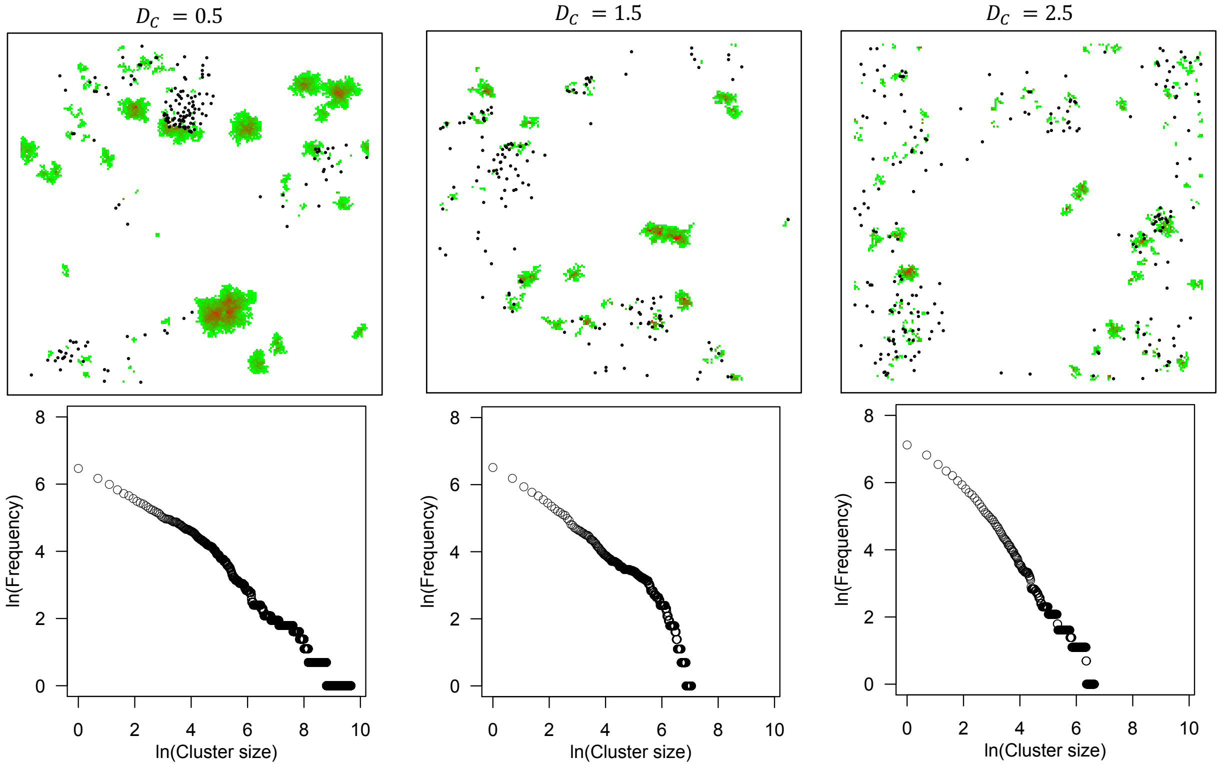

Figure 1.6: Shows a snap-shot from the individual based model of consumer resource interactions. The resources range in color from bright-green to red, where bright-green represent young resources, and red old resources. The black circles on the top row represent the consumers in the model. Note that the DSP emerges in clusters, where old resources are at the center and young resources on the periphery (older = redder and younger = greener). Also, note that consumer diffusion between patches of resources will result in young resources being encountered first. The bottom row shows the frequency distributions of cluster sizes that correspond to the parameters of consumer diffusion above. Note that larger clusters form with low diffusion with relative few small clusters and this shifts to no large clusters and many small clusters under high consumer diffusion.

Given the dependence of DSP in the model on the diffusion rates of the consumers we also expect that the extent to which the DSP can structure age-specific mortality will be also be influenced by relative diffusion. The results from both our model and long-term survey data tell a consistent story. The hypothesized impact of the DSP in regards to youngest resources having higher mortality due to their spatial arrangement on the periphery of the clusters observed in our model as well as our data (Figure 7 panels a and b.). As predicted the signal of the DSP in the age specific mortality is highest when resources are most clustered in space (e.g. consumers are dispersal limited – low diffusion), with the effect becoming less pronounced as consumer diffusion increases (Figure 7b). This is seen by looking at the rate in which age specific death rate decrease as function of nest age (Figure 7 panels a and b.). Here we attempt to isolate the role of the DSP in structuring resource death rates by focusing on the decreasing portion of age-specific mortality (see Figure 5a). We use the slopes of the age-specific death rates (Figure 7 panels a and b) to quantify the signal of where our model approximates observations from our empirical data (Figure 7c). We can approximate the same impact of the empirical DSP in our model occurring when consumer diffusion is around 2-2.5 times higher than resource diffusion (i.e.$D_{DI} \approx 0.5$).

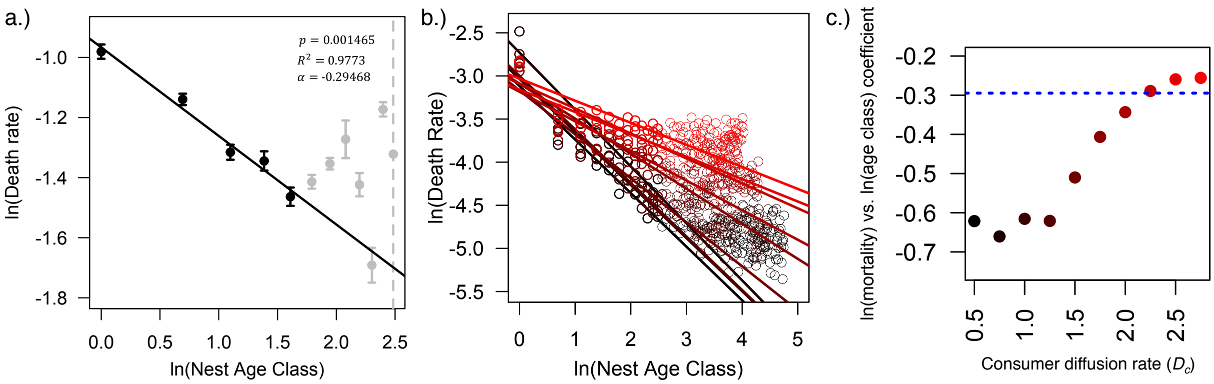

Figure 1.7: The death rate of specific age classes of resources (ant nests), in both the empirical data (a) and the model simulations (b). The data is plotted on a log-log plot to better quantify the relationship. The unlogged plots are in the supplementary material. (c) shows the slopes from the resource age vs death rate for the model (in black to red corresponding to Figure 6b, and the empirical data (dotted blue line). The data in (a) uses the empirical nest ages from 2016. Grey dots in (a) are excluded from the linear regression so we can see the scale at which the DSP impacts mortality (additional analysis in supplementary materials), and the dotted line on the oldest nest age signifies effectively infinite variance since we only have one data point. The colors in (b) and (c) show results from simulations with different diffusion parameters for the consumer, where consumer diffusion ranges from 0.5 (black) to 2.75 (bright red) by 0.25. Note that in both the model and empirical data we use relatively young nests, as older data induce noise due to their low abundance in addition with the termination of clusters

Given we can approximate the relative diffusion rate of our empirical system by using our model across a range of parameters, we can now see to what extent the spatial pattern corresponds as well. By isolating the diffusion rate of $\nabla_C = 2.25$ that is estimated from the age specific mortality, we see that it approximates our empirical data at the spatial scale detected by our test for DSP (Figure 8). The essential feature of the spatial pattern, as measured by the frequency distribution of cluster sizes correspond striking well with the slopes of the log-log cluster size frequency distribution plot being a quantification of the pattern. For the empirical cluster size frequency distribution the slope of the spatial pattern is *-1.26377* and for the simulation data at the scale detected in age specific mortality is *-1.27166*. This highlights the concordance between the age-specific mortality and the DSP which is closely related to the spatial pattern that emerges from the system. All of which is related to the essential idea of Turing's initial conceptualization of diffusive instability.

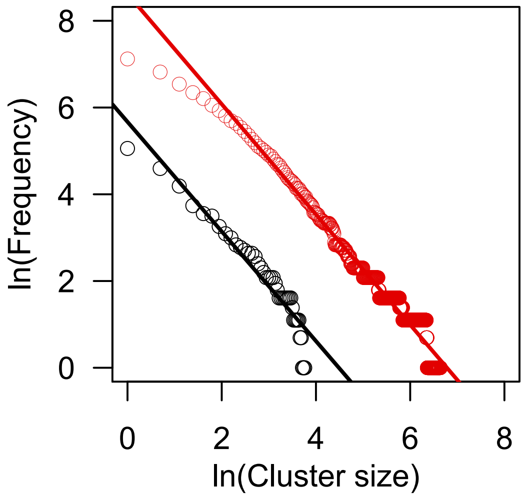

Figure 1.8: Shows the cluster size frequency distributions from empirical data at 20m cluster threshold (black) and for simulation data at $\nabla_C = 2.25$ *(red). Note the concordance between the slopes for both empirical (-1.26377) and simulation (-1.27166) spatial patterns.*

Conclusions

The confounding nature of ecological processes acting at distinct and often interacting spatial scales is a significant and well-known challenge in ecology (Weins 1989 ; Kotliar & Weins 1990; Levin 1992; Viana & Chase 2019; Vandermeer & Jackson 2019). Here we have attempted to confront a portion of this challenge by developing a multi-scale framework to understand pattern formation in consumer-resource systems, and by illustrating how the original spirit of Turing's insights into activator-inhibitor systems and diffusive instability can be applied directly to ecological systems. Through multiple lines of evidence, we show how fine-scale demographic structures in clustered resource populations can lend insights into the dynamics that generate large-scale spatial patterns. We then proposed and verified the existence of a demographic spatial pattern (DSP) in resource populations which we show to structure the consumer-resource population dynamics across spatial and temporal scales. Finally, we demonstrated how to extract information on the diffusive instability of the system through a cross-scale analysis of fine-scale and large-scale spatial pattern and demographic dynamics. By focusing on basic assumptions that stem from the spatially explicit population dynamics of consumer-resource systems, we presented a framework that can be applied to other consumer-resource pattern forming system in which there exists spatial time series data of resource populations.

Methods

Empirical Methodology

Phoridae predation across Azteca demography

Nests were selected haphazardly from a dataset that gave all *Azteca* nest ages on the 45ha plot on a coffee agroecosystem in southern Mexico. Once a nest was identified in the database it was then located on the 45ha plot. Once at the site of an *Azteca* nest, we slowly approached the tree containing the nest and attempted to identify where the majority of ant activity was prior to disturbing the nest. We subsequently killed 10 ants in an area of high activity by pressing them into the trunk of the tree. During this process, we used a stick or leaf to kill the ants and left it at the sight as to not carry *Azteca* pheromones between sites. Once the first ant was killed we started a stopwatch to time how long it takes for the first *Phoridae* parasitoid-fly to arrive to the local site of the disturbance. Once a *Phoridae* was spotted we turned off one stopwatch and triggered another one to track the duration of the attack. While the *Phoridae* were present at a site we monitored the number of them, the number of successful attacks, and the duration of the total attack for up to five minutes. If the attack duration for a nest surpassed five minutes then it was not included in the analysis presented in Figure 4c. When including the data points where attack duration was greater than five minutes the linear regression is not significant (p=0.184). If there were no successful attacks for 1 minute then we counted that as the attack being done. All sites were surveyed together with the same two people as to keep methodology consistent.

Long-term data collection of nest locations (2004-2016)

Each tree on a 45ha plot in a coffee agroecosystem in southern Mexico has been surveyed to look for the presence of *Azteca* nests since 2004. Data from this survey is used here from 2004 through 2016, to pick sites for fieldwork and also to look for trends in *Azteca* nest demography.

Analysis of long-term data

To calculate the age-specific mortality of the nests, we calculate the change in number of nests from one year to another divided by the number of nests in that age class. Doing this each year, we have the age-specific mortality on an annual basis. To understand long-term patterns in age-specific mortality we take the average values for each age class.

Model Methodology:

The resource is modeled essentially as a probabilistic cellular automata where a single resource is fixed in discrete space and offspring diffuse to neighboring sites with a fixed probability. The consumer is modelled on the continuous space overlying the discrete lattice and moves randomly across continuous space. The joining of both discrete and continuous space in our model here provides a unique way of modeling consumer-resource systems that reflects essential elements of the underlying biology of many systems where resources and sessile and consumers search for them. Furthermore, tracking the demographic data in our model resource allowed us to understand the implications of the DSP within the resources spatial distribution.

Model implementation: The model was built entirely in NetLogo 6.0 (Wilensky 1999), and can be found as a .nlogo file in the supplementary material.

The host (ant) dynamics occur on a square torus in which each point represents a shade tree potentially containing an ant nest. At each iteration each established ant nest increases its 'nest-population' by 1 and increases its 'nest-age' by 1. Each nest "buds" with a fixed probability to one of their unoccupied Moore-neighbors (the surrounding 8 patches). If an ant nest successfully buds to one of its Moore-neighbors then the budding nest divides its population in half, giving half of its population to the new ant nest.

The consumers (parasitoid *Phoridae* flies) are represented in the model as a distinct agent. They are randomly initialized on a given proportion, *beta*, of ant-nests and randomly walk across the lattice with step lengths drawn from a Gaussian distribution with a mean of two and standard deviation of one. When a fly encounters an ant-nest, it stops walking and begins reducing the ant-nest-population by α and converts it into fly-population via γ. Once the ant-nest-population reaches zero, the ant-nest dies and the fly continues to randomly walk the lattice. When a fly agent reaches a given threshold of fly-population, φ, it then produces a new fly which takes Ω fraction of the mother population. Flies also have an aging cost, ε, and die when their fly-population reaches zero. An outline pseudo code is presented in Figure S7. and parameters for the simulations can be found in Table. 1

Ants-Nests: Each ant has an integer representing *Nest-population* & *Nest-age*
Flies: Each fly has an integer representing *Fly-population*
Initial conditions: Randomly seed 20% of the lattice with Ant-Nests then randomly seed 20% of Ant-Nests with Flies

Pseudo-code for model

```
FOR Ant-Nests
    $Nest\text{-}population \leftarrow Nest\text{-}population + 1$
    $Nest\text{-}age \leftarrow Nest\text{-}age + 1$
    IF rand_float < prob_of_budding
        randomly select cell $C$ in Moore-neighborhood
        IF $C$ is unoccupied
            create new nest in $C$ with $Nest\text{-}age \leftarrow 1$ & $Nest\text{-}population \leftarrow 1$
            $Nest\text{-}population \leftarrow \frac{Nest-population}{2}$
    IF Fly on Ant-Nest
        $Nest\text{-}population \leftarrow Nest\text{-}population - \alpha$
    IF $Nest\text{-}population = 0$
        Ant-nest removed from lattice
FOR Flies
    IF Fly-population >= $\varphi$
        Fly-population $\leftarrow \frac{\text{Fly}-\text{population}}{\Omega}$
        Create new Fly in same coordinates
        new Fly rotate randomly 0-359 degrees and moves forward one
    IF on Ant-Nest cell
        $Fly\text{-}population \leftarrow Fly\text{-}population + \gamma$
    IF not on Ant-Nest cell
        rotate randomly 0-359 degrees and step length drawn from Gaussian distribution of mean 0 sd of 2
        Fly-population $\leftarrow$ Fly-population - $\varepsilon$
```

Figure 1.9: Schedule and pseudocode for agent-based model

parameter	value
beta	1.5
prob_of_buddding	5
α	65
γ	65
φ	150
ε	5
Ω	8

Table 1.1: Gives the parameter values of the model that were used in the simulations. Note that results in Figure 4 and Figure 3S only change the mean of the distribution Gaussian distribution used to pull consumer walks in the model.

Model analysis

For purposes of this analysis the model was run for 1000 iterations. During the last 50 iterations of each run the ‘ages’ of each *Azteca* nest patch is recorded in addition to the size of each cluster of *Azteca* nest patches. Clusters here are simply defined as a nest patches which are connected by their Moore neighborhood. All runs were conducted in NetLogo 6.0 (Wilensky 1999) and ‘Behavior Space’ was used for parameter sweeps. Data was exported via ‘Behavior Space’ and analyzed in R.

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Supplementary Material

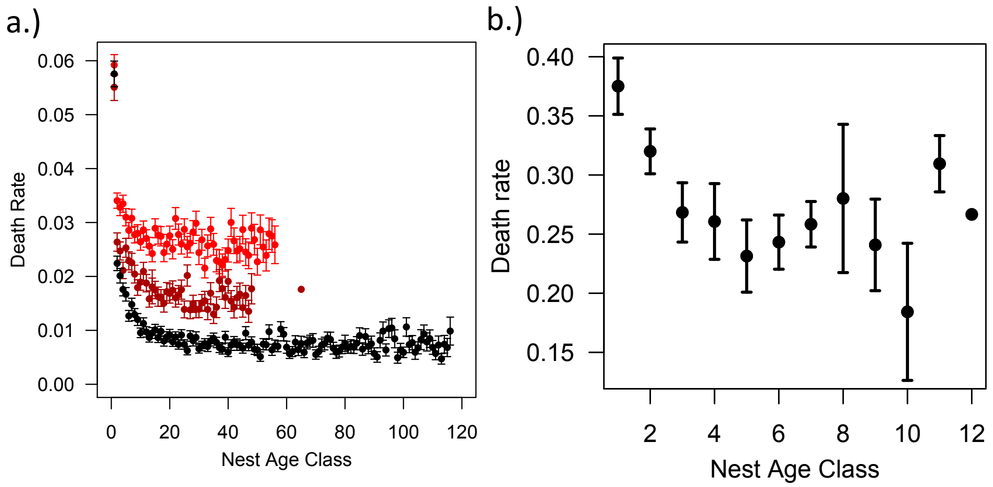

Figure 1.10: Shows the age class death rates for a.) the model simulations and b.) the empirical data. a.) shows the death rates for a range of parameters for the consumer diffusion rate. Red = 2.75, dark red = 2.00, black = 1.25.

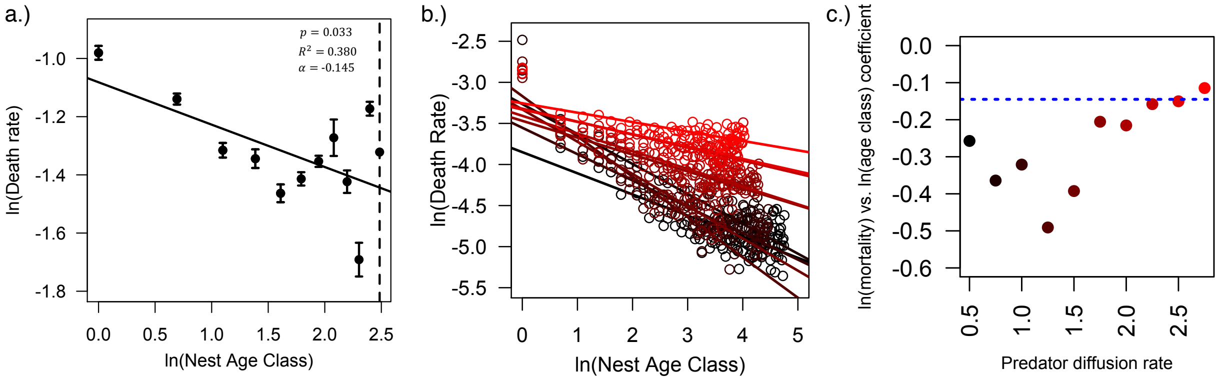

Figure 1.11: Shows the age specific mortality of the Azteca nests. Note that this figure is the same as Figure 5a but includes all of the age specific mortalities in the linear regression to quantify the impact of the DSP on mortality.

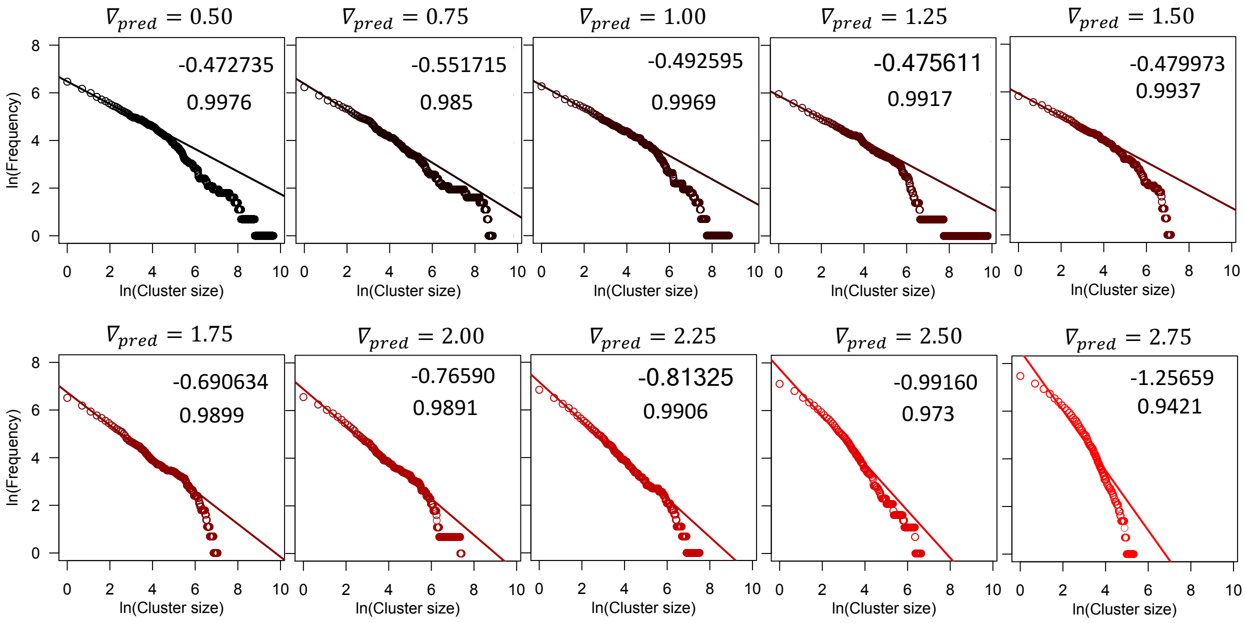

Figure 1.12: Shows the cluster size frequency distributions from model simulations across different predator diffusion rates. The colors in the figure correspond to the colors in Figure 5 panels b and c and the values used in Figure 5c. The first number in each panel is the slope (or coefficient) of the linear regression and the second is the R-squared. Note that the fit to a power function is done across the upper part of the distribution as is common practice when fitting power laws since the tail of the distribution is often under sampled.

Chapter 2 The Spatiotemporal Structure of Pilot Patterns and the Dynamics of Host-Parasitoid Systems

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Abstract

Environmental heterogeneity, in one form another, is appreciated as being present in all ecosystems. Furthermore, environmental heterogeneity has been shown to be central in attempts to understand the empirical patterns across spatial and temporal scales in ecosystems. Here we explore how spatiotemporal heterogeneity in the environment influences the simplest of all community ecology modules, consumer-resource interactions. By using a spatially extended Nicholson-Bailey, host-parasitoid model, we explore how patchiness in the model, as reflected by dynamically changing patch quality, influences the dynamics of the system. We show that if the environmental pattern is static then the system will persist indefinitely, but when the environmental pattern is dynamic that the system is quickly destabilized. The host-parasitoid system can be stabilized again only with time lags in the change of the environmental pattern. Additionally, we show that the spatial structure itself of the environmental patchiness plays a role in the persistence of the system. We suggest that these results from this simple toy model may highlight essential features of how the dynamics of organisms and their environment can match or mismatch in space and time resulting in unforeseen dynamics.

Introduction

The fact that no ecosystem is fully mixed means that all living organisms are confronted with environmental heterogeneity in one form or another (Levins 1989). Not only is heterogeneity omnipresent in ecosystems, but this environmental heterogeneity is often dynamic and changing on timescales that are relevant to the ecological dynamics of the organisms interacting within them. Heterogeneity is most often appreciated as being operative across space or time, and has been shown to be an important aspect of how we consider empirical patterns across spatial and temporal scales. Although this fact is acknowledged and growing in appreciation amongst ecologists, no general frameworks for our understanding of how spatiotemporal heterogeneity interacts with our basic understanding of community ecology has emerged. Here we explore how this basic idea of spatiotemporal heterogeneity with the simplest of all community ecology modules, consumer-resource interactions.

When ecologists first begun to explore the spatial dynamics of consumer-resource interactions, it was found that several unexpected observations emerged. It is now understood that simply putting consumer-resource interactions in space, the organisms themselves become a source of spatiotemporal heterogeneity that alter the fundamental dynamics of the system (Gause 1934; Huffaker 1958; Levin 1976). The classic theoretical example is that of the Nicholson-Bailey host-parasitoid model that has globally unstable oscillations in its most basic formulation but when extended to space can persist indefinitely (Hassell et al. 1994). By simply incorporating space into the Nicholson-Bailey model, spatiotemporal heterogeneity in the distribution of the host and parasitoid populations allow for host refugia that make a locally unstable system stable globally across space (May 1978).

Where suggest that in a broad sense, there are two ways in which heterogeneity can play a role in ecological systems. Frist, we can think of it has being imposed by some abiotic or environmental factor which may be conceived as impacting demographic rates of the organisms (Riolo et al. 2015). Second, the inclusion of space itself allows for the self-organizing spatial pattern of the interacting organisms. The first such case of a background pattern structuring the dynamics has been referred to as pilot pattern (Vandermeer and Jackson 2018), and can be thought of as being dynamic in space and time or static.

Here we attempt to gain an understanding of how these two forms of environmental heterogeneity in ecosystems interact in a simple model. The basic idea of an ecological pilot pattern has been explored by Vandermeer and Jackson (2018), and showed that the ratio of timescales between the dynamics of the pilot pattern and the ecological dynamics upon it can change the system from being stable to unstable. Here we explore a similar type of system but in a much simpler context than the cellular automata presented by Vandermeer and Jackson (2018), and use as simple spatially extended host-parasitoid model that plays out upon a dynamic environmental pattern. We first attempt to understand if the relationship of the disjoint timeframes between a pilot pattern and the host-parasitoid dynamics exists. We then explore the details of the underlying pilot pattern and ask how that impacts the host-parasitoid dynamics.,

Methods

Consumer-resource coupled map lattice

The basic formulation of the model follows Nicholson and Baileys original conception with the absence of density dependence on the host.

$$H_{t+1} = \lambda H_t e^{-\alpha P_t}$$

$$P_{t+1} = H_t(1 - e^{-\alpha P_t})$$

It is well known that this model in the absence of space produces unstable oscillations resulting in a collapse of the system. Here we make the simple modification to the model and put it on a coupled-map lattice.

$$H_{t+1}(k) = \lambda H_t(k)e^{-\alpha P_t(k)} + D_H \nabla^2 H_t(k)$$

$$P_{t+1}(k) = H_t(k)\left(1 - e^{-\alpha P_t(k)}\right) + D_P \nabla^2 P_t(k)$$

$$\nabla^2 H_t(r) = \sum_{j}^{q} H_t(j) - q\, H_t(k)$$

The simple inclusion of a diffusion operator, ∇^2, where q = 4 are the four closes neighbors of the focal cell, otherwise known as a the Von Neumann neighborhood puts the model on the lattice. All of our simulations used periodic boundary conditions and we employed a threshold cutoff for survival of hosts and parasitoids, where if H(k) or P(k) < 1X10^-6 = 0.

<u>*Spatiotemporal heterogeneity*</u>

By using a model developed by Vandermeer and Jackson (2015) we are able to not only study the impact of the dynamically changing environment but we also have the ability to quantify what that spatial pattern looks like and ask how that impacts the dynamics of the system itself. They made a simple cellular automaton that proposes the existence of a single population growing in space. The degree of density of dependence the population experiences is governed by the sum of the cells in its Moore neighborhood, $N_i(i,j)$, which is given by:

$$N_i(i,j) = \sum_{a=i-1}^{a=i+1} \sum_{b=i-1}^{b=i+1} B(a,b)$$

Where B is the operator that allows to us to sum the states surrounding or ith cell. Given the local density of the population around a focal cell, there is a probability that the cell will become occupied is given by:

$$P_O = \alpha_0 + \alpha N_i(i, j)$$

and a probability that the cell will die is given by:

$$P_D = \gamma + \beta N_i(i, j)$$

When $\alpha_0 = 0$ and $\gamma = 0$, the whole system is governed by local dynamics only where death and birth are determined by the Moore Neighborhood densities. Thus, $\alpha_0 > 0$ and $\gamma > 0$, model regional dispersal and stochastic death in the population. Further detail regarding the model can be found in Vandermeer and Jackson (2015).

Given a resultant spatial pattern which emerges from the Vandermeer-Jackson CA model, we use the same approach they do to quantify the spatial pattern. By using the frequency distribution of cluster sizes, as defined by cells connected via their Moore neighborhood, we can use the fit to a power function for a quantitative description of the pattern. Not only can we use the parameter of the power function, but we can all gleam information about the pattern by looking at deviations from the power law.

Coupling the spatiotemporal heterogeneity with the coupled map lattice.

Although there are various ways to formulate the ways in which spatiotemporal heterogeneity might influence a consumer-resource interaction, here we start with the simple assumption that the host population's underlying resource is of variable quality in space and time. Thus, we have a parameter, δ, associated with each cell in the couple map lattice that gives us a modification of the host growth rate, where for a given patch via, $\lambda = \delta\lambda_0$. Where λ is the realized growth rate of the population and $\lambda_0$is the maximum growth rate. For all the simulations presented here, there are only two values of δ that are given by the state of N(i,j) of the Vandermeer/Jackson CA model. We are modeling the system as if high quality resources are dynamically patchy with low quality resource matrix, thus when N(I,j) = 1, $\delta = 1$ and when N(I,j) = 0, $\delta < 1$. This creates a system that effectively acts as if it were a metacommunity constrained to a self-organizing environment or high quality patches for hosts. Thus, the environmental pattern has it independent dynamics that largely constrain the host distribution when then constrains the parasitoid distribution. For all simulations presented here when N(I,j) = 0, $\delta = 0.2$.

Results

Under the parameters used for the simulations here, the basic dynamics of similar models are relatively well know. Figure 1**.** Shows the spatially extended Nicholson-Bailey model for our parameters when there is a homogenous environment. The spiral patterns produced here are characteristic of similar models of host-parasitoid dynamics (Bascompte Sole Varlies 1995). Constraining the host-parasitoid system to a statically heterogeneous environment where patches are high-quality resource and matrix is low quality resource (as reflected in the growth rates of the host, λ, in those environments), also allows the system to persist (Figure 1b). Although the characteristic spiral spatial pattern observed in homogenous space is no longer present, and both populations are at lower densities this seems to simply be a reflection of the number of high quality patches accessible. Note that both system have stable oscillatory attractors that seem to persist indefinitely (Figure 1).

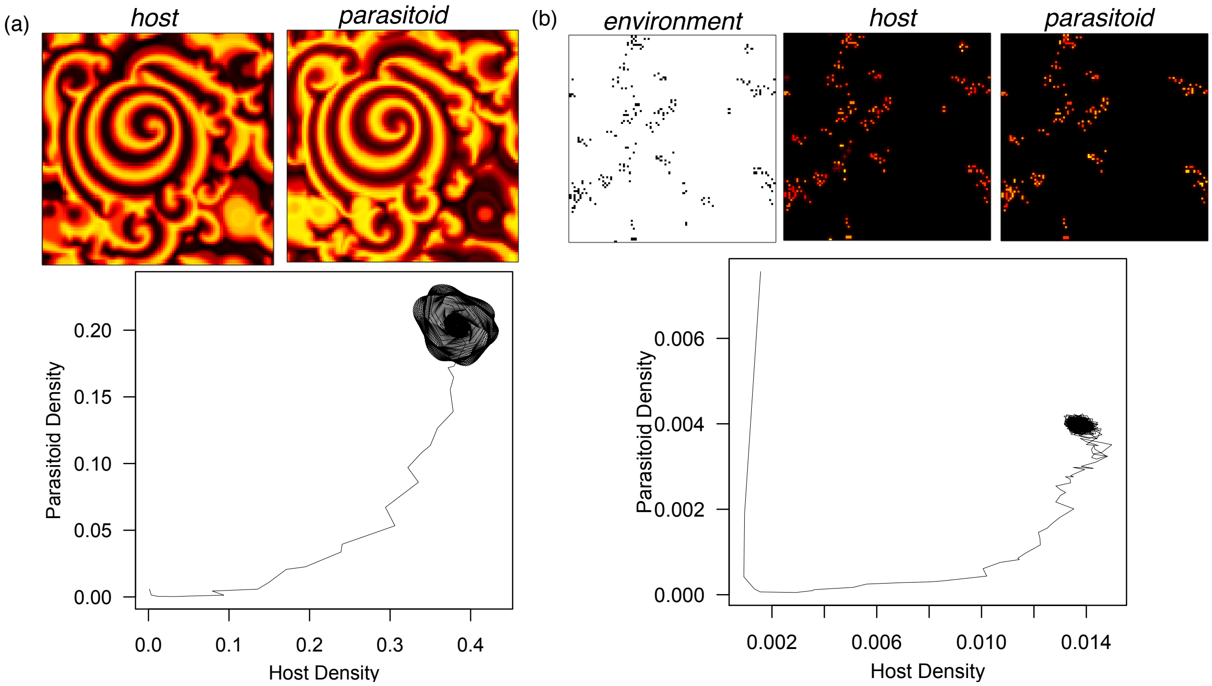

Figure 2.1: (a) The dynamics of the spatially extended host-parasitoid system in the absence of spatial heterogeneity after 2000 runs with the parameters $D_P = 0.1$*,* $D_H = 0.05$*,* $\lambda = 4$*, and* $\alpha = 4.25$*. (b) the dynamics of the model with a structured environment and the same parameters of (a) but with* $\delta = 0.2$*. The background environmental pattern was obtained by 1000 runs of the Vandermeer & Jackson (2015) cellular automata.*

Given this starting point of space, both homogenous and heterogeneous and static, can stabilize locally unstable host-parasitoid systems, we now ask to what extent can the system persist on an environment that has spatiotemporal heterogeneity. Our simulations show that with no time lag between the dynamics of the spatial pattern and the dynamics of the host-parasitoid system largely constrained to it, the system will always collapse (Figure 2). Observations from of these simulations suggests that this likely always happens because the parasitoid population goes extinct which in turn results in exponential growth of the host. The suggested importance of the disjoint timeframes between the dynamics of a background spatial pattern and the dynamics of the system upon it, was explored next to see if time lags associated with the self-organization of the spatial pattern have the ability to stabilize the system as found in other system (Vandermeer and Jackson 2018).

We found that as the time lag (τ) increases the probability that the system will persist for more time, mirroring the result from Vandermeer and Jackson 2018 (Figure 2). Interestingly there is a relatively large amount of variability for a given value of tau in the dynamics of the environmental spatial pattern. The simulations presented here are constrained up to 2000 iterations of the model, so the hard stop for $\tau = 4$ in Figure 2 is a result of that.

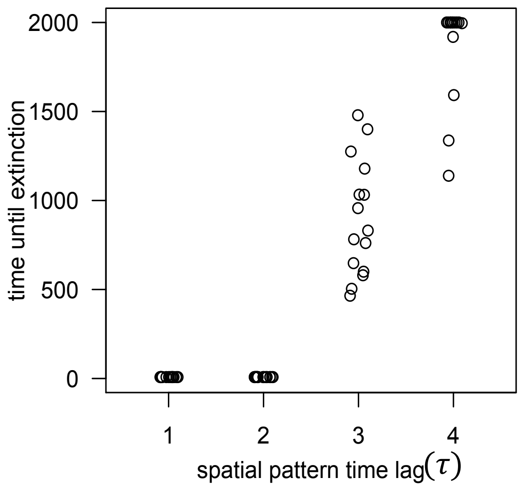

Figure 2.2: Shows the time until extinction of the host-parasitoid system with dynamic environmental pattern formation. Note that the cluster of points at τ = 4 emerges from the maximum number of iterations that were used in the simulations being 2000.

We suggest that the variability seen in Figure 2 as to how long the system will persist is dependent on the underlying spatial pattern that governs the host parasitoid system. As mentioned above, the system most frequently crashes due to the parasitoid metapopulation becoming extinct. Figure 3 shows the snapshots of characteristic model runs after 2000 time steps for different values of τ. Note that as we increase Tao the basic dynamics of the model changes as well. Note that the host generally tracks the environmental background pattern quite well, where the environmental pattern almost fully constrained the spatial distribution of the host. Importantly, the hosts ability to track the underlying environment increases with the time lag between the dynamics. The panel with the parasitoid in Figure 3, show that the reason why the system is crashing at low tau is due to the parasitoids inability to track the host populations. Much like the host's ability to track to the environment increases with time lags, as does the parasitoids ability to track the hosts spatial distribution.

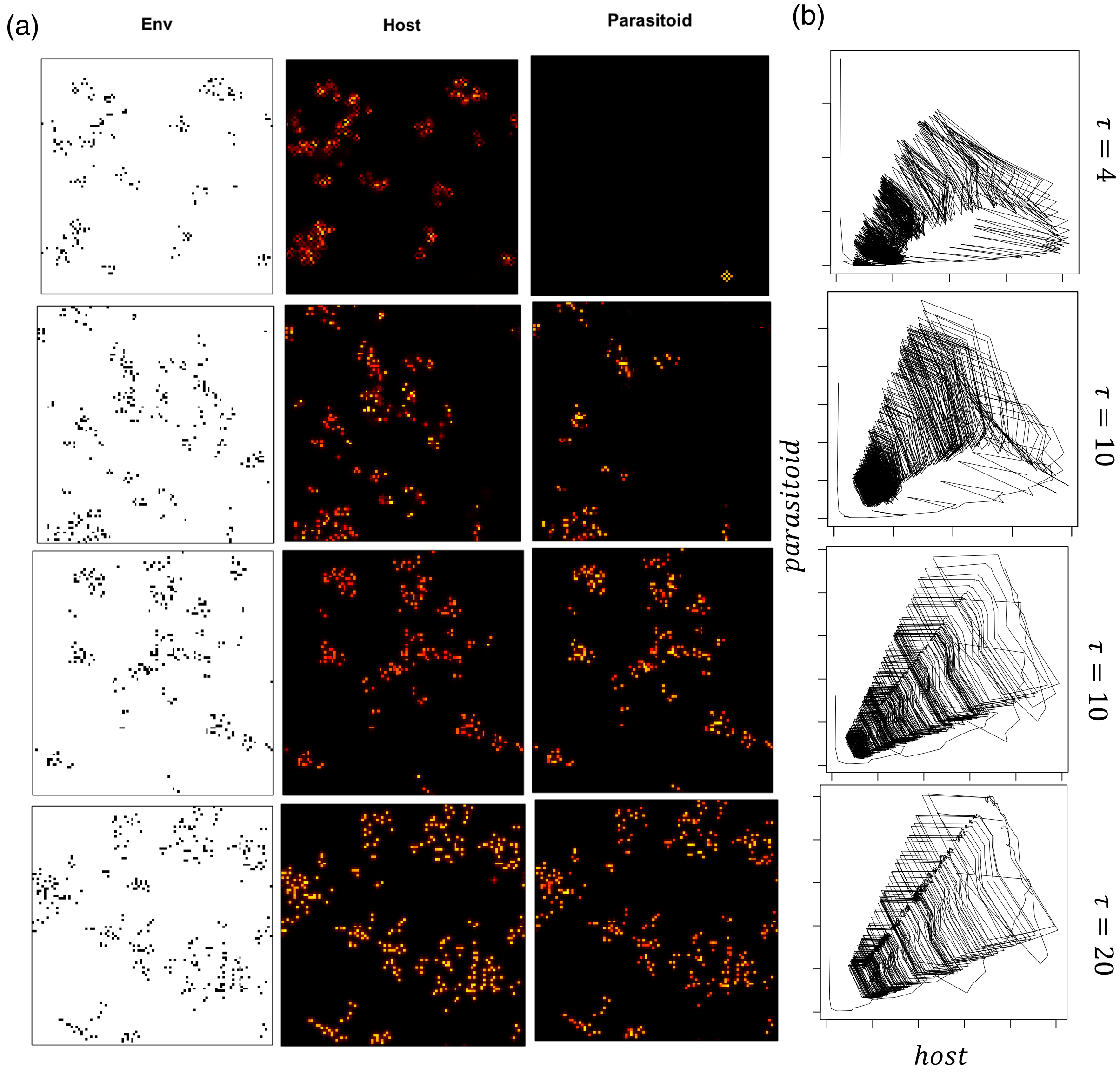

Figure 2.3: Illustrates the dynamics of the host-parasitoid model as τ increases. (a) shows the underlying spatial pattern of the environment where hosts can access resources of high quality (black squares) and where hosts cannot (white squares). The first column of panels is followed

by the host and parasitoids spatial distributions. (b) shows the phase space diagrams for the host-parasitoid population through time.

In order to understand how the underlying spatial distribution of the environment, which constrains all of the trophic levels built upon it, influences persistence of the system, we took a value of $\tau = 3$ where extinctinos are inevible, but highly variable to explore the spatial pattern of the environment. By using the slope and fit to a power function we are provided an intuitive understanding of the spatial pattern present. Figure 4 Shows that the slope of the initial environmental pattern has no relationship with the time until extinction. Interesting there is a significant negative relationship with the time until extinction and the slope of the environmental pattern power law. This suggests that some high-quality habitat cluster distributions are more strongly associated with persistence of the system than others. In particular, we found that more negative slopes are associated with persistence. Somewhat counterintuitively, we find the opposite pattern with the fits to the power laws, where the initial fit has a negative relationship with the persistence but the final fit does not.

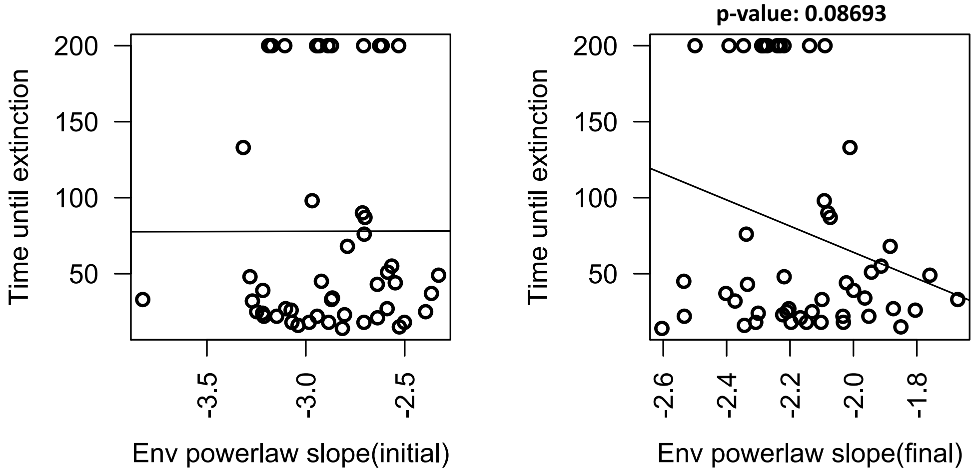

Figure 2.4: Shows the time until extinction for the host-parasitoid system and the initial lope of the environmental heterogeneity and the final slope. Note that the initial Environmental heterogeneity power law slope had not relationship with the time until extinction, but the final slope had a significantly negative relationship.

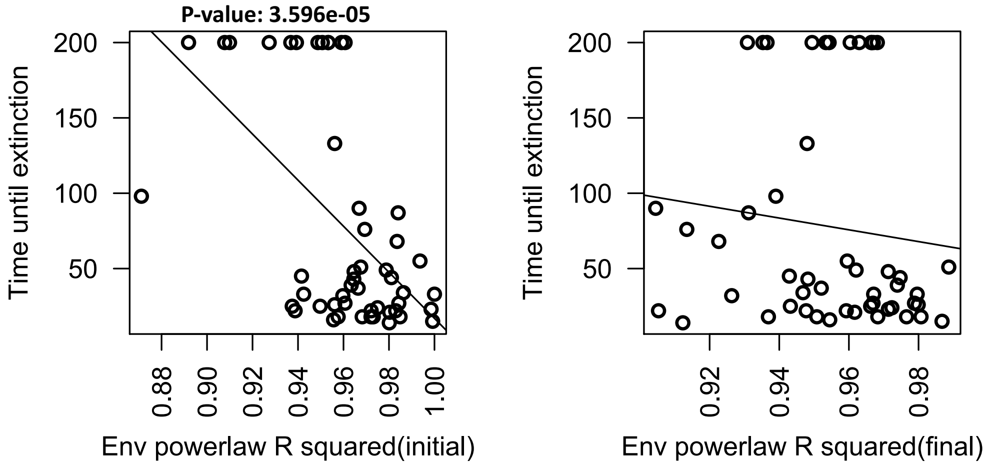

Figure 2.5: Shows the relationship between the time until extinction and the fit R-squared fit to the power function of the initial environmental pattern and the final environmental pattern. Note a significant negative relationship between the initial fit to the power law and the time until extinction.

Discussion

The inclusion of temporally static heterogeneity does not change the fundamental stable oscillatory dynamics of the host-parasitoid system, but as soon as the environmental heterogeneity, or the pilot pattern, becomes dynamic the system is quickly destabilized. Given strikingly similar patterns observed in more complicated models (Vandermeer and Jackson 2018), this may suggest some type of generality in how structured environments constrain ecological interactions.

The longer the time lags in the dynamic spatial pattern of the environmental allows for the host parasitoid system which was constrained upon it to persist longer. Figure 3. Shows the qualitative dynamics of how the time lag impacts dynamics. Unlike Vandermeer and Jackson (2018) we did not calculate the critical value of τ in our model, although it does look like it maybe relevant to our system. Note that in Figure 1b, where we have a spatially heterogonous but temporally static environment, the system exhibits stable oscillations. This is in contrast to Figure 3b, where all of the dynamics show damped oscillations but approach the origin, suggesting that the system may be on its way to extinction. Quite clearly, the analysis here needs to be revisited with much longer simulation times to see, first if the system is on its way to extinction for the parameters in Figure 3, and if so to see if a critical τ exists as it does for the Vandermeer Jackson model (2018).

In our model, it seemed as if the spatial distribution of the pilot pattern plays an important role in how long a system may persist. When the dynamics of the clustered environment, organizes itself in such a way where there are many small patches and very few large patches (more negative slows to the power law) then the system is more likely to persist. The slope of the power law used to describe the spatial patterning of the pilot pattern allows us to conceptually organize the types of patterns that emerge. With steeper slopes being characteristic of what some may describe as a metapopulation or many small patches and few if any larger patches and shallower slopes being more of a mainland-island type of spatial arrangement where very large clusters can act as sources for the populations (Jackson et al. 2014). Figure 4 and Figure 5 suggest that having a power law distribution that approximates any power law well early on in its dynamics will likely go extinct soon, but if the environment self-organizes into a metapopulation type spatial arrangement it can persist longer. Figure 3 suggests that this metapopulation structure may be most important for the parasitoids which are constrained by the distribution of the hosts which are then constrained by the distribution of the resources in space. It may be that when we have more small patches the distance needed to traverse across the lattice is less allowing for effective dispersal of the parasitoids and thus persistence of the system.

Here we show that the often-assumed role of heterogeneity in allowing for the persistence of ecological systems is not often the case, and the timescales at which dynamics play out play a central role to the persistence of the system. Furthermore, we have shown that the underlying pilot pattern that constrains ecological interactions can also impact the outcome of the system. Thus, it is both the spatial structure of heterogeneity as well as the time scales at which it is dynamic. This becomes an issue of practical importance when we consider how climate change will increases the variability of most of the worlds ecosystems. Understanding how that will these changes in the dynamics of the environment relative to the dynamics of the organisms embedded with them will be of the utmost importance for trying to anticipate the impacts of the climate change. The use of a simple toy model here, illustrates that the rate of environmental change relative to the rate of ecological dynamics is far from trivial. Analogous forms spatiotemporal heterogeneity in ecosystems which will be influenced by climate change include seasonality, which in turn determines the dynamics of phenology, precipitation, and temperature. Thus, many of the approaches being employed by ecologists today trying to predict range shifts and the like may be moot in light of the ecological dynamics. A consideration of elementary ecological dynamics in the presence of spatiotemporal heterogeneity in the environment may provide basic insights into modern day as well as future ecosystems.

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Chapter 3 Emergent Spatial Structure and Pathogen Epidemics: The Influence of Management and Stochasticity in Agroecosystems

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Abstract

Organisms susceptible to disease, from humans to crops, inevitably have spatial geometry that influence disease dynamics. Understanding how spatial structure emerges through time in ecological systems and how that structure influences disease dynamics is of practical importance for natural and human management systems. Here we use the perennial crop, coffee*, Coffea arabica*, along with its pathogen, the coffee leaf rust, *Hemileia vastrix*, as a model system to understand how spatial structure is created in agroecosystems and its subsequent influence on the dynamics of the system. Here, we create a simple null model of the socio-ecological process of death and stochastic replanting of coffee plants on a plot. We then use spatial networks to quantify the spatial structures and make comparisons of our stochastic null model to empirically observed spatial distributions of coffee. We then present a simple model of pathogen spread on spatial networks across a range of spatial geometries emerging from our null model and show how both local and regional management of agroecosystems interact with space and time to alter disease dynamics. Our results suggest that our null model of evolving spatial structure can capture many critical features of how the spatial arrangement of plants changes through time in

coffee agroecosystems. Additionally, we find small changes in management factors that can influence the scale of pathogen transmission, such as shade tree removal, and result in a rapid transition to epidemics with lattice-like spatial arrangements but not with irregular planting geometries. The results presented here may have practical implications for farmers in Latin America who are in the process of replanting and overhauling management of their coffee farms in response to a coffee leaf rust epidemic in 2013. We suggest that shade reduction in conjunction with more lattice-like planting schemes may result in coffee being more prone to epidemic-like dynamics of the coffee leaf rust in the future.

Introduction

Organisms susceptible to disease, from humans to crops, inevitably have spatial geometry that influences disease dynamics. While it may be argued that spatial components of disease-host systems in mixed environments are less important (e.g. plankton), it is certainly true that most plants and animals have non-trivial spatial structure, whether exogenously imposed by abiotic environment (Gratzer et al. 2004) or emerging endogenously from ecological dynamics (Li et al 2016). It has been a standard epidemiological question to ask how disease propagates through space (Keeling et al. 1999; Park et al. 2002; Balcan et al. 2009; Craft et al. 2010), but less obvious is how the space is constructed in the first place and how that space influences subsequent disease dynamics. At one extreme, a feedback likely exists between host and disease, where hosts may alter their spatial distribution in response to the presence of disease, such systems may include humans (Levine & Levine 1994). On the other hand, there exist many hosts-pathogen systems where hosts do not alter their spatial distribution over the course of pathogen dynamics, such as plants.

The construction of spatial structure becomes complicated when considering human managed systems such as agroecosystems. The spatial arrangement of crops varies across agroecosystems due to a suite of interacting cultural, social, economic, and ecological factors. Here we focus our attention on perennial agroecosystems where plant mortality and replanting can occur iteratively, generating spatial distribution with a signature of the prior spatial arrangements, continuously inherited from one harvest to the next. This contrasts with annual systems which will be effectively fixed during the course of pathogen spread, due to the seasonal harvest/destruction and replanting of all plants. In perennial systems, the spatial arrangement is a consequence of farmer decisions about initial planting combined with continual replanting in spaces where individual plants had become damaged or die. The initial planting frequently begins with a lattice-like structure consisting of ordered rows and semi-constant interplant distances, but evolves over time with the dynamics of replanting. Replanting can be understood as a response to thinning, from a variety of causes, including the pathogens themselves. Consequently, the pattern of disease occurrence in agroecosystems is conditioned first by the structure of the plant distributions (effectively a socioecological process) and second by the dynamics of transmission (mainly an ecological process).

The coffee agroecosystem and its most notorious pathogen, the coffee leaf rust, *Hemileia vastatrix*, provides a useful model system to interrogate the interaction of spatial pattern construction and its subsequent influence on pathogen dynamics. Coffee (both *Coffea arabica* and *Coffea robusta*) is a long-lived plant subject to a variety of management styles from intensive latticed monocultures to polycultures beneath the shade of forests (Mogul & Toledo 1999). Transmission of the pathogen operates at two distinct spatial scales, locally, from coffee bush to coffee bush, and regionally, from farm to farm (Vandermeer et al. 2015; Vandermeer and

Rohani 2014). While regional pathogen dynamics is clearly important (Avelino et al. 2012), here we focus on the local dynamics in which the spatial distribution of coffee plants is evidently important to local transmission (Vandermeer et al. 2018). At this local scale, transmission likely results from a number of interacting factors, for example from plants being so densely planted that their leaves touch, or spore dispersal via air turbulence to neighboring plants, all of which are, in practice, influenced by management decisions such as how many and what kind of shade trees are incorporated in the system.

Prior work on coffee and the coffee leaf rust has employed a network approach to understanding spatial dynamics (Vandermeer et al. 2018), and here we build on that work. By focusing on local transmission dynamics, an intuitive approach for modeling pathogen dynamics is evident. We presume there exists some critical distance (D_{crit}) for which the pathogen is able to spread from plant to plant. We conceptualize the distribution of plants and the implied spread of the pathogen, as a network where the nodes consist of the plants and the edges are defined by the D_{crit}. Figure 1 illustrates the approach on three 20x20m coffee plots from a coffee farm in southern Mexico and shows the clear interaction of the scale of transmission (D_{crit}) and the underlying spatial arrangement of coffee plants. The sub-networks within a given plot show us the extent to which the pathogen could theoretically spread if any member of the sub-network were infected. In one case (Vandermeer et al. 2018) the emergent spatial sub-networks predict observed pathogen dynamics, showing that plant to plant pathogen transmission is more likely within a sub-network than between subnetworks, suggesting a utility in employing the subnetwork framework to more generally study pathogen dynamics.

Our proposed time-dependent process of spatial reorganization of plants via death and replanting within a plot is in part inspired by observations from the field with areas under cultivation for different periods of time. The three plots in Figure 1 correspond to a one-year-old plot (Sandino), a four-year-old plot (Che), and a fifteen-year-old plot (Leon). Note how the youngest plot has a lattice-like spatial pattern and the distributions become more disorganized as the plots age. Exploring the mortality/replanting mechanism, we propose a null-model to simulate the socio-ecological processes of plant death and replanting. Initiating a perfect lattice arrangement of plants, we simulate stochastic death and replanting within a fixed radius of the plant's prior position. The emergent spatial patterns are then compared to empirical spatial distributions (Figure 1.), and the range of spatial patterns from the null-model are used simulate pathogen spread to understand how the scale of pathogen transmission (D_{crit}) interacts with the underlying spatial pattern.

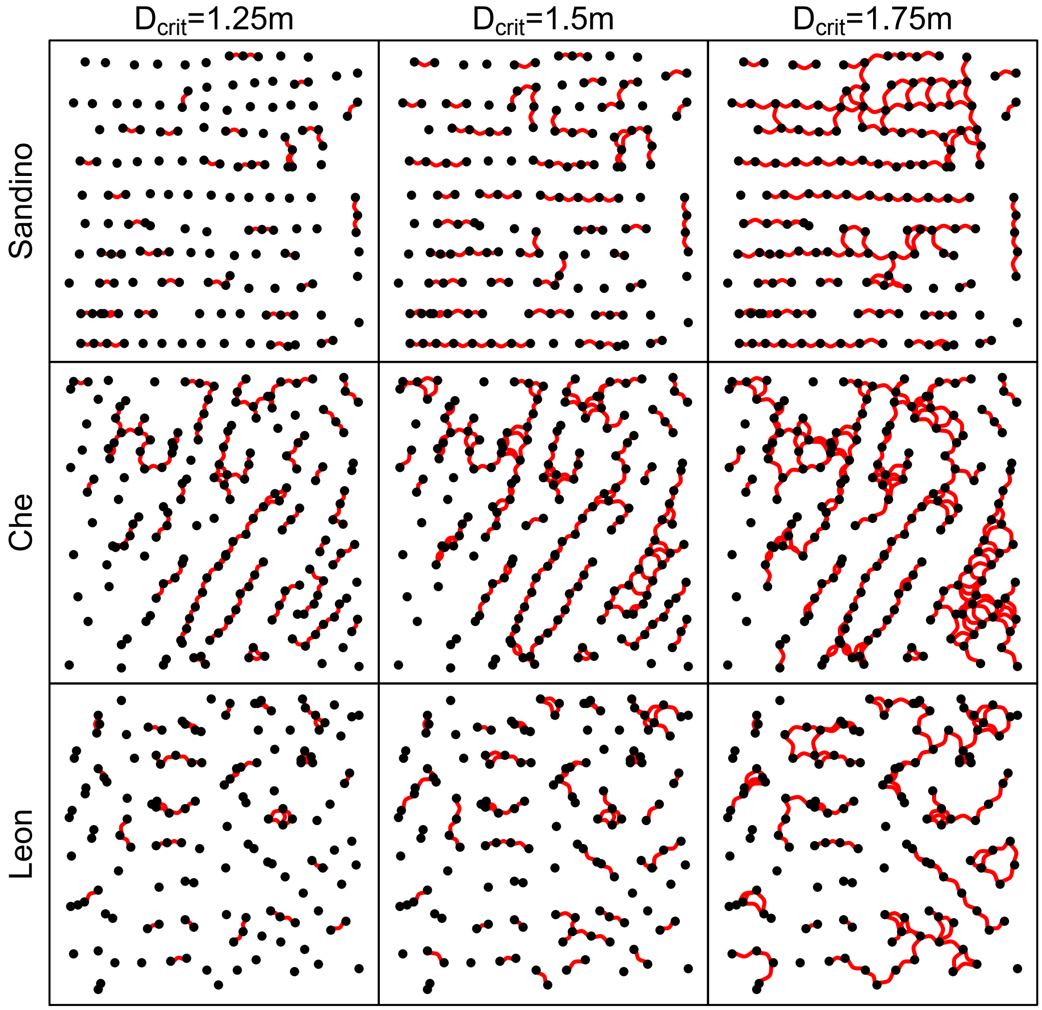

Figure 3.1: The spatial distribution of coffee plants on three 20x20m plots in southern Mexico and the subsequent spatial networks that emerge from different spatial scales of pathogen transmission (D_{crit}), illustrating how the underlying spatial distribution of plots changes through time where Sandino is a one-year-old plot, Che is a four-year-old plot, and Leon is a 15 year-old plot. The spatial pattern moves from highly organzed lattice-like (1 year old plot - Sandino) to disorganized spatial structure (15 year old plot - Leon). We suggest that this gradient of organization emerges from the mortality/replanting phenomenon.

Figure 1.

Methods

Model of Spread on Spatial Networks

Given that the intensity of pathogen infection is empirically correlated with the sub-network structure (Vandermeer et al. 2018), we stipulate D_{crit} , the maximum distance the pathogen can spread to neighboring plants (the spatial scale of transmission) and create a community of sub-networks for which dynamics are simulated (see Figure 1, which illustrates how D_{crit} creates sub-networks). Given the coordinates of each plant, as they emerge from the simulations from the plot spatial evolution, a spatial scale of pathogen transmission is stipulated via particular values of D_{crit} which in turn creates a collection of spatial sub-networks (frequently referred to as "connected components"), called C,

$$C \ = \{C_1, C_2, C_3 \dots C_m\}$$

Where m is the number of sub-networks in the system. Note that each subnetwork in C contains a unique collection of plants corresponding to a given scale of pathogen transmission D_{crit}. For example, from a collection of n plants we might obtain,

$$C \ = \{\{p_1, p_2\}, \{p_{3,}p_4, p_5\}, \{p_6\}, \dots \{p_a, p_b, p_c, \dots p_n\}\}$$

for a particular D_{crit}. Note that the indices for each plant, p, are unique across all subsets within C, and come from the set P,

$$P = \{p_1, p_2, p_3 \dots p_n\}$$

Where n represents the total number of plants in the system.

In the model, we keep track of all the infected plants with the set I, which is initialized as an empty set.

$$I = \{\}$$

For each time step in the model we iterate through all nodes (plants) in P, and there is a fixed probability, β, that a given plant becomes infected. If P_i (the i^{th}plant in P) becomes infected via

$$p_i \lambda(\beta)$$

Where

$$\lambda(\beta) = \begin{cases} 0, & \beta \geq \mathcal{U}(0,1) \\ 1, & \beta < \mathcal{U}(0,1) \end{cases}$$

then the whole cluster, C_j, which is a subset of C and contains p_i, is join in union with I. This is done for all p's where $\lambda(\beta) = 1$ (i.e. when there is a successful infection).

$$I(t+1) = I(t) \cup C_j$$

Conceptually, each sub-network represents the extent to which the pathogen instantaneously spreads from a single infected plant to all plants in that sub-network. We use the inevitability of the spread within a sub-network as a simplifying assumption and assume that all plants that fall within the sub-network denoted by the scale of the spread, D_{crit}, become infected instantaneously. This abstraction simplifies the system and provides for a focus on the interplay of pathogen dynamics and the spatial geometry. With the assumption of instantaneous spread within a sub-network, our model only has one parameter associated with the epidemic process, the probability of a random plant in the plot being infected β, which can be thought of as being a measure of the regional pathogen propagule density.

When simulating pathogen spread, we allowed simulations to proceed until 90% of the plants became infected to quantify the time to epidemic of the pathogen on the spatial geometries arising from the null model. To account for the inherent stochasticity of the null model and the spreading process we replicated time step snapshots from the null model five times with subsequent ten replicate simulations of the spreading process for the D_{crit}ranging from 0 to 3. We then used the mean time until 90% infected hosts.

Null model of evolving plant spatial geometry

Despite the fact that coffee bushes are often planted with the intention of a strict lattice structure (planted in rows), the real distribution of coffee plants on a farm rarely reflects perfectly that initial intent. As time goes by, some coffee bushes die and usually are replanted, but rarely in precisely the same location, leading eventually to a loss of the initial planting pattern. To the farmer these small deviations may not seem consequential for the dynamics of pathogens and pests, yet they can accumulate significantly to change the basic spatial pattern (e.g., Figure 1.). Although a host of complicated local factors are involved in planting decisions, we initially approach the problem with a null model of planting spatial evolution.

We begin with plants arranged in a lattice bound within a x and y coordinate range and modify the structure over time. The simple model simulates stochastic death and replanting within an area of relatively proximity of the prior plant position. The coordinates change over time according to,

$$x_i(t+1) = x_i(t) + \xi(\phi)\mathcal{D}(\alpha)$$

$$y_i(t+1) = y_i(t) + \xi(\phi)\mathcal{D}(\alpha)$$

Where

$$\xi(\phi) = \begin{cases} 0, & \phi \geq \mathcal{U}(0,1) \\ 1, & \phi < \mathcal{U}(0,1) \end{cases}$$

and $x_i(t)$ and $y_i(t)$ represent the two coordinates corresponding the position of plant i at time t. $\xi(\phi)$ is the death/replanting rate and ϕ is the mortality probability for plant i. $\mathcal{U}(a,b)$ is a uniformly distributed random variable with range (0,1) and $\mathrm{D}(\alpha)$ is a random variable drawn from a uniform distribution with mean α, that stipulates the “replanting radius” of the new plant. For all simulations, $\phi = 0.05$ and $\alpha = 0.25$. The simulations were run iteratively for each plant in the plot 100 times.

To understand how our null model approximates the planting arrangements of real agroecosystems, we use an empirical data set of three 20x20 m plots on an organic coffee farm in the Soconusco region of Chiapas, Mexico. Each of the three plots have different ages (time since the area had all plants removed and replanted) corresponding to approximately one year, four years and fifteen years (Figure 1.). They represent what we propose to be the progression of spatial structure across the lifecycle of an area in cultivation. Given these three 20x20m plots with differing numbers of plants, for each comparison, the simulated evolution of spatial structure was done with the same planting density as the real plot it was intended to simulate. Our empirical plots have 177, 147 and 140 plants. To approximate the lattice-like initial conditions of each of these plots we used 12x15, 15x10, and 14x10 planting arrangements for the simulated plots. By controlling for the planting density, our null model of plot spatial evolution allows us to make comparisons with our empirical 20x20m plots and understand to what extent our null model approximates the empirical spatial geometry across the ontogeny of the plots through time.

Quantification of spatial structure

Similar to modeling the spread of the pathogen in space as described in the previous section, to quantify the spatial pattern of a plot we focus again on the sub-networks that emerge from imposing D_{crit}. By looking at a range of D_{crit} for a given spatial pattern we quantify how the number of sub-networks changes across spatial scales and can subsequently make comparisons to our empirical spatial patterns. Figure 1. illustrates how different spatial patterns give rise to varying numbers of sub-networks for a single D_{crit}. The variability in the number of sub-networks reflects the clustering and over-dispersion and various spatial scales within a particular plot. The number of sub-networks not only uses the same tools for modeling pathogen spread, but also provides biologically relevant information for the dynamics of the pathogen that the use of a traditional dispersal kernel does not. For example, a given distribution of sub-networks for a D_{crit} gives us the minimum number of outside infections needed to infect a total area in cultivation.

To understand the extent to which the simulations approximate the empirical patterns, we use Δ_s, or the difference in the number of sub-networks in the empirical spatial patterns minus the number of sub-networks in the simulated spatial patterns. For a perfect spatial approximation in terms of number of subgraphs we expect a Δ_s= 0. Importantly, we are interested in Δ_s across a relatively wide range of D_{crit} to quantify the spatial pattern, although we are constrained at the low end where no plants are connected and the high end where the whole plot is connected. For each simulation, we extracted the pattern at the first step and subsequently every 10 steps through 100 rounds of replanting. For our analyses, we used D_{crit} that ranges from 0 to 3m to quantify the spatial structure.

Results

Plot evolution and approximations of empirical structure

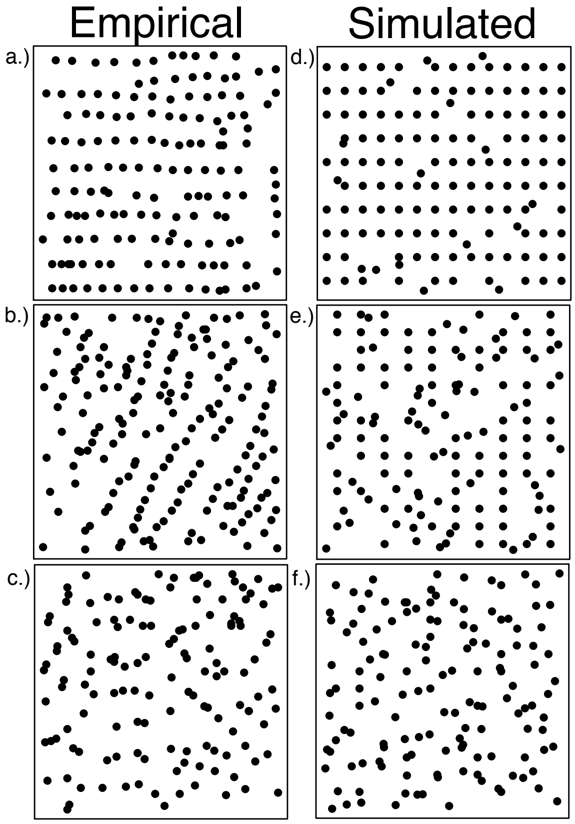

Figure 3.2: Three 20 x 20M plots illustrating the position of all coffee plants. a. a one-year old plot, b. a 4 year old plot, c. approximately a 15 year old plot d, simulated plot after 25 time units, e. simulated plot after 50 time units, f. simulated plot after 100 time units.

Considering the pattern of sub-network emergence as a function of D_{crit}, we expect that as time advances (iterations in the model), early iterations will approximate the younger empirical plots and later interactions of the model will approximate the older empirical plots (as is evident in Figure 2). Data for the three empirical plots are roughly approximated by the null model for various spatial scales (values of D_{crit}), and the range of colors in Figure 3. show the variation in plot evolution, where light grey is the lattice and dark red is after 100 rounds of replanting. It is apparent that simulations start far from the empirical distributions and move towards them (i.e., Δ_s,=0) with continued plant death and replanting.

The largest deviations Δ_s) are typically found at the distance that separates rows of the lattice, which ranges from 1.3-1.6m. This suggests that the empirical planting geometries are more clustered and over dispersed at scales that the model cannot approximate. For example, the empirical plot in Figure 3a. shows the model consistently unable to approximate at D_{crit} from 1.3-2m, and we see in the empirical data that this likely emerges from irregularities within row structure. It is evident from Figure 3a. that the deviation from the lattice emerges from missing plants and clustered plants but within the row structure itself. While simulations move plants away from the lattice structure randomly, the empirical data suggest that attempts to maintain semblance of row structure results in plants being replanting within the row but in an over dispersed or clustered fashion. Similar deviations are found between the empirical plots and simulations in Figure 3b and c and are consistent prior to the scale that join rows of the lattice, as denoted by the lite grey line from the simulations. These deviations occur because the simulated plots are more clustered at these smaller distances as shown by the approximations being below the zero line.

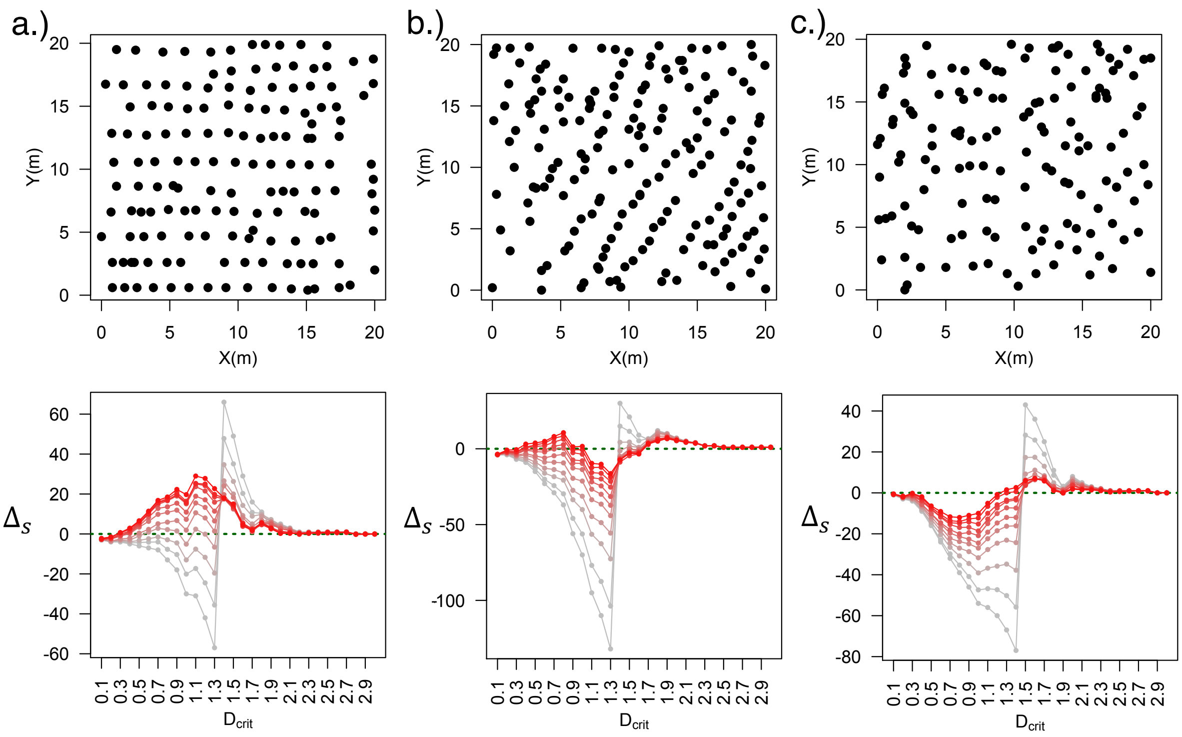

Figure 3.3: (a-c) Δ_s*as a function of the critical distance (parameter a in equation set 1), at various stages in the evolution of plot structure using the null model. Shading goes from light (the first stage in the simulation) to dark red (final step of simulation). Note that the dashed horizontal line corresponds to a 1:1 approximation of the model to the empirical plots. Note that the y-axes differ for each of the sub-network comparison plots.*

Modeling pathogen spread on spatial networks

Using time to reach 90% infection as a state variable, we illustrate its response to the two variables of interest, "plot evolution time" which is to say the time the null model is permitted to run, and the D_{crit} parameter which stipulates the threshold scale of transmission between plants. In Figure 4., we summarize the general dynamics of the system from a two-dimensional parameter sweep of, 1) the scale of the pathogen transmission (D_{crit}), 2) the time steps involved in the plot evolution simulation, and 3) the state variable, time to epidemic (time to reach 90% of the trees infected). A pathogen spreading across the different plot geometries (represented by plot evolution time) reaches epidemic status regardless of spatial geometries due to the fixed probability of outside infection of plants β. At low transmission levels, it is apparent that plants become more clustered as the plot geometry evolves away from a lattice-like structure resulting in a small but detectable difference in the time to epidemic. At large scales there are few differences in the dynamics pathogen transmission due to almost the entire plot being connected resulting instantaneously infection once a colonizing infection reaches the plot.

It is intuitive that at very large transmission values, the pathogen will move quickly to infect the whole plot and at smaller scales it will move slowly, with little effect of the planting geometry. It is at intermediate transmission levels that we find non-obvious interactions with the geometry of plants. For these intermediate scales of transmission we find that lattice-like geometries are sensitive to small increases in transmission and generate a drastic jump in pathogen dynamics where the time to epidemic shows a pattern similar to that of a critical transition (Figure 4.). As the plot becomes less lattice-like through stochastic plant death and replanting this critical transition-like dynamic becomes less pronounced. At the two extremes of plant geometries, we see critical transition-like behavior for highly organized lattice-like arrangements and a gradual change in time to epidemic for more unorganized pseudorandom arrangements as the scale of pathogen transmission changes. These results suggest that a more random-like pattern of the plants buffers drastic changes in the overall dynamics of the pathogen.

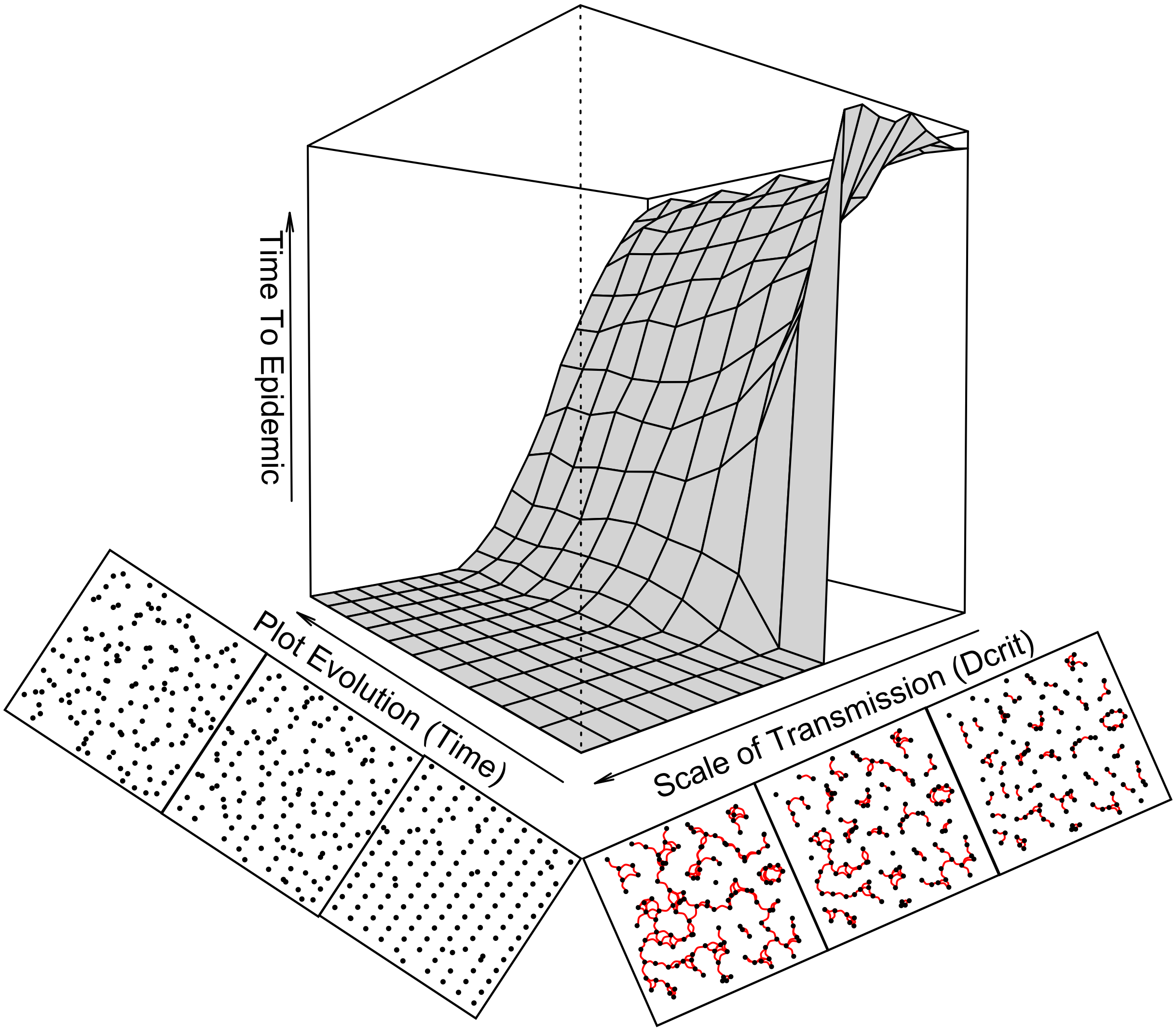

Figure 3.4: Shows the time until 90% infection across a range of scales of pathogen transmission (Dcrit) as well as planting geometries generated by the plot evolution model. Plots along the two axes are to illustrate the changing spatial network structure along scale of spread and the changing panting geometry in the plot evolution model. Note that the regional infection probability, $\beta = 0.1$.

Given the basic biology of most pathogens, it makes sense to think about not only the dynamics within a plot but also how the regional dynamics impact the system. Our model results suggest that the dynamics of the spatial host-pathogen system changes as the probability of plants being infected from outside of the plot increases (Figure 5.). As the regional infection probability increases, the interaction between the spatial geometries of the plants and scale of pathogen transmission becomes less pronounced. The critical transition-like behavior observed for relatively low regional infection probabilities is buffered as the regional infection probability increases, suggesting that under epidemic levels of a pathogen in the environment, the spatial arrangement of plants on a given farm becomes less important for the overall dynamics of the system.

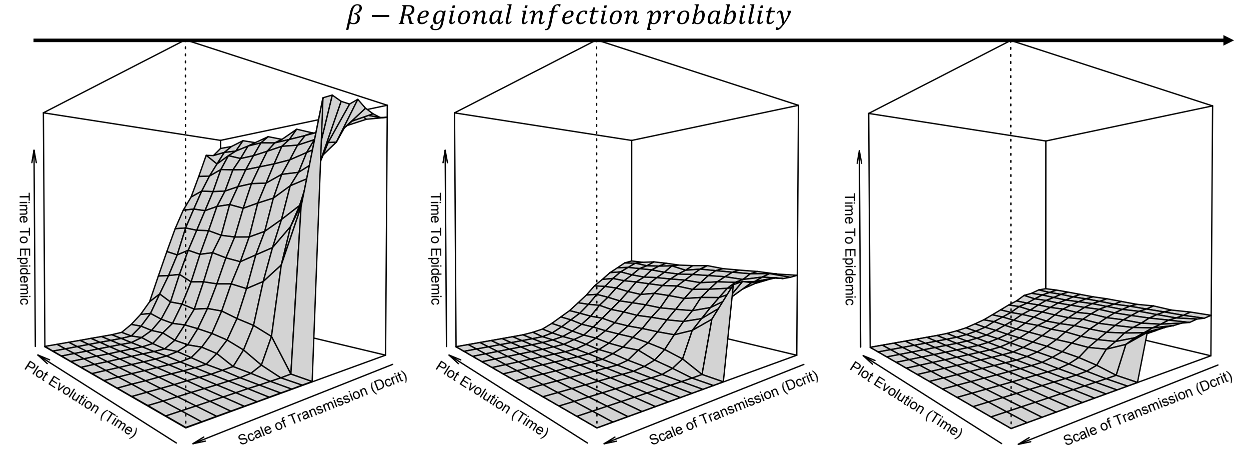

Figure 3.5: Shows how the pathogen dynamics change as the regional infection probability increases. The first figure is β = 0.1, then β = 0.2 then β = 0.5.

Discussion

The management practices that create the spatial geometries of plants in agroecosystems emerge from socioecological processes structured by a number of influences, from cultural practices to the economic position of the farmer among other factors. Our approach here has been to try and recreate the range of observed spatial planting geometries by using a simple null model that strips away most of these real-world complexities. We show that a simple process of stochastic plant death and replanting within a small radius surrounding the dead plant can recreate many of the features observed in the real distribution of planting geometry. Furthermore, we suggest that the observed spatial geometries in agroecosystem can be the result of different snapshots in time of this dynamic process (Figure 2.). The comparisons between our model and empirical data (Figure 3.) provides support for the idea that at least for the sampled plots, the distributions of plants fall along different times of this stochastic death and replanting process. For the most lattice-like geometry of our empirical plot (Figure 3a.) the model passes through the 1:1 approximation of our empirical data for a wide range of spatial scales, suggesting that early stages in the simulations that move away from the lattice approximate it better than later more unorganized steps in the model. Furthermore, our simulations pass that same 1:1 approximation but at a much later time in the simulations for our plot of intermediate lattice structure (Figure 3.b), while our plot farthest from the lattice structure (Figure 3c.) is never well approximated by our model across the full range of D_{crit}.

The interaction of spatial structure and spatial transmission of the pathogen suggests that they interact in a non-linear way. We observe that there is a critical transition-like behavior that emerges from the interaction of both the scale of pathogen transmission and the underlying spatial pattern of the hosts. Relatively small changes in pathogen transmission (D_{crit}) with lattice-like spatial geometry can lead to a dramatic jump in dynamics of the pathogen (Figure 4.). Thus, with lattice-like planting, the pathogen may be held at relatively low densities, but a small change in management that may influence of scale of pathogen spread (discussed below) can result in a devastating shift in dynamics. The uniform nature of the lattice creates conditions such that, once the threshold that connects rows is met, the whole plot becomes a connected network on which the pathogen can spread across. As the death and replanting process moves the spatial pattern away from a lattice planting geometry, it disrupts row structures and subsequently buffers the critical transition-like jump in pathogen dynamics. Thus it might be expected that uniform lattice-like planting geometries are far more sensitive to small changes in the scale of transmission of the pathogen and even a relatively small amount of disruption from the highly organized state can buffer against variability in pathogen spread. As we move away from the lattice-like geometry, there may be higher pathogen infection at low transmission due to some clusters of plants, but that same geometry ultimately prevents the pathogen from spreading through the whole area. Furthermore, as the regional infection probability increases the qualitative results of the model stay the same however they are damped, and the critical transition-like behavior is almost non-existent for high regional infection probabilities.

The results presented here have practical significance for the management of pathogens in agricultural systems, and in particular for the system which inspired the study, the coffee leaf rust (CLR). The CLR propagates both as a random propagule rain, spores arriving from the regional pool of spores in the environment, and from plant to plant on a local level through local wind current instabilities, branch-branch-contact, and splashing (Vandermeer et al. 2017, Avelino et al. 2015). Our model simulations mainly focused on the local level transmission and how that interacts with the planting geometry of the agroecosystem. There are a number of management factors within coffee agroecosystems that have the potential to influence parameters associated with the scale of the CLR transmission (Avelino et al. 2004). Shade is one of the most commonly managed aspects of coffee agroecosystems and its impact on the dynamics of the CLR has been contentious with some reporting beneficial impacts of shade reducing CLR (Soto-Pinto et al, 2002), and others reporting the opposite (Lopez-Bravo et al. 2012). The classic recommendation has been to reduce shade to manage the CLR, as the microclimatic implications of shade such as increasing humidity could potentially be beneficial to the germination of spores (Staver et al. 2001), but it is important to understanding that the transmission of spores and the viability of spores are two different forces that need to be simultaneously managed. Bourot et al.

(2016) provided evidence that shade within coffee agroecosystems reduces the spread of spores, thus providing support for the idea that shade trees within a coffee plantation act as a wind breaks and prevent local dispersal. In Avelino et al. (2012) the surrounding landscape of pasture land was correlated with the CLR on individual farms. Shade is a single management factor that has the potential to influence the local scale of pathogen transmission and probability of the pathogen establishing infection. In the context of the analysis presented here, we suggest that the amount of shade locally will modify $D_{crit}$by creating wind breaks which reduce the plant to plant (local) transmission.

While the question of what initially caused the outbreak of the CLR in 2013 in Latin America is still unclear, it set up the necessary conditions to overhaul many coffee agroecosystems throughout the region. Due to the prevalence of plant death from the epidemic itself, in conjunction with the promotion of resistant varieties, most farmers throughout Latin America are likely replanting whole farms now. This is particularly important moment in the dynamics of the CLR in Latin America, as following classical agronomical recommendations for combating the CLR would mean a reduction in shade, thus potenitally increasing the scale of CLR transmission locally, as well as replanting with resistant varieties, will likely lead to planting geometries that are more lattice-like when the whole system is replanted. Studies have found that this process is already underway in parts of Central America (Valencia et al. 2018), and as this study shows, the combination of shade reduction and moving towards a uniform planting structure, increases the likelihood of the critical transition-like epidemic dynamics observed in our model.

Acknowledgments

We would like to thank Gustavo Lopez-Bautista for help with setting up the plots to measure the empirical spatial distributions of coffee plants. Wardell Gray and Ferdinand LaMothe both provided useful feedback on the models. This work supported by NSF grant number DEB – 1853261 and USDA grants NIFA/USDA 2017-67019-26292 & NIFA/USDA 2018-67030-28239

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<u>Supplementary material</u>

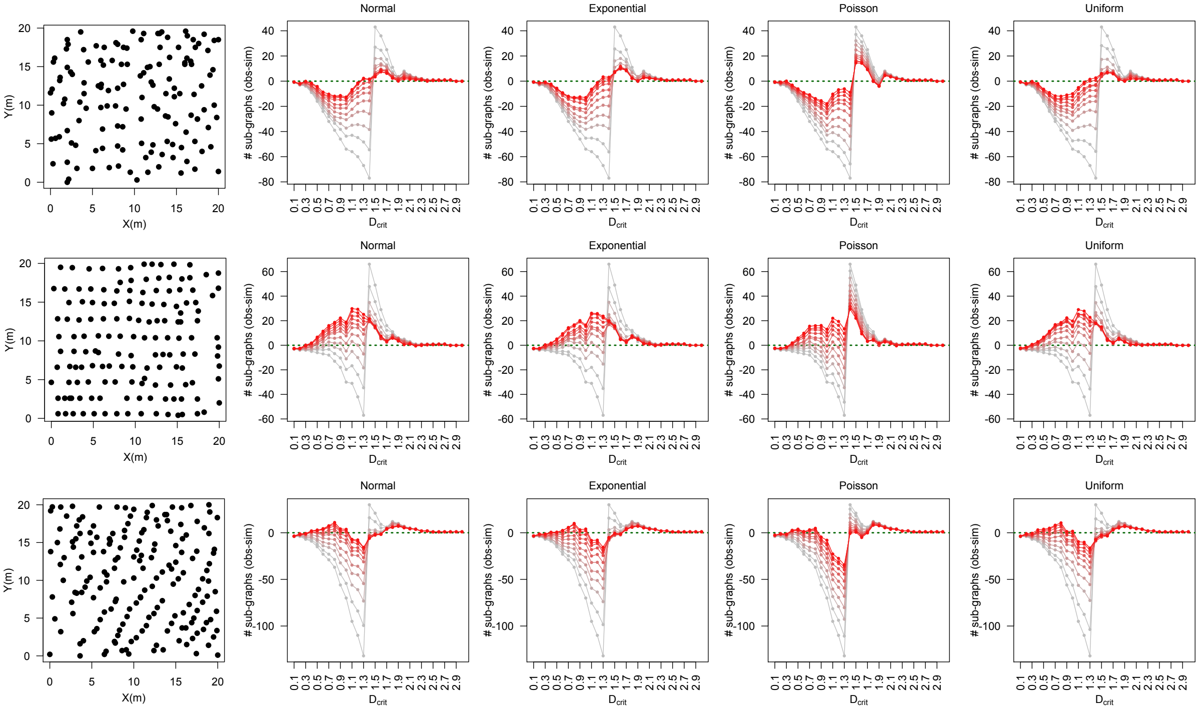

Figure 3.6: Δ_s (the different in the number of sub-graphs/sub-networks) as a function of the critical distance (parameter a in equation set 1), at various stages in the evolution of plot structure using the null model. Shading goes from light (the first stage in the simulation) to dark red (final step of simulation). Note that the dashed horizontal line corresponds to a 1:1 approximation of the model to the empirical plots. Note that the y-axes differ for each of the sub-network comparison plots. Rows correspond to the three empirical plots, and the columns show different probability distributions, $\mathcal{D}(\alpha)$,used for the replanting. Note that alpha is equal to 0.05, consistent with the simulations in the main manuscript.

Chapter 4 Trophic-Specific Responses to Migration in Empirical Metacommunities

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Abstract

The metacommunity, as it evolved from Levins's metapopulation, provides a framework to consider the spatial organization of species interactions. A defining feature of metapopulations and metacommunities is that organisms (populations or communities) are connected via migration. An important result from Levins's metapopulation work—that increasing migration lowers regional extinction probability—is often incorporated into conceptions of metacommunities; however, this may not hold true for multiple interacting metapopulations (metacommunities). We report results from a metacommunity field experiment conducted with a tropical terrestrial leaf litter macro-arthropod community. We show that migration induces regional extinctions of predators without changing the predator community composition. For non-predators we found no evidence of regional extinctions, but a significant change in community composition. Our result corroborates the findings of a prior similar metacommunity experiment with a temperate forest leaf litter community. The concordance between these

experiments, even with vastly different communities, highlights the importance of considering trophic and non-trophic community structure to understand metacommunity dynamics, and suggests a potential connection between migration rates and trophic-specific responses in ecological communities.

Introduction

The theory of metapopulations has become a standard way of thinking about simple population dynamics, and its success has stimulated a seemingly obvious extension, the metacommunity (Levins 1969; Wilson 1992). As originally envisioned, a metacommunity is a collection of interacting populations of different species in which extinction and migration occur on a regular basis. This results in patchiness that creates subcommunities, which may be distinct in species composition. It might be argued that MacArthur and Wilson's theory of island biogeography was the first metacommunity theory, and perhaps the most elegant, in which patchiness is provided by the existence of islands (MacArthur and Wilson 1964). From these formulations, an important conclusion of metapopulation theory has been tacitly incorporated as an obvious corollary of metacommunity theory—that increasing migration lowers overall extinction probability. While it may be a reasonable proposition at first glance, further reflection on the assumption suggests that the expectation of lowered extinction is not universal in the metacommunity context (Vandermeer et al. 1980; Caswell and Cohen 1991).

Huffaker's classic experiment might be thought of as a canonical case study that supports a link between increasing inter-patch migration and lower extinction. When isolated to a small feeding area, both predator and prey mites go extinct (predator eats prey to extinction then itself goes locally extinct)--yet when many smaller feeding areas were arranged to facilitate local dispersal of prey (but not predators), apparently stable oscillations result (Huffaker 1958). A similar experimental set-up that yielded stable oscillations also included predator-focused dispersal limitations (Huffaker 1958). A similar pattern was also observed in Gause's experimental system of protozoans twenty years prior (Gause et al. 1936). In these examples, migration appears to decrease the probability of extinction.

Alternatively, it is not difficult to imagine the reverse outcome in other systems: a case in which migration might increase extinction probability. For example, in a two-predator one-prey situation in which spatial structure allows for a segregation of the two predators in space, increasing the predator migration rate could increase intraguild antagonism, leading to one of the predators dominating, and a reduction of total species diversity from three to two. Even in cases without intraguild competition, the simple dispersal of any intermediate predator can theoretically cause trophic instabilities due to more lag in population dynamics (Jansen 1995). Thus, elevated migration rates could result in either increased or decreased species diversity, depending on the strength or timescale of antagonistic (or even facilitative) interactions across ecological guilds (Guzman et al. 2019). The simple migration-extinction equilibrium of island biogeography and metapopulation theory may yield predictions that are not generalizable for more complex community structures.

The role of migration in rescuing unstable populations has been highlighted so often that it is usually taken for granted, but that result is not theoretically inevitable (Simberloff and Cox 1987). The ability to simulate a wide range of metacommunity dynamics suggests the need for an empirical approach. One of the key shortfalls of much of the experimental metacommunity work lies in its simplification of community interactions (Polis et al. 1989), where studies often only consider a subset of species with simple trophic structure (e.g. consumer-resource pairs) Warren 1996; Shurin 2001; Kneitel and Miller 2003; Cadotte 2006; Fox et al. 2017). Although there are some notable experiments which attempt to include some of the trophic and non-trophic realism of communities (Neill 1974; Vandermeer et al. 1980), surprisingly few experimental studies have focused on empirically realistic metacommunities.

One of the early attempts to study the role of migration in empirical metacommunities used leaf litter macro-arthropod communities and found that the predator guild (defined taxonomically) decreased in richness when random migration was induced, while non-predator richness was unaffected by migration (Vandermeer et al. 1980). These results suggest that conclusions about metacommunity structure may, at least in some contexts, be trophic-specific. The dependence of community dynamics on trophic structure has been noted in some well-known debates, for example, in considering whether communities tend to be controlled primarily by consumers (top-down) or producers (bottom-up) (Hairston et al. 1960), and why trophic cascades operate differently in aquatic versus terrestrial systems (Strong 1992). Clearly, a wide range of ecological processes interact with migration in real metacommunities, including higher-order interactions (or trait-mediated indirect interactions), which recent work suggests may be more determinant of community structure than the more direct, lower-order or pairwise species interactions (Werner and Peacor 2003; Bairey et al. 2016; Grilli et al. 2017; Terry et al. 2017).

The empirical result that experimental migrations make a difference in metacommunity structure for predators, but not for non-predators (Vandermeer et al. 1980), was found in a species-poor temperate deciduous forest (Michigan, USA). Here we revisit the experiment conducted by Vandermeer et al. (1980) in a more speciose montane tropical agroecosystem. We considered that in the tropics, the hypothesized stability-preserving aspect of high biodiversity (McCann 2000) could overwhelm any special effect of a strongly antagonistic predator species, which was proposed to explain the results of the earlier temperate zone study. Accordingly, we sought to investigate how migration affects leaf litter community richness and composition, focusing especially on the effects at different trophic levels. Based on underlying assumptions about the importance of migration in maintaining biodiversity, we hypothesized that curtailing local migration would reduce local species diversity, and that this effect would be observed at all trophic levels.

Methods

Study region and design

This study was conducted at Finca Irlanda*,* an organic shaded coffee agroecosystem in the Soconusco region of Chiapas, Mexico. The study site was on a subset of land recently transitioned from rustic coffee production to a forested reserve. The experimental set-up was positioned adjacent to a patch of invasive golden bamboo, the litter of which created a uniform mat.

Leaf litter was collected from a well-forested area of the reserve, homogenized, and separated into 10 mesocosms, each of which were 0.5 m^2 in area and separated from one another by 1 meter. Five mesocosms were positioned on either side of a walking trail. No physical barriers prevented migration between mesocosms. Inter-patch migration was therefore possible, but we assumed it was sufficiently infrequent such that it could be ignored. We assumed organisms would not prefer to leave a mesocosm of leaf litter of the same composition from which they were originally collected to migrate across a relatively inhospitable mat of dried litter from an invasive bamboo species.

Half of the mesocosms were assigned as controls and half as treatments. To simulate migration among treatments, one-quarter of the litter in each mesocosm was removed and replaced with the same amount of litter from a different mesocosm. The transfer schedule was set so that a different quarter of the mesocosm was migrated during each transfer event, and the replacement pattern was randomized so that each mesocosm received and contributed litter to a different, randomly assigned mesocosm. Transfers were done every 4 days for 16 days. Migration was not manipulated among control mesocosms, though one-quarter of the litter was lifted, agitated, and replaced in the same mesocosm every four days to control for the disturbance of the litter transfers between treatment mesocosms. All mesocosms were harvested on day 20. This time scale is comparable to Vandermeer et al.'s 1980 experiment which ran for 30 days.

After harvesting, the litter was sieved using 3-mm meshes to remove coarse detritus. Each sample was searched by four people for 20 minutes, and all encountered organisms were individually removed and placed in alcohol. This technique did not likely capture all organisms found within the mesocosms, but we expect that any bias toward certain groups of organisms was standardized across all samples, which we assured by blinding the sample labels throughout the sorting process. Individuals were sorted into orders or families and identified to morphospecies. Morphospecies were then classified as either predators or non-predators, where predators included spiders, *Staphylinidae* beetle larvae, pseudo-scorpions and centipedes.

Statistical methods

To compare the number of species in our control and migration treatments, individual-based rarefaction curves were calculated for the whole dataset and for each trophic group (predators and non-predators) separately. Rarefactions followed the now standard methodology of resampling the list of species observations with replacement at increasing numbers of individuals (Gotelli and Colwell 2001). 100 resamples were conducted for each level of individuals sampled, and the mean number of species for a given density of individuals was calculated.

While there are standard methods to extrapolate the number of species (Colwell and Coddington 1994; Chao et al. 2014) and compare the overall shape of rarefaction curves (Cayuela et al. 2015), we were interested in the statistical differences between our rarefaction curves across the range of resampled levels. To assess differences between the control and migration treatments, we conducted a bootstrapping procedure to compare the difference in the mean number of species at every re-sampling level, x_i, along the rarefaction curves. For a given x_i,100 random draws from the observed datasets for the control and migration, D_c and D_m, were used to calculate the mean observed number of species,$\overline{S_c}$ and $\overline{S_m}$, for sampling level x_i.These values were used to calculate the observed difference in the number of species, $\overline{S_c} - \overline{S_m} = \Delta_{OBS}$ for resampling level x_i. The observed data, D_c and D_m, were then pooled together to create D_p, which was then randomly partitioned into null data sets 100 times for the control and migration treatments, N_c and N_m. N_c and N_m were then randomly sampled 100 times at x_i sampling level to calculate mean number of species, $\overline{S_{N_c}}$ and $\overline{S_{N_m}}$, sampled at x_i for both null data sets. These values were then used to calculate the null difference in the mean number of species sampled, $\overline{S_{N_c}}$- $\overline{S_{N_m}} = \Delta_{NULL}$. This gives us a distribution of Δ_{NULL} which was then compared to Δ_{OBS} to calculate the probability of observing Δ_{OBS} for a given x_i if D_c and $D_m$come from the same statistical population. The probability, p, is calculated by $p = \frac{1}{n}\sum q$ where q is the number of times that $\Delta_{OBS} \geq \Delta_{NULL}$ and n is the number of Δ_{NULL} values in the distribution. This procedure was repeated for every value of $x_i$where the rarefactions of both treatments overlap. The supplementary material contains a graphical walkthrough of the statistical test (Figure S1) and a link to a repository with the R code for the test.

To look at patterns in community composition for both treatments (increased migration and control) we used both Bray-Curtis and Jaccard distances as measures of dissimilarity at the patch scale. This allowed us to look at the data as weighted by abundance of morpho-species (Bray-Curtis) as well as just looking at the presence-absence (Jaccard). Analysis of Similarity tests (ANOSIM) were used to calculate statistical differences in community composition for both dissimilarity measures between our control and migration treatment. The NMDS plots, ANOSIM tests, and calculations of dissimilarity measures were implemented with the 'vegan' package (Oksanen et al. 2010) in R (R Core Team 2019). The 'anosim()' function of the 'vegan' package used with 5000 permutations to calculate the R statistic and the p-values. For the Bray-Curtis distance ANOSIM we created a community matrix where the rows are the separate patches, the columns are morpho-species, and the entries are the number of morpho-species for a given patch. With the Jaccard distance ANOSIM we created a similar matrix, but where the entries are the presence (1) or absence (0) of morpho-species.

To quantify the impact of migration in the communities across treatments we infer the local extinctions dynamics in our experiment by using the distribution of rare species across treatments. Given that the leaf-litter substrate was homogenized prior to the experimental set-up we assume that observed differences result from the dynamics in different treatments. We defined rare species in two ways here. First, by being a singleton (i.e. having an abundance of 1 in a single patch) across all patches (control and migration), and second by having an abundance that is less than the mean morpho-species abundance in the community ("relatively rare species") (5.12 for predator community and 4.44 for non-predator community). This comparison of 'rare' morpho-species is done with both the community of predators and non-predators separately to understand how dynamics differ across trophic position across treatments.

Results

While there was no statistically significant difference between the control and migration treatments for the whole community (Figure 1A) or the non-predator community (Figure 1C), we did observe a significant difference in species richness between the control and migration treatments within the predator community (Figure 1B). This difference between control and migration treatments for the predators starts at just nine individuals sampled and remains significant for the rest of the overlap between the two curves.

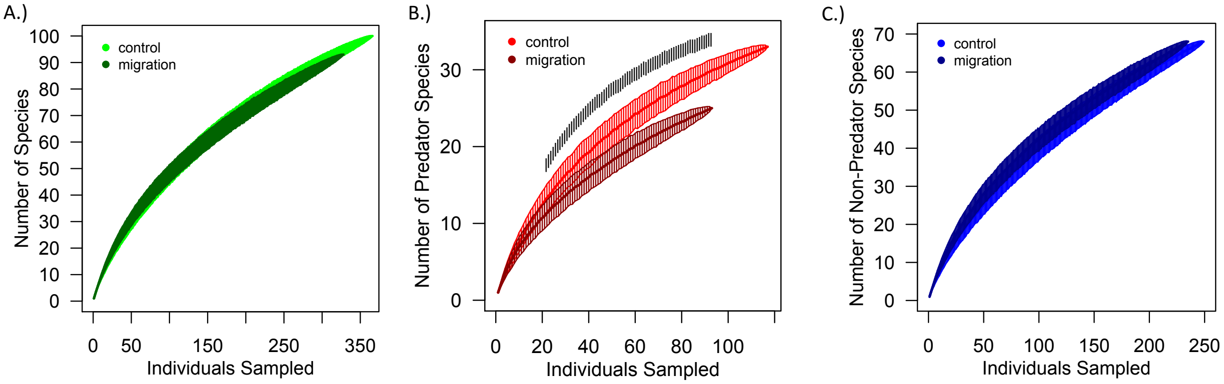

Figure 4.1: (A-C) Individual-based rarefaction curves for A.) whole community (green), B.) predators (red), and C.) non-predators (blue). Treatments are shown in lighter colors (control) and darker colors (migration). One standard deviation (based on the 1000 random draws) is plotted in the shaded areas around the curves. The vertical dashes above the curves in in B.) represent a statistically significant ($p < 0.05$) difference in the number of species for a given number of individuals sampled between the control and migration treatments.

<u>Community analysis</u>

Analysis of similarity (ANOSIM) showed no differences between the community composition for the predators for both Bray-Curtis (R=0.12, p=0.182) and Jaccard distance (R=0.16, p=0.081), while the non-predator community showed significant differences for both Bray-Curtis (R=0.478, p=0.0172) and Jaccard distance (R=0.332, p=0.0523) (Figure 2). The amount of species overlap between control and migration treatments was 51% for predators and 40% for non-predators. Additionally, we see that rare morpho-species, as defined by being singletons and less abundant than the mean morpho-species abundance in the community are more common the non-migration treatment for predators with no apparent difference in the non-predator community Table 1. This suggests that relatively rare morpho-species in the predator community are more prone to local extinctions than rare morpho-species in the non-predator community when migration occurs.

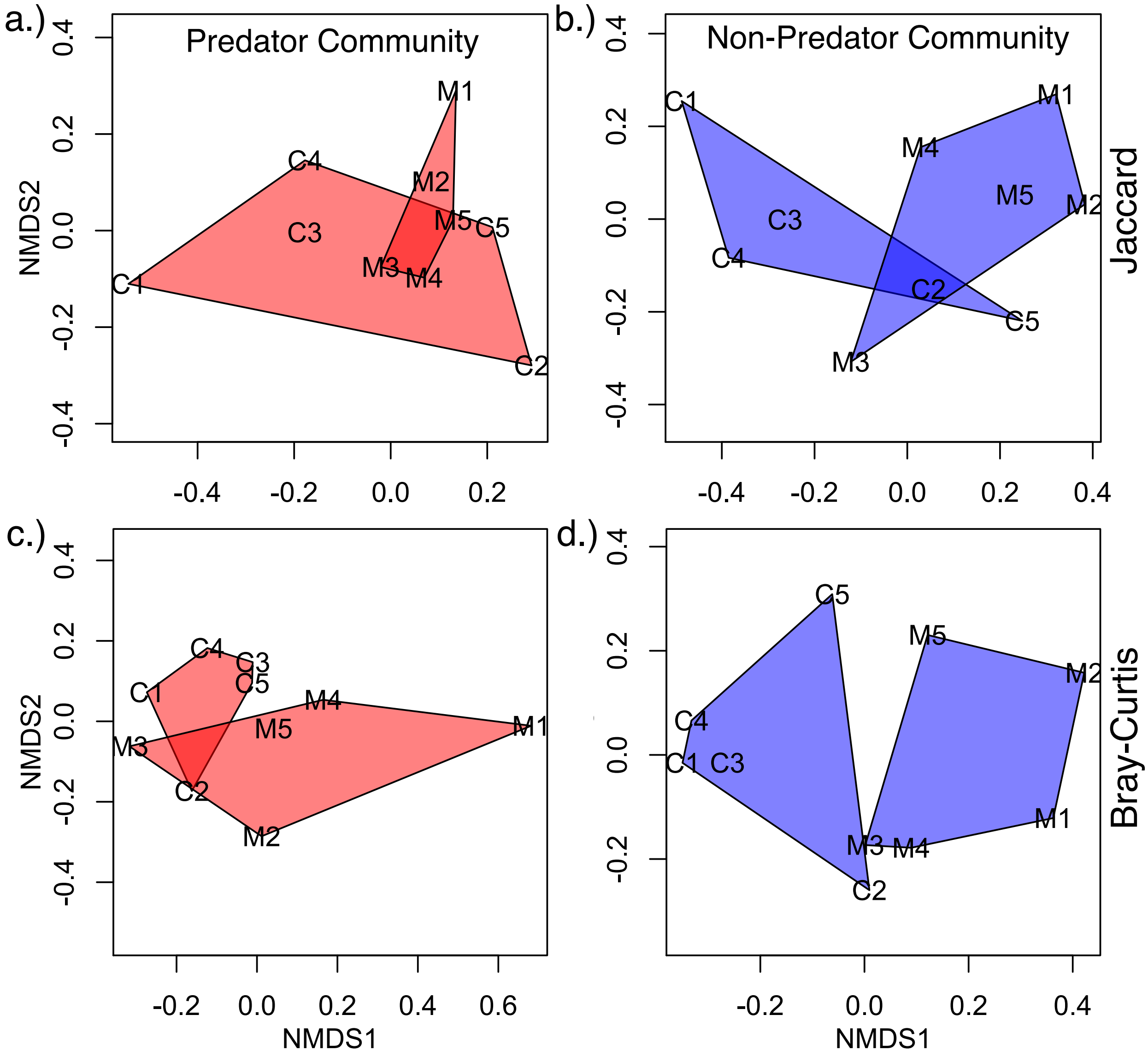

Figure 4.2: NMDS plots for predator community and non-predator community. a.) and b.) are made using Bray-Curtis dissimilarity and c.) and d.) are using Jaccard. ANOSIM showed no differences between control and migration treatments for the predators (Bray-Curtis R=0.12; p=0.182 & Jaccard R=0.16 p=0.081) and significant differences between control and migration treatments for non-predators (Bray-Curtis R=0.478; p=0.0172 & Jaccard R=0.332, p=0.0523). The same analysis was conducted using Jaccard distance and is reported in the results section. C1-C5 refer to the control patches while M1-M5 refer to the migration patches.

Predator Community	%	*Non-Predator Community*	%
Singletons		**Singletons**	
Control	69	Control	49
Migration	31	Migration	51
Relatively Rare		**Relatively Rare**	
Control	75	Control	56
Migration	24	Migration	44

Table 4.1 :Shows the percentage of rare species in the predator and non-predator communities for the control and migration treatment of the experiment. Two definitions of "rare" are used here: first, a morpho-species as a singleton in the dataset (top-half) and second, a given morpho-species as less abundant than the mean abundance of all morpho-species in the community ("relatively rare").

Discussion

Our results showed that, even after scaling up the biodiversity background to a tropical leaf litter community with over 100 species, predator guild species diversity decreased significantly with migration. It is notable that even the coarsest distinction of trophic complexity (predators and non-predators) provides insights that do not emerge when analyzing the community as a whole. These findings echo those of the earlier study (Vandermeer et al. 1980) which was done with a lower-biodiversity temperate leaf litter community. Results from both this and the earlier study seemingly contradict a main conclusion of basic metacommunity theory: that migration increases species' persistence, and thus also regional richness. While theoretical treatments of metacommunities acknowledge the potential complexity of community structure and its effect on migration (Caswell and Cohen 1991; Mouquet and Loreau 2002; Economo and Keitt 2008), it remains that simplified metacommunity theory generates the prediction that migration will tend to cause species diversity to increase, a result in concordance with the original MacArthur-Wilson, Levins-Heatwole framework (Heatwole and Levins 1972; 1973; Levins et al. 1973). Importantly, there is also no evidence, to our knowledge, that suggests that leaf litter communities in the temperate or tropical zones are organized in such a way that predisposes them to the results of both of these studies. These consistent results with distinct communities in distinct regions suggest that there may be some generality in the way that migration impacts trophic guilds.

While it is of particular interest that effects of migration fall along the lines that delineate trophic position in the community, that does not necessarily imply a trophic mechanism to explain the observed dynamics. The type of detailed observations of community interactions that would be necessary to understand the mechanisms that generated our experimental results were not feasible in our study; we could only look at patterns of community richness and composition to attempt to shed light on potential mechanisms at play. The two key findings are that first, predator richness decreased significantly with migration, but community structure did not significantly change, and secondly, while non-predator richness did not change significantly, community structure did (Figure 1 & Figure 2). For the predator community, this suggests that although there is a reduction in the number of morpho-species, the relative abundance and presence in the rest of the community was not significantly impacted by migration. This indicates that migration may have had a very species-specific impact within the predator guild, the effects of which then rippled through the non-predator community. We suggest that a highly antagonistic and relatively rare (possibly initially isolated to only a single patch) predator may be shaping the community when dispersed among patches, as was suggested in Vandermeer et al. (1980). Support for this hypothesis is in the higher percentage of rare predator morpho-species in the treatment with no migration (Table 1.). Non-significant compositional changes in the predator community may be the result of the extinction of relatively rare predator morpho-species, an effect not present in the non-predator community. While rare predators are impacted by migration, rare non-predators are not. The R statistics reported from the ANOSIM tests suggest a similar story, where the larger R for the Jaccard index compared to Bray-Curtis observed in the predator community suggest targeted species specific changes to the communities.

Based on patterns in community richness and composition, we suggest that an antagonist and relatively rare predator may be shaping these leaf litter communities, but it remains that both trophic and non-trophic mechanisms acting within and between guilds could be drawn upon to explain these results. Intraguild effects among predator communities are common and may manifest in the form of indirect competition among predators or intraguild predation. Impacts of predators on community structure are often hypothesized as acting through lower trophic levels such as predator-mediated coexistence or keystone predation (Shurin and Allen 2002). It is also possible that the changes observed resulted from non-trophic interactions such as trait-mediated indirect interactions (Werner and Peacor 2003; Bairey et al. 2016; Grilli et al. 2017; Terry et al. 2017), which may be acting within or between trophic levels. As is widely documented in ecological communities, the addition of new species (i.e. by migration) can result in local changes to the magnitude, and even sign, of other species' pairwise direct interactions, often caused by behavioral changes. For example, the mere presence of a predator at a low density can decrease the maximum observed foraging activity and thus fitness of a prey (Werner and Peacor 2003). In a metacommunity context, higher-order anti-predator effects have also been shown to shape metacommunity dynamics when migration is induced in simple experimental systems

(Kneitel and Miller 2003; Hauzy et al. 2007; Howeth and Leibold 2010). If there are differences in the structure of indirect interactions within trophic levels, we may predict different dynamics for each trophic level. For instance, there may be more strong negative indirect interactions among predators in a system, but weaker positive indirect effects among prey; this could cause more exclusion and lower richness among predators, yet little to no change in prey richness. Ultimately, a myriad of trophic and non-trophic mechanisms may be important in shaping metacommunity dynamics, and we emphasize their consideration in developing modern metacommunity theory (Guzman et al. 2019) .

Community organization, which encompasses the ways in which trophic levels are connected across scales also mediates the ways in which predators shape metacommunity dynamics (Shurin 2001, Shurin and Allen 2001, CadotteCodetta and Fukami 2005). The context dependency associated with metacommunity dynamics is likely a reflection of the complex ways in which communities can be organized trophically and non-trophically. The ability to account for the true distribution of interactions in ecosystems is likely limited in natural systems, but will further our understanding of the plethora of theoretical and empirical results regarding trophically specific roles in metacommunities (Shurin 2001; Kneitel and Miller; Caswell 1978; Caswell and Cohen 1991). Most frequently, experimentalists look at the impacts of predators on the overall diversity of the metacommunity, and have found examples of predators increasing regional diversity (Shurin 2001) as well as decreasing it (Codette and Fukami 2005). What has been less frequently explored is the impact of migration on the predator and non-predator guilds separately. Most hypotheses associated with trophic guilds and metacommunities are related to the rate of migration in the system or simply the presence of predators (Kneitel and Miller 2003). Regarding our study system, the relatively small literature on the community ecology of terrestrial leaf litter arthropod communities makes it difficult to narrow potential mechanisms that may explain our results.

In our experiment, we manipulated migration rates such that there were equivalent potential migration rates for predators and non-predators. This could be an important caveat to our study's generalizability, given the potential differences in the realized predator and non-predator migration rates. Migration should increase diversity initially, as homogenization occurs, but trophic and non-trophic interactions can act to increase or decrease diversity after this initial homogenization. Our result of lower predator richness with migration runs counter to this expectation of increased diversity with homogenization, and thus indicates that our experimental time frame was appropriate to assess changes in these communities. We found no change in the richness of non-predators, but have no reason to suspect that homogenization effects would operate on a different time scale for predators and non-predators in the leaf litter community, particularly given that we manipulated the potential migration rates to be equal across trophic levels.

The work reported herein sits comfortably with the current enthusiasm for metacommunities, a framework originally suggested by Wilson (1992). It is substantially similar to the framework of MacArthur and Wilson's original offering, in which 1) ecological dynamics occur locally, with species interactions (of various forms) determining which species will survive and which will locally perish, while 2) the more regional process of migration continually feeds these local communities, countering local extinctions with regional migrations to provide the expected equilibrium (MacArthur and Wilson 1964). Eschewing some recent complexities (Leibold et al. 2004), we consider a metacommunity as structured in the original sense of Wilson (1992), wherein ecological dynamics occur at a local level, but local patches affect one another through dispersal. Our experiment interrogates the consequences of migration, but more specifically explores the interaction between community structure and the dynamics of migration. Our results highlight the importance of considering trophic and non-trophic structure when evaluating metacommunity dynamics.

Acknowledgments

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Supplementary Material

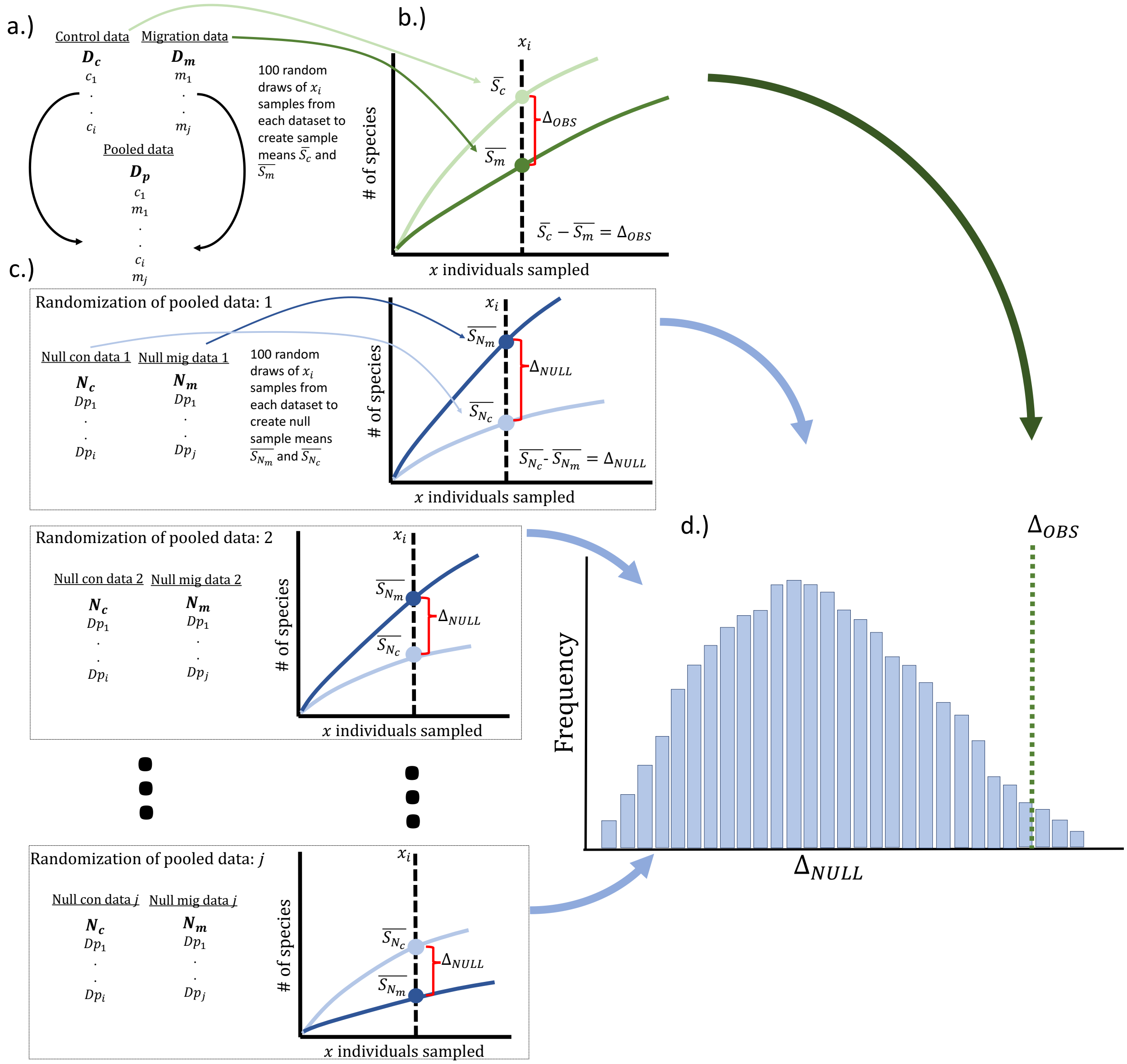

Figure 4.3: This figure presents a graphical walkthrough of the statistical test to compare the rarefaction curves. ***a.)*** *shows the observed list of species incidences from the control and migration datasets.* ***b.)*** *each one of the datasets (D_c and D_m) are respectively sampled 100 times to calculate a sample mean for a given level of x individuals sampled (x_i). The difference between those samples give us our observed statistic.* ***c.)*** *pooled data (D_p) from D_c and D_m are then randomly partitioned and the procedure in* ***b.)*** *I then repeated 100 times to create a null distribution* ***d.)*** *where the probability of finding our observed statistic can be calculated. Note*

that the random partitioning of data and resampling done in ***c.)*** *is done 100 times for a given* x_i *which then creates the null distribution. R code for statistical test can be found at https://github.com/ZHAJIANF/Hajian-Forooshani_Oikos_2019_rarefaction_test*

Chapter 5 Viewing Communities as Coupled Oscillators: Elementary Forms from Lotka and Volterra to Kuramoto

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Abstract

Ecosystems and their embedded ecological communities are almost always by definition collections of oscillating populations. This is apparent given the qualitative reality that oscillations emerge from consumer-resource interactions, which are the elementary building blocks for ecological communities. It is also likely always the case that oscillatory consumer-resource pairs will be connected to one another via trophic cross-feeding with shared resources or via competitive interactions among resources. Thus, one approach to understanding the dynamics of communities conceptualizes them as collections of oscillators coupled in various arrangements. Here we look to the pioneering work of Kuramoto on coupled oscillators and ask to what extent can his insights and approaches be translated to ecological systems. We explore the four ecologically significant coupling arrangements of the simple case of three oscillator systems with both the Kuramoto model and with the classical Lotka-Volterra equations. Our results show that the six-dimensional analogous Lotka-Volterra systems behave strikingly similarly to that of the corresponding Kuramoto systems across all possible coupling combinations. This qualitative similarity in the results between these two approaches suggests

that a vast literature on coupled oscillators that has largely been ignored by ecologists may in fact be relevant in furthering our understanding of ecosystem and community organization.

Introduction

Interacting species assemblages are composed of consumers and their resources. If pairs of consumer-resource systems are persistent in a given community, then the fundamentals of ecological theory suggest that these communities are, in principle, assemblages of oscillators. To the extent that the consumers tend to overlap in their diets, or the resources interact with one another, ecological communities may be thought of as systems of coupled oscillators. Although ecologists have long been interested in understanding large assemblages of interacting species, relatively little research in community ecology has drawn on the body of theory associated with coupled oscillators to conceptualize such systems. In many branches of science, coupled oscillators have been used as a key metaphor for developing general theory, from electronics to neurobiology (Norton et al., 2018; Laing, 2017; Fukuyama, and Okugawa, 2017). Here we suggest that consumer-resource oscillators can be thought of as the building blocks of ecological communities and the analogy of coupled oscillators can potentially be used as an abstraction for community ecology.

The inevitability of oscillatory dynamics in ecological systems stems from one of ecology's most foundational models of consumer-resource interactions, where the simplest assumptions of one population consuming another generates persistent oscillations (Lotka 1926; Volterra 1926). Adding Holling's functional response (Holling, 1959), this basic framework can generate persistent oscillations in the form of stable limit cycles, a form that could be considered as a starting point for envisioning ecological communities, which is to say, as coupled oscillators (Vandermeer, 1993; 1994; 2004; 2006). Restricting the analysis to the parameter space within which limit cycle solutions exist, while limiting from a complete ecological point of view, is potentially a useful simplification explored here.

In this work we deal with three oscillators, which means three consumers and three resources. Since there are six variables with the only necessary restriction that resources get consumed by consumers, the number of ways one could couple the variables together is large. Conceptualizing the system as three oscillators (a consumer and one of the resources) restricts the possible combinations, but there are still many. Yet there is a way in which some ecological assumptions can make the landscape simpler and perhaps more intuitive. Suppose that oscillatory consumer-resource pairs function in two distinct and ecologically relevant ways (Vandermeer, 2004). First, when two consumers share two resources they can be thought of as coupled with one another via trophic cross-feeding, the case of resource competition between the two consumers. Second, resources that are in direct competition with one another can be thought of as being coupled via competition for some external resource. Here we refer to these two qualitatively distinct forms as trophic-coupling and resource-coupling respectively. When coupling is weak, surprising generalizations emerge in the phase dynamics for these arrangements. For weak trophic-coupling, the oscillators converge on a pattern of relative in-phase synchrony, and for weak resource-coupling the oscillator pairs will converge on a pattern of relative anti-phase synchrony (Vandermeer, 2004) (Figure 1). It is almost certainly the case that consumer-resource pairs are not exclusively resource-coupled or trophic-coupled in nature, and incorporating both coupling types can lead to complicated dynamics such as chaotic oscillations (Vandermeer, 2004). Even given these complications, Benicà et al. (2009) demonstrated that the insights from these particular forms of coupled oscillators can be successfully applied to complex empirical communities.

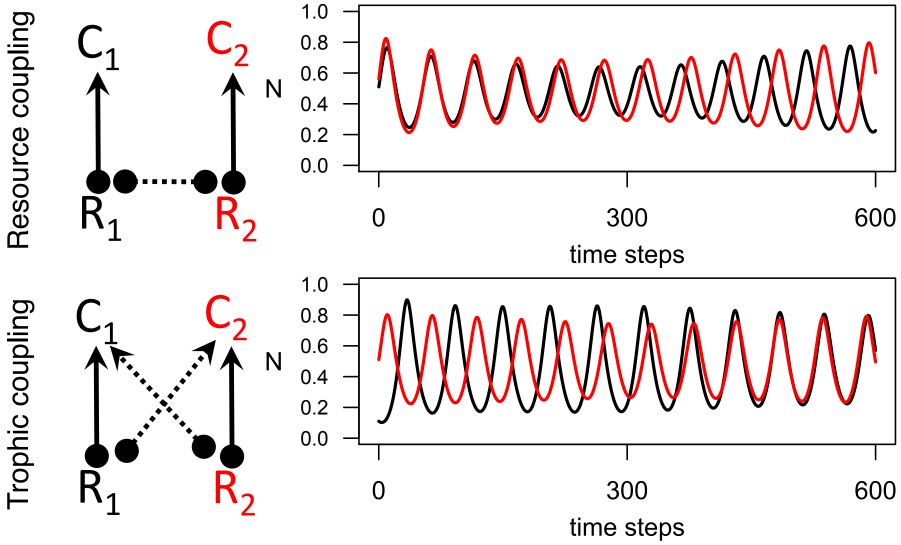


Figure 5.1: The two qualitatively distinct coupling arrangements for consumer-resource oscillators and their dynamic outcomes (Vandermeer, 2004). Resource coupling (competition between resources) leads to asynchrony and trophic coupling (cross-feeding) leads to synchrony. Circles represent negative effects, arrows positive effects, and dotted lines oscillator coupling.

Although oscillations emerge from many nonlinear systems, oscillators themselves have been the focus of understanding systems. One elegant perspective on coupled oscillators is the abstraction of Yoshiki Kuramoto (1975; 1984), which was partially inspired by the pioneering work by Arthur Winfree on biological oscillators (1967). Kuramoto envisioned collections of coupled oscillators as *weakly-coupled* limit cycles on the circle and the oscillator conditions indicated as the angle Θ made by the point of resource and consumer on the unit circle, taken to represent the limit cycle of the oscillator. Presuming that synchronization will occur, Kuramoto writes;

$$\frac{d\Theta_i}{dt} = \omega_i + \frac{K}{N}\sum_j \sin(\Theta_i - \Theta_j) \tag{1}$$

where ω_i is the intrinsic frequency of oscillator *i* (the rate of advancement on the circle dictated by the inherent oscillations), *K* is the intensity of coupling, and *N* is the number of oscillators.

Clearly the intent of the model is to view the phase of the oscillations (not the amplitude) as the key dynamical variable. All oscillators are identical (with the possible exception of the intrinsic frequency) and couplings are taken to be universal (all to all). A rather remarkable result emerges from this simple model -- with random initiations, no synchrony occurs when coupling strengths are small, but a critical point of coupling intensity is reached where rapid attainment of synchrony of all oscillators is achieved. There is now a large technical literature on this model, as well as a long history, both of which are summarized in a reader-friendly way by Strogatz (2000).

In an ecological context, Kuramoto's limit-cycle oscillators could be thought of as resource-consumer pairs in the parameter regimes that generate limit-cycle behavior . Although it is apparent to ecologists that oscillations are an essential feature that results from the most elementary of ecological interactions, approaches used in the field of complex systems, like those pioneered by Kuramoto, have gained relatively little traction in the field of ecology. It is most frequently the practice in ecology, especially in the food web literature, to couple together large networks of ordinary differential equations (e.g. Lotka-Volterra) representing individual populations of consumers and resources. Although this approach has been fruitful, it sometimes leads to unwieldy parameterization, limiting analytical questions to those amenable to linear stability analyses. To explore the potential usefulness of employing approaches such as those of Kuramoto, we here study the concordance between his model and the classical Lotka-Volterra models used in ecology, for the most elementary formulation of an ecological community.

Methods

Modifying Kuramoto's model, we write:

$$\frac{d\Theta_i}{dt} = \omega_i + \frac{K}{N}\sum_j \Gamma_{i,j}\sin(\Theta_i - \Theta_j) \qquad (2)$$

where Kuramoto's mean field approach has been disaggregated with the adjacency matrix Γ stipulating the coupling of each pair of oscillators. Note that $\Gamma_{i,j} > 0$ indicates the oscillators i and j will synchronize "in phase" while $\Gamma_{i,j} < 0$ indicates they will synchronize "anti-phase." If we stipulate that $|\Gamma_{i,j}| = 1.0$, the sum of the upper triangle of the adjacency matrix [= $\frac{1}{2}\sum(\Gamma_{i,j})$] can be -3, -1, 1, or 3 for a three oscillator system. Figure 2 illustrates the basic combinations of a three oscillator system with expected outcomes of oscillator phases based on coupling.

Taking the classic Lotka-Volterra consumer resource equations we write:

$$\frac{dC_i}{dt} = \frac{aC_i \sum_{j=1}^{3} \beta_{ij} R_j}{1 + h\sum_{j=1}^{3} R_j} - mC_i \tag{3a}$$

$$\frac{dR_i}{dt} = bR_i\left(1 - \sum_{j=1}^{3} \alpha_{ij} R_j\right) - \frac{aC_i \sum_{j=1}^{3} \beta_{ij} R_j}{1 + h\sum_{j=1}^{3} R_j} \tag{3b}$$

Where C and R denote "consumers" and "resources" respectively and i ranges from 1 to 3. The basic parameters of the model are: a = the attack rate of the consumers, m = the mortality rate of the consumers, h = the functional response term of the consumer, b = the birth rate of the resource, α_{ij} = the competitive effect of resource j on resource i (note, $\alpha_{ii} = 1$), and β_{ij} = the strength of cross feeding (note, $\beta_{ij} = 1$). The parameter α represents the strength of competition (resource coupling) between resources and β represents the strength of cross-feeding (trophic coupling).

In the spirit of Kuramoto's model, we first located parameter space where individual consumer-resource pairs oscillate in limit cycles (equation set 3). Given a persistent oscillator in the Lotka-Volterra formulation, we then couple them in four paradigmatic combinations outlined in Figure 2, where trophic-coupling implies eventual synchrony and resource-coupling implies asynchrony. Manipulating α_{ij} and β_{ij} in equation set 3, we create the parameter states for all four coupling arrangements depicted in Figure 2 (See appendix for long form equations for each coupling scenario). For all simulations presented here we used low values of coupling coefficients (α =0.01 and β =0.1).

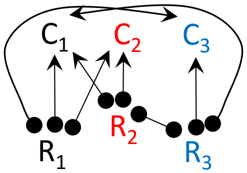
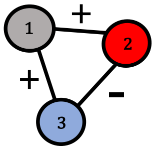
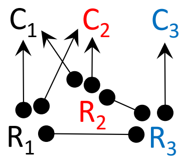
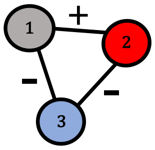
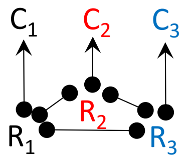
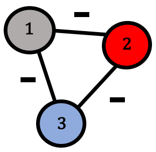
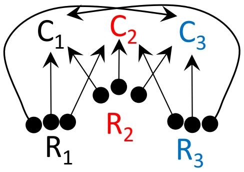
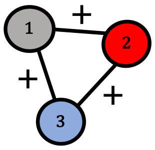
Lotka-Volterra diagram	Kuramoto diagram	$\frac{1}{2}\sum\Gamma$
		1
		-1
		-3
		3

Figure 5.2: Diagrammatic representation of the analogous forms of Lotka-Volterra and Kuramoto for three oscillator communities. ***Lotka-Volterra diagram:*** *Illustrates the core idea of three consumer/resource coupled oscillators, C_i is the biomass of the ith consumer and R_i is the biomass of the ith resource. Connectors indicate a positive effect with an arrowhead and a negative effect with a closed circle.* ***Kuramoto diagram:*** *illustrates the three oscillators as nodes in a graph and their connections, edges, with the elements of the adjacency matrix (+=1 or - = -1) indicated near the edges.* $\frac{1}{2}\sum\Gamma$ *shows the sum of the elements of half of the adjacency matrix to simply represent the four unique coupling arrangements. Note that the coloring scheme of the oscillators is consistent throughout the article.*

Results

Employing the Kuramoto model (equation 2) if $\frac{1}{2}\sum\Gamma_{i,j} = 3$, the system synchronizes in-phase (i.e., all oscillators are effectively on the same point in circle space, as in Fig. 3d), if it is -3 the system synchronizes precisely anti-phase (each oscillator separated from each other by $2\Theta/3$ radians, as in Fig. 3c), if it is -1 two oscillators are in-phase and the third is anti-phase against the two in-phase oscillators (Fig. 3b). However, if the sum is 1 an intransitive situation emerges in which oscillator 3 is in-phase synchrony with oscillator 1, oscillator 1 is in-phase synchrony with oscillator 2, while oscillator 2 is anti-phase synchronous with oscillator 3, but, qualitatively stable. The three oscillators are separated from one another by $\Theta_{1,2} = \Theta_{1,3} = \Pi/3$ and $\Pi_{23} = 4\Pi/3$ (Fig. 3a). In all four cases (Fig. 3), while all oscillators retain the same relative position with respect to one another, they all together progress around the state space according to the intrinsic frequency.

Employing the LV model (equations 3), typical time series results of all four ODE simulations are presented in Figure 3. It is clear that the L-V predictions for all four qualitatively distinct cases (Figure 2) are precisely what we get from the simpler Kuramoto approach. It is worth noting that the LV simulations are quite robust as long as the coupling is not strong. As reported elsewhere (Vandermeer, 1993; 1994; 2004; 2006) as coupling becomes stronger, frequently complicated behavior, including chaos and quasiperiodicity, typically emerge from these structures. Regarding the Kuramoto simulations, the results are seemingly completely robust in that we found no examples of coupling (in the range 0 – 1) that did not yield the same qualitative results as visualized in Figure 3.

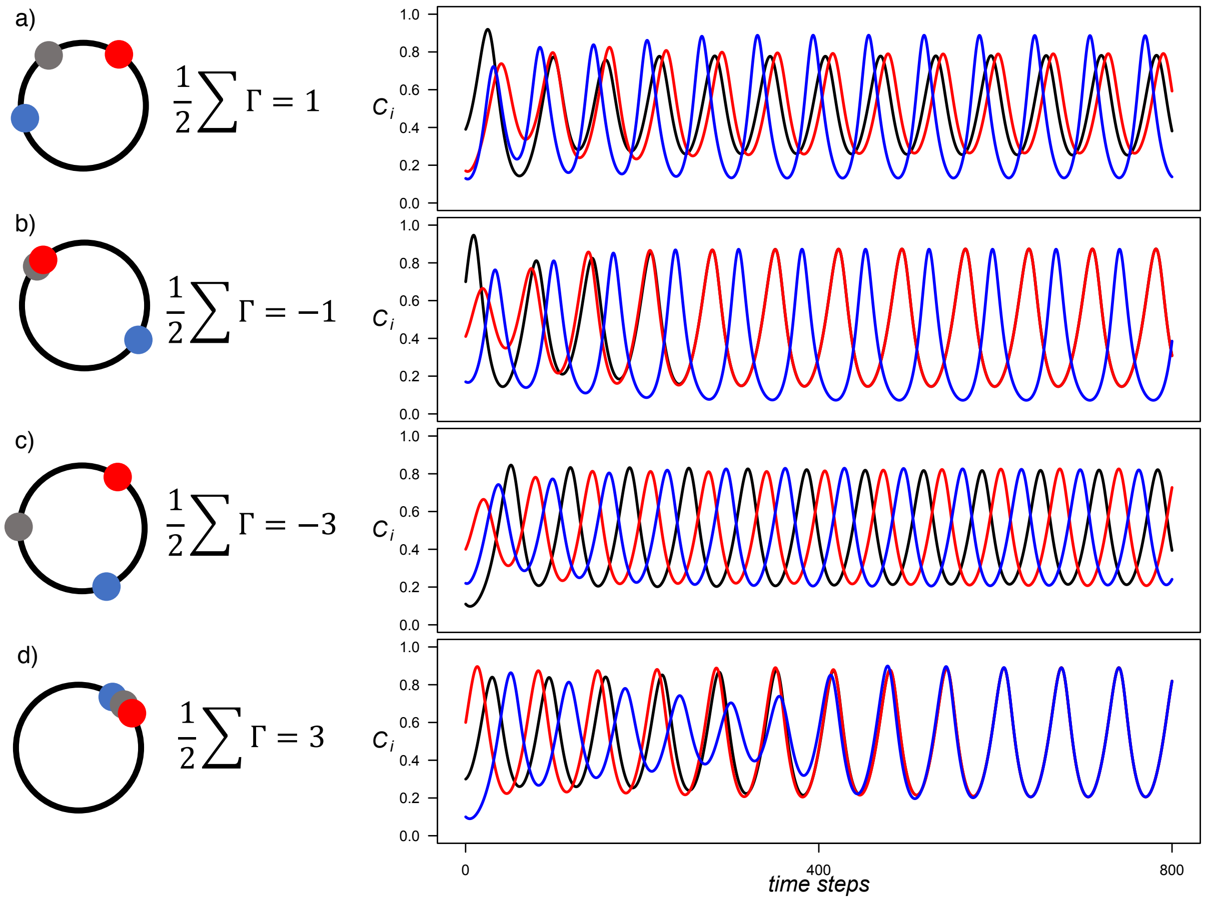


Figure 5.3: Time series from the four separate coupling configurations of the three dimensional Kuramoto and six dimensional Lotka-Volterra systems. a)-d) show the oscillator phases from the Kuramoto systems and the time series for the analogous six dimensional Lotka-Volterra systems. The clear concordance between the Lotka-Volterra time series and the Kuramoto oscillator phases is evident by the end of the Lotka-Volterra time series plots. Note that only the consumers are plotted in the time series to more clearly illustrate the correspondence in oscillatory dynamics between LV and Kuramoto. The parameters and initial conditions for all Lotka-Volterra simulations are found in appendix. For the Kuramoto model simulations K=0.01, ω =.01, and the model was run for 200 time steps.

Discussion

The ubiquity of oscillatory dynamics in ecology has long been appreciated (Platt and Denman, 1975; Huisman and Weissing, 2001; Blasius et al., 2020). Empirically, across a range of spatiotemporal scales from large scale dynamics of the hare-lynx system (Blasius et al., 1999) to the microcosm experiments of Huffaker (1958), and theoretically emerging from the simplest conceptualizations of consumer-resource interactions (Lotka, 1928; Volterra, 1926), synchronization of coupled consumer-resource oscillators is well-known, both from an implied spatial coupling (e.g., predator or prey migrating among habitat patches (Koelle and Vandermeer, 2005)) and direct energy transfer [e.g., different predators coupling among different prey in the same habitat (Vandermeer, 2006)]. Here we demonstrate that for the four most obvious qualitatively distinct yet ecologically significant coupling patterns in a six-species community (three oscillators), weak coupling leads to precisely the pattern predicted by Kuramoto's phase coupled system. These results suggest a wholly distinct vision of ecological communities in which the "agents" are not population densities, but rather oscillators.

There are evident limitations in the analysis as presented here, but, we argue, those limitations suggest that the approach holds much potential. For example, the introduction of dissipating oscillators into the mix is an evident expansion of the system, one that has not been examined, at least not in the context of the Lotka/Volterra and Kuramoto connection. Another important element is the possibility of studying coupled chaotic oscillators with the Kuramoto framework, certainly a challenging possibility. Blasius and colleagues (1999) have already indirectly entered this topic with their UPCA pattern (uniform phase chaotic amplitude), which is, in a sense, putting chaotic dynamics in a Kuramoto-like framing (although chaotic, the lynx/hare cycle synchronizes phases across Canada). Contrarily, one might ask what a UACP pattern (uniform amplitude, chaotic phase) would look like and how it could be generated, perhaps a more direct application of the Kuramoto metaphor since amplitudes are fixed and the interest is in the dynamics of the phases. On the other hand, the existence of chimeric elements (individual oscillators that refuse to synchronize in any way with synchronous groups of oscillators) may already be examples of chaos or chaos-like behavior in the Kuramoto framing (Kotwal et al., 2017; Laing, 2009).

There is a rich and diverse literature on synchronization, popularly summarized for a generalist audience by Steven Strogatz in his book “Sync.” (2012). Ecological applications are less common but the field is growing. For example, some authors have examined correlations with external forcing, either regular or stochastic (Vasseur, and Fox, 2007; Reuman et al., 2008) in driving or sometimes quenching synchronized systems, and spectral analysis (Vasseur and Gaedke, 2007) recalls the original insights of Platt and Denman (1975). And, of course, it has long been acknowledged that a metapopulation in which subpopulations oscillate in sync are far more likely to undergo global extinction (Matter, 2001).

By reorienting the focus of ecological analogy from individual populations to collections of oscillators, the dynamical nature of the system becomes the central focus rather than questions of stability or persistence. As in other sciences, the collective dynamics of coupled oscillators can provide a useful heuristic for exploring the general properties of large and complex systems of the sort that ecologists have long cited with awe (Hutchinson, 1961; Lawton, 1999; Vellend, 2010). Furthermore, by highlighting the ability to move between classical models in ecology and classical models in the coupled oscillator literature, we suggest that both approaches can be used in tandem and exploited for their strengths. Approaches á la Kuramoto effectively increase the tractability of large complex systems by halving the dimensionality and providing an elegant and intuitive way to visualize the oscillatory dynamics, while approaches á la Lotka-Volterra permit investigation of how basic biological parameters influence dynamics. The most obvious utility of such an approach is where synchronous dynamics are the focus of investigation (e.g. Earn et al.,1998; Blasius et al., 1999; Liebhold et al., 2004), and may have practical implications for the management of fisheries (Kaemingk et al., 2018), the planning complex biological control systems in agroecosystems (Vandermeer et al., 2019), or conservation (Earn et al., 2000).

The once popular idea that ecosystems are at, or moving towards, Lyapunov stability is considered passé (e.g., Morozov et al., 2019). The growing appreciation amongst ecologists that ecosystems and communities are dominated by nonlinear processes often outside of equilibrium (DeAngelis & Waterhouse ,1987) suggests that our tool kits to understand ecosystems need to evolve along with our analogies of them, as suggested long ago (Platt and Denman, 1975). We suggest that networks of oscillators, rather than networks of populations, represent a potentially new paradigm for the examination of ecological communities.

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The students in the "Complex Systems in Ecology" course in Fall 2019 at University of Michigan participated in stimulating discussions related to the ideas presented here. Chatura Vaidya and Kristel Sanchez provided feedback on an earlier draft of the manuscript. Several examples from Ferdinand LaMothe and Oscar Peterson gave some intuition into the dynamics of coupled oscillators that were useful in the development of this manuscript.

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Supplementary Material

Appendix

$\frac{1}{2}\sum \mathbf{\Gamma} = 1$ for the Lotka-Volterra system of ordinary differential equations has C1 with trophic-coupling on R2 and R3, C2 with trophic-coupling on R1, C3 with trophic-coupling on R1, and R2 and R3 resource coupled. Initial conditions and parameters for Figure 3 are:

R_1=0.38, R_2=0.16, R_3=0.12, C_1=0.39, C_2=0.17, C_3=0.13, β=0.01, α=0.21

$$\dot{R_1} = bR_1(1 - R_1) - \frac{aR_1C_1}{1+h(R_1+\beta(R_2+R_3))} - \frac{\beta aR_1C_2}{1+h(R_2+\beta R_1)} - \frac{\beta aR_1C_3}{1+h(R_3+\beta R_1)}$$ (eq. 4a)

$$\dot{C_1} = -mC_1 + \frac{aR_1C_1+\beta aR_2C_1+\beta aR_3C_1}{1+h(R_1+\beta(R_2+R_3))}$$ (eq. 4b)

$$\dot{R_2} = bR_2(1 - R_2 - \alpha R_3) - \frac{aR_2C_2}{1+h(R_2+\beta R_1)} - \frac{\beta aR_2C_1}{1+h(R_1+\beta(R_2+R_3))}$$ (eq. 4c)

$$\dot{C_2} = -mC_2 + \frac{aR_2C_2+\beta aR_1C_2}{1+h(R_2+\beta R_1)}$$ (eq. 4d)

$$\dot{R_3} = bR_3(1 - R_3 - \alpha R_2) - \frac{aR_3C_3}{1+h(R_3+\beta R_1)} - \frac{\beta aR_3C_1}{1+h(R_1+\beta(R_2+R_3))} \quad \text{(eq. 4e)}$$

$$\dot{C_3} = -mC_3 + \frac{aR_3C_3+\beta aR_1C_3}{1+h(R_3+\beta R_1)} \quad \text{(eq. 4f)}$$

for $\frac{1}{2}\sum \mathbf{\Gamma} = -1$ for the Lotka-Volterra system of ordinary differential equations has C1 with trophic-coupling on R2, C2 with trophic-coupling on R1, R2 and R3 with resource-coupling and R1 and R3 with resource-coupling. Initial conditions and parameters for Figure 3 are:

R_1=0.69, R_2=0.40, R_3=0.16, C_1=0.70, C_2=0.41, C_3=0.17, β=0.06, α=0.09

$$\dot{R_1} = bR_1(1 - R_1 - \alpha R_3) - \frac{aR_1C_1}{1+h(R_1+\beta R_2)} - \frac{\beta aR_1C_2}{1+h(R_2+\beta R_1)} \quad \text{(eq. 5a)}$$

$$\dot{C_1} = -mC_1 + \frac{aR_1C_1+\beta aR_2C_1}{1+h(R_1+\beta R_2)} \quad \text{(eq. 5b)}$$

$$\dot{R_2} = bR_2(1 - R_2 - \alpha R_3) - \frac{aR_2C_2}{1+h(R_2+\beta R_1)} - \frac{\beta aR_2C_1}{1+h(R_1+\beta R_2)} \quad \text{(eq. 5c)}$$

$$\dot{C_2} = -mC_2 + \frac{aR_2C_2+\beta aR_1C_2}{1+h(R_2+\beta R_1)} \quad \text{(eq. 5d)}$$

$$\dot{R_3} = bR_3(1 - R_3 - \alpha R_2 - \alpha R_1) - \frac{aR_3C_3}{1+hR_3} \quad \text{(eq. 5e)}$$

$$\dot{C_3} = -mC_3 + \frac{aR_3C_3}{1+hR_3} \quad \text{(eq. 5f)}$$

for $\frac{1}{2}\sum \mathbf{\Gamma} = -3$ has pairwise resource-coupling between all resources and no trophic-coupling.

Initial conditions and parameters for Figure 3 are:

R_1=0.10, R_2=0.39, R_3=0.21, C_1=0.11, C_2=0.40, C_3=0.22, α=0.09

$$\dot{R_1} = bR_1\left(1 - R_1 - \alpha R_2 \ - \alpha R_3\right) - \frac{aR_1C_1}{1+hR_1} \quad \text{(eq. 6a)}$$

$$\dot{C_1} = -\mathrm{m}C_1 + \frac{aR_1C_1}{1+hR_1} \quad \text{(eq. 6b)}$$

$$\dot{R_2} = bR_2\left(1 - R_2 - \alpha R_1 \ - \alpha R_3\right) - \frac{aR_2C_2}{1+hR_2} \quad \text{(eq. 6c)}$$

$$\dot{C_2} = -\mathrm{m}C_2 + \frac{aR_2C_2}{1+hR_2} \quad \text{(eq. 6d)}$$

$$\dot{R_3} = bR_3\left(1 - R_3 - \alpha R_1 \ - \alpha R_2\right) - \frac{aR_3C_3}{1+hR_3} \quad \text{(eq. 6e)}$$

$$\dot{C_3} = -\mathrm{m}C_3 + \frac{aR_3C_3}{1+hR_3} \quad \text{(eq. 6f)}$$

for $\frac{1}{2}\sum \mathbf{\Gamma} = 3$ has pairwise trophic-coupling between all consumers and resources and no resource-coupling. Initial conditions and parameters for Figure 3 are:

R_1=0.29, R_2=0.59, R_3=0.09, C_1=0.30, C_2=0.60, C_3=0.10, β=0.02

$$\dot{R_1} = bR_1(1 - R_1) - \frac{aR_1C_1}{1+h(R_1+\beta(R_2+R_3))} - \frac{\beta aR_1C_2}{1+h(R_2+\beta(R_1+R_3))} \ - \frac{\beta aR_1C_3}{1+h(R_3+\beta(R_1+R_2))}$$

(eq. 7a)

$$\dot{C_1} = -mC_1 + \frac{aR_1C_1+\beta aR_2C_1+\beta aR_3C_1}{1+h(R_1+\beta(R_2+R_3)} \quad \text{(eq. 7b)}$$

$$\dot{R_2} = bR_2(1 - R_2) - \frac{aR_2C_2}{1+h(R_2+\beta(R_1+R_3))} - \frac{\beta aR_2C_1}{1+h(R_1+\beta(R_2+R_3))} - \frac{\beta aR_2C_3}{1+h(R_3+\beta(R_1+R_2))}$$

(eq. 7c)

$$\dot{C_2} = -mC_2 + \frac{aR_2C_2+\beta aR_1C_2+\beta aR_3C_2}{1+h(R_2+\beta(R_1+R_3))} \quad \text{(eq. 7d)}$$

$$\dot{R_3} = bR_3(1 - R_3) - \frac{aR_3C_3}{1+h(R_3+\beta(R_1+R_2))} - \frac{\beta aR_3C_1}{1+h(R_1+\beta(R_2+R_3))} - \frac{\beta aR_3C_2}{1+h(R_2+\beta(R_1+R_3))}$$

(eq. 7e)

$$\dot{C_3} = -mC_3 + \frac{aR_3C_3+\beta aR_1C_3+\beta aR_2C_3}{1+h(R_3+\beta(R_1+R_2))} \quad \text{(eq. 7f)}$$

Chapter 6 Ecological Perspectives on the Coffee Leaf Rust

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Introduction

The yellow blotches spotted on coffee leaves in Ceylon (Sri Lanka) in 1869 turned out to be a symptom of what would become one of the most devastating diseases of one of the most important crops in the world. British authorities rushed one of their most brilliant pathologists, Henry Marshall Ward, to one of their most intensively planned agroecosystems in one of their most profitable colonies, to solve what was correctly seen as the tip of a disease iceberg. A keen observer of natural history, Ward determined the cause to be a fungus and meticulously worked out the details of its natural history, most of which remain the central core of our biological understanding yet today. As much as the current authors regard Ward as a hero, British authorities of the nineteenth century regarded his work as worthless, since he failed to find a solution to the problem. Providing detailed information on the underlying biology and ecology of the disease was regarded by the plant pathologists of the day as rather unimportant if such information did not lead to immediate solutions, reflective of nineteenth century British imperial attitudes about their empire.

The rolling appearance of the coffee leaf rust (CLR) coupled with its devastating impact on local coffee economies, as told brilliantly by historian Stuart McCook in his recent book “Coffee is not forever” (2019) is remarkable for its qualitative predictability – if you have coffee, CLR will come, if the rust comes, your economy will be devastated. From the mid nineteenth century in Ceylon, to the beginning of the twentieth century in East Africa, to the middle of the twentieth century in West Africa to the end of the twentieth century in the Americas, much like other species invasions, a plant invades a new area and prospers initially (coffee), followed by one or more natural enemies (CLR), which stifle its initial prosperity. The only difference here is the interest generated among the individuals of the species *Homo sapiens*, due to its propensity for drug addiction.

The Americas represent something special. As documented in great deal by McCook, the so-called "Great Rust" occurred sort of without warning in 2012/2013. Having arrived in Brazil in 1970, coffee farmers throughout the Americas, cognizant of what had happened in Sri Lanka and elsewhere, panicked. Warnings with admonitions to do everything from pruning coffee bushes, to increase fertilization, to reducing or eliminating shade, to prophylactic spraying of fungicides were common throughout the area for the next 30 or 40 years. Yet as time wore on, farmers began to realize that the rust was here to stay, never did cause the sort of devastation the nineteenth century epidemic in Sri Lanka caused, and was effectively treated as just one more of the yield-reducing nuisances they had learned to live with. Major problems with the disease were periodically reported in isolated areas throughout the Americas, but all seemed local and temporary. Then quite suddenly, the Great Rust hit them with devastating force. Walking through a coffee field in December of 2012 one's clothes would become yellow with the incredible abundance of rust spores seeking new victims (Lopez-Bautista, personal communication).

The history of research on the disease (see McCook, 2019) seems oriented much like the original British establishment who judged Ward a failure. Genetics and chemistry seem to be the reining discourses where the ultimate solution will be found. Ward's careful consideration of biological and ecological factors are acknowledged, to be sure, but a reading of the disease's history cannot help but suggest that a sort of technocentric or instrumentalist, as the philosophers say (Dear, 2008), point of view has prevailed. The search continues for genetic solutions, which is to say resistant varieties, as well as chemical ones, which is to say fungicides. Less common, albeit important, is an approach the philosophers would call intelligibility (Dear, 2008), seeking the underlying mechanisms as to why, for example, open landscapes seem to favor the rust (Avelino et al., 2012), or fungicides are effective only when fine-tuned at a local level (de Souza, et al., 2011). The technocrat (instrumentalist) might say, if moisture favors the rust, reduce moisture. The ecologist, interested in the intelligibility of nature, would ask what is it about the natural history of the rust that results in its rapid growth when moisture is high? This latter approach, the ecological, we feel should represent an important compliment to the more direct search for technological solutions.

In this chapter, we attempt to at least in part refocus an ecological approach to the problem of CLR. First we provide a brief overview of the research which has stemmed from a more technocentric approach to understanding and subsequently control CLR. We intentionally keep this section brief, but try to highlight areas which are of potential ecological and evolutionary interest within this thread of research. This technocentric approach has been the main line of inquiry regarding CLR and there are various resources available which provide in-depth information for ongoing research on these topics for interested readers (see section on Further Readings). Next we synthesize and discuss the sparsely available information about the community ecology and natural enemies of CLR around the world. We then present two case studies about CLR which we feel represent a more ecological (i.e. intelligible) approach to understanding the pathogen.

Technocentrism and control of the coffee leaf rust

The prevailing wisdom on control of CLR has long considered fungicides and resistant coffee varieties to be the two main factors to be explored, with the tacit assumptions that these two strategies will be the most effective (Talhinhas et al., 2017). There is a long history of developing and deploying fungicides with mixed results due to a variety of reasons ranging from the relatively fast evolution of resistance (Avelino et al. 1999), incorrect application technique (Belan et a., 2015), the economic costs to producers (Narayana, 2014) and environmental health concerns (Loland & Singh 2004). While fungicides have been shown to be an important component of pathogen management under certain circumstances (Virginio Filho, 2017), it is almost certain that application impacts non-target organisms that occur in coffee agroecosystems communities, such as mycoparasitic fungi that attack CLR (Vandermeer et al., 2009; Pico Rosado 2014). The extent to which fungicide application may have unintended consequences such as inhibiting biological control of CLR by fungal mycoparasites is not fully appreciated but preliminary evidence suggests this may be the case (Carrión & Rico-Gray 2002; Pico Rosado 2014). Apart from potentially interfering with biological control of CLR, there are examples of fungicide application benefiting other devastating pests of coffee, such as reports from Kenya that a popular triazol used to control CLR, resulted in promoting the Coffee Berry Disease (CBD) (Kushalappa and Eskes 1989, 100). A consideration of the ecology of the agroecosystem will be prerequisite to understanding how non-target effects of fungicide applications impact other pests as well as biological control agents in coffee agroecosystems.

In addition to the fungicides, the development of resistant coffee varieties has been thought to be an effective way of controlling CLR (Silva et al., 2006, McCook and Vandermeer, 2015). The history of this approach is long and complex, beginning with coffee's evolution under domestication. As a tetraploid, *Coffea arabica* is likely of hybrid origin from two diploid species, one perhaps similar to the other commercially important *Coffea* species, *C. canephora* (popularly known as Robusta coffee and a main source for instant coffee today). Prehistoric Arab traders brought *C. arabica* to Yemen from where it made its way, through international commerce, to south India, Sri Lanka and Java in the 1690s. Most modern varieties stem from two sources, the variety "Typica" transferred from Java to the botanical garden in Amsterdam by the Dutch in 1706, and variety the "Bourbon" taken from Yemen to Reunion Island and then on to South America by the French. Thus, only two original accessions, historically, provide a rather narrow genetic basis for further evolution under domestication (Ferwerda, 1976). One of the most popular modern varieties, extremely susceptible to CLR and planted extensively before arrival of CLR is "Caturra," derived as a single dwarf mutant in Brazil, from Bourbon stock. By the 1930s, it was acknowledged that variety of coffee had implications for the severity of CLR infection, and that there was also substantial genetic diversity of the CLR which could be classified into different strains or races. The CIFC rapidly identified several dozen CLR strains of varying virulence, and today more than 50 races of the pathogen are recognized (Talhinhas, et al, 2017). With the discovery that both the variety of coffee as well as the strain of CLR impact the outcome of CLR infection, a number of efforts spawned focusing on breeding of resistant varieties, and exist to this day.

Unfortunately, as early as resistant breeding programs arose, so did the observation that CLR can eventually overcome resistance (Mayne 1932). Although breeding programs have undoubtedly become more sophisticated through time, the loss of resistance for most and if not all varieties seems inevitable due to the relatively rapid evolution of CLR in response to selective pressures from varieties. The recent breakdown in resistance of the Lempira variety in Honduras in 2017, following almost 20 years of widespread use, illustrates how rapidly resistance can be overcome and the dangers of relying on a small number of varieties (Morales & Yonis 2018; Avelino & Records 2018). Although widely documented, the evolution of resistance presented somewhat of a paradox for biologists working on the CLR as the pathogen was long thought to clonally reproduce (Gouveia et al. 2005; Caralho et al. 2011), suggesting that the genetic variability needed to evolve the ability overcome resistance should be relatively difficult to attain. There have been a number of hypotheses proposed to explain CLR genetic variability, from cryptosexuality, based on evidence of meiosis in urediniospores (Caralho et al. 2011), to hybridization of different ancestral lineages of CLR that attack different species of *Coffea* species (Silva et al. 2018). While an active area of research, there seems to be an emerging picture that mechanisms of reproduction are likely not homogenous everywhere CLR is present (Ramírez-Camejo et al. 2021). The complex picture of the population genetics of the CLR around the world suggests the need for a regionally specific approach to understanding the dynamics of different CLR strains with different coffee varieties.

The community ecology of coffee leaf rust

The community of organisms associated with CLR has largely been considered a question of natural history curiosity rather than one of practical importance, something illustrated by the relatively small body of literature on this topic when compared to classical or technocentric research briefly described above. Rust fungi, evolutionarily a very ancient group, are known to have communities of organisms which regularly consume them (Anikster & Wahl

1979; Henke et al. 2011). Currently little is known about the general ecology of these assemblages of natural enemies of rust fungi and what, if any, impact they have on the dynamics of the pathogen. Better understanding these communities of natural enemies will likely have practical implications for our understanding of how rust fungi are controlled in both "natural" and agricultural settings. The context in which organisms are regulated in their native environment undoubtedly lends insight into the dynamics of how they escape control when exported elsewhere, something that has been long appreciated with classical programs in biological control. Understanding how and why pests and pathogens are released from control by natural enemies is an area of active research (Keane & Crawley 2002; Liu & Stiling 2006; Horrocks et al., 2020), but with regard to CLR little is known. We suggest that understanding the dynamics of CLR in the regions where it has been and remains "under control" can potentially shed light on how exactly it has escaped control historically in regions such as Sri Lanka and more recently in Central America, and where it might escape control in the future.

A growing body of work conducted in coffee's native range in Ethiopia sheds some light on the community ecology of CLR in its native range. With regard to CLR's natural enemies, Zewdie et al., (2021) collected three years of data on CLR and its fungal mycoparasite, *L. lecanii* and showed that there is a signature of top-down control of CLR. It was found that *L. lecanii* was most abundant in the wet season, and that its intensity in the wet season was negatively associated growth of CLR in the subsequent dry season, which is when CLR typically reaches its peak. Another recent study by Stüber et al., (2021) found that arboreal nesting *Crematogaster* sp. ants throughout parts of the coffee producing region of Ethiopia were associated with lower amounts of CLR. These studies provide to our knowledge the first reports of the community ecology of coffee and CLR in its native range.

Similar relationships with CLR, L. lecanii and arboreal ants are known from Mexico, and have been extensively studied, revealing a complex network of direct and indirect ecological interactions (see Vandermeer et al, 2009; Vandermeer et al., 2010; Jackson et al., 2012; Vandermeer et al., 2019). The similarities between these systems that have vastly different ecological and evolutionary histories suggests that generalities in interaction structures may exist and that interactions networks may assemble in introduced areas of coffee production that mirror those in the native range, as suggested earlier in a different context (Perfecto & Vandermeer 2015). Although similar work is sparse around the world, the little information that is available suggests potentially informative connections that span across novel ecological communities assembled in coffee agroecosystems.

While much remains to be understood about the community ecology of coffee agroecosystems in coffee's native range, much also remains to be discovered in the many regions around the world where coffee has been introduced and cultivated. As noted above, each introduction into a new region results in the assembly of a novel community with its own distinct assemblage of organisms and subsequent ecological dynamics. Simply documenting these communities could help piece together gaps in our understanding and serve as a basis to form hypotheses about the potential for control by natural enemies. Coffee researchers generally acknowledge the existence of these complex communities, but for a variety of reasons they are rarely reported in the literature. For example, *Cecidomyidae* consuming CLR in Latin America was not reported until 2016 (Hajian-Forooshani et al., 2016), although we have heard anecdotal reports of researchers having observed it for years in the region. It is likely the case that many more such ecological interactions are observed regularly but go unreported. Although potentially very important, creating incentives to report this type of information in the literature will likely be difficult, as documentation of natural history is seemingly less and less valued in the ecological literature and without direct practical application this information is similarly not highly valued in the agronomic literature.

As more information is accumulated about the organisms associated with CLR and their potential impact on the pathogen's dynamics, determining how environmental factors and management interact with this community of natural enemies will be exceedingly important. Given that CLR is a resource for its natural enemies, the first step is to understand how these factors impact the dynamics of CLR itself since that will constrain the natural enemy community. In short, although regionally variable, some generalities have emerged in our understanding of environmental factors and management impacts on CLR. For example, the negative relationship between attitude and CLR has been widely documented (Bock 1962; Avelino et al., 2006; Belachew et al., 2020; Zewdie et al., 2021). Various climatic factors such a participation and temperature are known to impact the development of the CLR as well (Brown et al., 1995; Avelino et al., 2015). Due to the interaction of temperature and precipitation on CLR, management factors which impact these variables have been proposed to be important for explaining realized CLR dynamics although there remains considerable controversy surrounding the topic. One of the most well-known examples of management in coffee agroecosystems is that of shade trees, which have shown variable effects in different systems with some finding positive impacts (Lopez-Bravo et al., 2012), others negative impacts on CLR dynamics (Soto-Pinto et al., 2002; Zewdie et al., 2020), and some finding an interaction of shade effects depending on context (Pico Rosado 2014). Shade trees in coffee agroecosystems present a variety of plausible pathways to impact CLR from increasing germination through microclimatic modifications

(Lopez-Bravo et al., 2012), decreasing wind speeds in coffee farms (Orozco & Jaramillo 1978), to modifying rain-drop kinetics below shade trees (Avelino et al., 2020).

While a nuanced and growing literature carefully teases apart these effects on the CLR itself, there is some information emerging as to how these same factors may impact natural enemies, and in particular attention has been paid to fungal mycoparasites such as *L. lecanii*. Recently Zewdie et al., (2021) found that higher levels of shade are associated with an increase in *L. lecanii* and Pico Rosado (2014) found similar results with shade favoring *L. lecanii*. Pico Rosado's (2014) results suggest that natural enemy control by *L. lecanii* is more effective than the fungicide application and that fungicides inhibit *L. lecanii* ability to grow in the field. With regard to other natural enemies, there is currently little known about how environmental factors or management may impact their distribution or ability to control CLR. Basic ecological theory suggests that in systems where there are multiple natural enemies consuming the same resource there will likely to be competition for that resource. In Puerto Rico gastropods have been documented as consuming CLR both in the field and laboratory settings, and the invasive snail, *Bradybaena similaris,* was also shown to consume *L. lecanii* infected lesions of CLR. The extent to which resource competition and intrigued predation between natural enemies in the field shapes ecological dynamics remains to be explored in detail although preliminary observations suggests they are important factors for the natural enemy communities Puerto Rico (Personal observations).

The natural enemy community of coffee leaf rust

Here we focus on summarizing the relatively small body of literature on the communities of organisms which are known to interact with CLR in various parts of the world.

Cecidomyidae

The first notes on what we might call the community ecology of CLR's natural enemies were published by H.F. Barnes when describing the species of *Cecidomyidae* associated with coffee (Barnes 1939). Barnes provides a taxonomic description of both the larvae and adult of *Mycodiplosis hemileiae* which lives among and feeds on CLR urediniospores in what is today Tanzania and Madagascar. Barnes also published notes from A.H. Ritchie on the ecology of *M. hemileiae* dated June 4th 1935 from the Boos' Plantation, Kaboia District, Bukoba, Tanganyika Territory. Ritchie provides a brief description of the life-cycle, noting patterns in pupation and population densities that reach as high as 25 to 30 larvae per leaf. He also gives some insight into the community of organisms indirectly associated with the coffee rust through interactions with *M. hemiliea*, describing a fungus that attacks larvae just prior to pupation which arrests development and results in the desiccation of the larvae. This unknown fungus is said to sporulate in the pupal webbing and sign of past attack is noted by the fawn to brownish color in the larvae. Mention of this fungus attacking *M. hemiliea* is absent from all subsequent literature, and has not been observed by the authors in Mexico or Puerto Rico. In addition to *M. hemiliea* being attacked by fungi, Barnes describes another *Cecidomyidae*, *Lestodiplosis sp.*, which he suggests is predaceous on *M. hemiliea*. Predation of *M. hemiliea* by *Lestodiplosis* sp. was not mentioned by Richie in his notes.

After Richie's initial observations of *M. hemiliea* in Tanzania and Madagascar, two *Cecidomyidae, Lestodiplosis sp.* and *Mycodiplosis sp.,* were reported to be commonly found in CLR pustules eating urediniospores in Kenya, (Crowe 1963), although it is unclear if these two species are the same as observed by Richie. It seems unlikely that *Lestodiplosis* is a fungus feeder given that most reports of species in the genus describe it to be an arthropod predator. In addition to noting these two natural enemies of CLR, Crowe makes note of two parasitoids that attack both species of *Cecidomyidae* larvae, *Leptacis kivuensis* Risbec and *Synopeas sp.* (Hymenoptera: *Platygasteridae*), and suggests that these parasitoids may be vectors of long range dispersal of CLR urediniospores. Crowe describes observations of the searching behavior of parasitoids within and around pustules with coffee rust and documents the accumulation of CLR urediniospores on their bodies. He found an average of 37 spores per individual and estimated the population of the parasitoids to be approximately 20,000 per acre. The next mention of *Cecidomyidae* associated with CLR came again from Kenya by D.L. Miline in 1975, where he notes relatively low densities of *M. hemiliea* (seven or eight per leaf), completely clearing leaves of rust spores (Miline 1975). Miline speculated that under certain conditions the larvae may play a role in controlling CLR stating:

> *"The coffee rust fungus unfortunately produces spores on such a prolific scale that even under conditions favorable for infestation by this midge, it is doubted whether the insect could ever be considered as more than a contributory factor to rust control. However in areas where rust infections are light, it is possible that M. hemileiae could play quite an important role in reducing the spore load."*

Given the potential for a *Cecidomyidae* community to contribute to the control of CLR, it is somewhat surprising that no subsequent work was done to understand the impact of these organisms on CLR dynamics. It took over forty years until *Cecidomyidae* associated with the coffee rust were mentioned again in the scientific literature, when they were noted in Southern Mexico and Puerto Rico (Hajian-Forooshani et al. 2016), although CLR researchers seem aware of its existence and potential to consume CLR. While the realized distribution of *Cecidomyidae* that consume CLR is unclear, it seems likely that in areas where they have been described (Mexico and Puerto Rico) they have likely been co-introduced with CLR. Analyses have shown that *Mycodiplosis* genera overwhelming tends to be rust species specific (Henk et al. 2011). This suggests that although there are likely native *Mycodiplosis* or other *Cecidomyidae* in both regions feeding on native rust fungi, the organisms found feeding on CLR are likely non-native. Work on both the molecular identification and population genetics of CLR-feeding *Cecidomyidae* could help elucidate their origins and potential as biological control agents.

Thrips

In Richie's summary published by Barnes (1939), there are brief notes on a number of thrips associated with coffee, but he makes particular mention of *Physothrips xanthoceros* feeding in CLR pustules. Since Richie's notes, various thrips associated with and potentially feeding on CLR have been mentioned sporadically throughout the literature of the 20th century (see references in Kushalappa & Eskes p. 163-164), but largely dismissed, seemingly in absence of detailed observational or experimental work. Knowledge of the ranges and occurrences of thrips associated with CLR mainly come from taxonomic descriptions. Interestingly some of these thrip species seem to be relatively widespread and associated with CLR. Two African species *Craspedothrips antennatus* and *C. xanthocerus* have been found in Uganda, Kenya, Tanzania, and Angola (Mound 2012). Additionally another thrips, *Megaphysothrips subramanii,* was recently observed in Timor Leste and was said to be found exclusively in pustules of CLR and not exploring any other portions of the coffee leaf (Mound 2018). *M. subramanii* was found to be covered in CLR urediniospores and it is suggested that *M. subramanii* consumes CLR to complete its life cycle while not causing feeding damage to coffee leaves themselves.

Mites

Coffee is known to host a community of mites that are likely facilitated by the presence of acadomatia on some coffee leaves. While these mites have a variety of life histories, some of them are associated with CLR. Flechtmann (1976) first suggested that the mite *Ricoseius* *loxocheles* feeds on CLR, and recently a detailed study of its biology and behavior was reported by Oliveira et al. (2014), including the important observation that for the females to oviposit, they need to be fed a diet that includes CLR rust urediniospores. Once eggs are ovipoisted in pustules of CLR urediniospores, they are covered in additional CLR urediniospores and take about nine days to develop from egg to adult. It is suggested that *R. loxocheles* is a specialist on CLR, given it would not consume alternative food sources common to predatory mites (specifically *Oligonychus ilicis*). It was additionally noted that *R. loxocheles* exhibited the behavior of carrying CLR urediniospores on its body.

It is unclear how widespread *R. loxocheles* is in coffee producing regions around the world. While the only published data we are aware of comes from Brazil, we have personally made observations of mites associated with CLR both in southern Mexico and throughout the central coffee producing region of Puerto Rico. While we have not identified the species of mite, the description of behavior from both Flechtmann (1976) and Oliveira et al. (2014) suggest it is likely *R. loxocheles*. The behavior of laying eggs and aggregating in pustules of CLR urediniospores as well as coating their bodies in urediniospores has been observed numerous times in both regions. In Puerto Rico, these mites are widespread across the island and quite commonly found on rust infected leaves (personal observations). While seemingly the same mites occur in Southern Mexico they are less common than in Puerto Rico.

Gastropods

Although gastropods are not widely known to consume rust fungi (although see Ramsell and Paul 1990) , both field surveys and laboratory experiments have recently shown gastropods to consume CLR in Puerto Rico (Hajian-Forooshani et al. 2020). Bright orange excrement left behind on leaves was found to be associated with leaves cleaned of urediniospores and were identified as being from gastropods consuming CLR. Laboratory experiments conducted with

Bradybaena similaris showed that the snail consumes CLR as well as the mycoparasitic fungus *L. lecanii*, approximately halving the percentage of the coffee leaf covered in CLR urediniospores in 24 hours as well as reducing the *L.lecanii* coverage. *B. similaris* as well as other unidentified gastropods (see Hajian-Forooshani et al. 2020 for photographs), are widespread across the coffee producing region in Puerto Rico (personal observations), but it is currently unknown if or to what extent they may be altering the dynamics of CLR on the island.

Notably, *B. similaris* is a non-native species that has been introduced to Puerto Rico as well as a number of other coffee producing regions and is often considered a pest in various forms of agriculture (Idris and Abdullah 1997). Many questions remain unanswered regarding the impact that *B. similaris* and other gastropods may have in other parts of the world. Given its widespread distribution it seems likely that they may consume CLR in other parts of the world, although thus far no other reports are in the literature. Additionally, and of potential importance, it is unclear if spores are viable after passing through the digestive system of these gastropods.

Mycoparsitic fungi

The first report of mycoparasitic fungi attacking CLR came from Stanleyville Congo in 1929 (Seyert 1930). Seyert notes that when strolling through coffee plantations near the railroad they were examining CLR on plants (he notes that coffee rust was rare in the region) and noticed a blackish (*noirâtre*) mass in the center of CLR lesion. Upon examination under the microscope they discovered that the mycelia was not in the host plant tissue but surrounding the urediniospores of CLR. Seyert denotes a new species, *Cladosporium Hemileiae n.sp.* (now *Digitopodium hemileiae* see Heuchert et al. 2005) and notes that this first record of a mycoparasite of CLR could very well contribute to efforts to control the pathogen (Seyert 1930). Since this initial documentation, there is growing appreciation of a highly diverse and widespread community of CLR fungal mycoparasites occurring across the globe which likely has the potential to impact coffee rust dynamics (Pirozynski 1977; Lim & Nik 1983; Shaw 1988; Kushalappa & Eskes 1989; Carrión & Rico-Gray 2002; James et al. 2016; Gómez-De La Cruz et al. 2018; Colmán et al. 2021).

Given that over 15 fungal mycoparasites of CLR have been documented (see references above), to what extent they may contribute to control of the coffee rust has been a point of inquiry for many researchers and practitioners. Within coffee's native range, the well-known mycoparasite *L. lecanii* is widespread (Zewdie et al., 2021), as in the Central African Republic (Kushalappa & Eskes 1989 p.163). Outside of coffee's native range, many fungal mycoparsites have been documented. Carrión and Rico-Gray (2002) note that the region in Mexico where they documented six mycoparastic fungi, does not use fungicides for CLR due to its low prevalence in the region. They speculate that this community of fungal antagonists may play a role in controlling CLR in the region. Furthermore, Carrión (1989) compared the attack by *L.lecanii* in two states in Mexico, Veracruz and Chiapas, and found that Veracruz which had less CLR had 21.2% attack by *L. lecanii* as compared to Chiapas which only had 2.9% attack. A similar comparative study was done with Mexico and Puerto Rico and found similarly that regions with lower CLR had a higher attack rate by *L .lecanii* (Hajian-Forooshani et al. 2016). Aside from observational studies there is mixed evidence that this mycoparasitic community of fungi could be manipulated to control CLR in the field. Laboratory experiments show that CLR urediniospores can be inoculated with *L.lecanii*, but with mixed results (Carrión & Ruíz-Belin 1988). Some field trials have successfully demonstrated the efficacy of *L.lecanii* (Carion 1988), while others showed mixed to no results from field applications of *L.lecanii* and *Vertucillium leptobactrum* (Kushalappa & Eskes 1989 p.165-167).

Mixed results in field and laboratory manipulations may be a result of isolating this mycoparasitic community from the context of the interactions in which it is typically embedded. Research in southern Mexico emphasized the fact that *L. lecanii* is a natural enemy not only of CLR, but also of the green coffee scale (*Coccus viridis*), suggesting the potential for complicated indirect effects, where the scale insect might provide a reservoir of *L. lecanii* that would attack the coffee rust (Vandermeer et al. 2009; Vandermeer, et al., 2012; Jackson et al., 2012; Galvão and Bettiol, 2014). The community of alternate hosts of *L.lecanii* in particular is widely acknowledged (Jackson et al., 2012), and understanding the dynamics of host utilization under different biotic and abiotic conditions will likely shed light on the potential for mycoparasites to control CLR. In addition to insects as alternative hosts for *L. lecanii*, the mycoparasite, *Digitopodium tectonae*, discovered in 1930 by Seyert, has been reported attacking an alternative rust host *Olivea tectonae* in Brazil (Colmán et al. 2021).

It is clear that a complicating factor in most field studies of CLR mycoparasites is a lack of certainty in their identification. For example, Carrión & Rico-Gray (2002) document five fungal mycoparasites of coffee and note that all of them are white to some extent when cultured. One notable expectation from the white colored fungal mycoparasites is *Cladosporium hemileiae*, described as olive brown by Kushalappa & Eskes (1989 p.163), and blackish by Seyert (1930). James et al. (2016), highlighting the inadequacy of visual identification of mycoparasites in the field, used molecular methods to identify fungal communities from samples of rust lesions that contained apparent mycoparasites in Mexico and Puerto Rico, finding 15 species of fungi belonging to clades that contained at least one species of known mycoparasite. In James et al. (2016) sampling material was simply collected from CLR lesions that had white fungal growth on them. These results suggest that the true identities of fungal mycoparasites are likely obfuscated from simple field identification, and what often looks like a single white mycoparasite is in fact harboring a cryptic community of which we know relatively little. Microscopic structural and morphological characterizations of these fungal mycoparasites may also offer little hope of elucidating the true diversity given what seems to be convergent evolution of structures (Colmán 2021). While documentation of the fungal communities associated with *Coffea* is ongoing (see Vega et al. 2009; James et al. 2016), it is clear that much remains unknown about these communities and their potential impacts on the dynamics of CLR around the globe. Approaches that prioritize not only identification but also elucidation of the ecology of these fungal communities will be particularly informative.

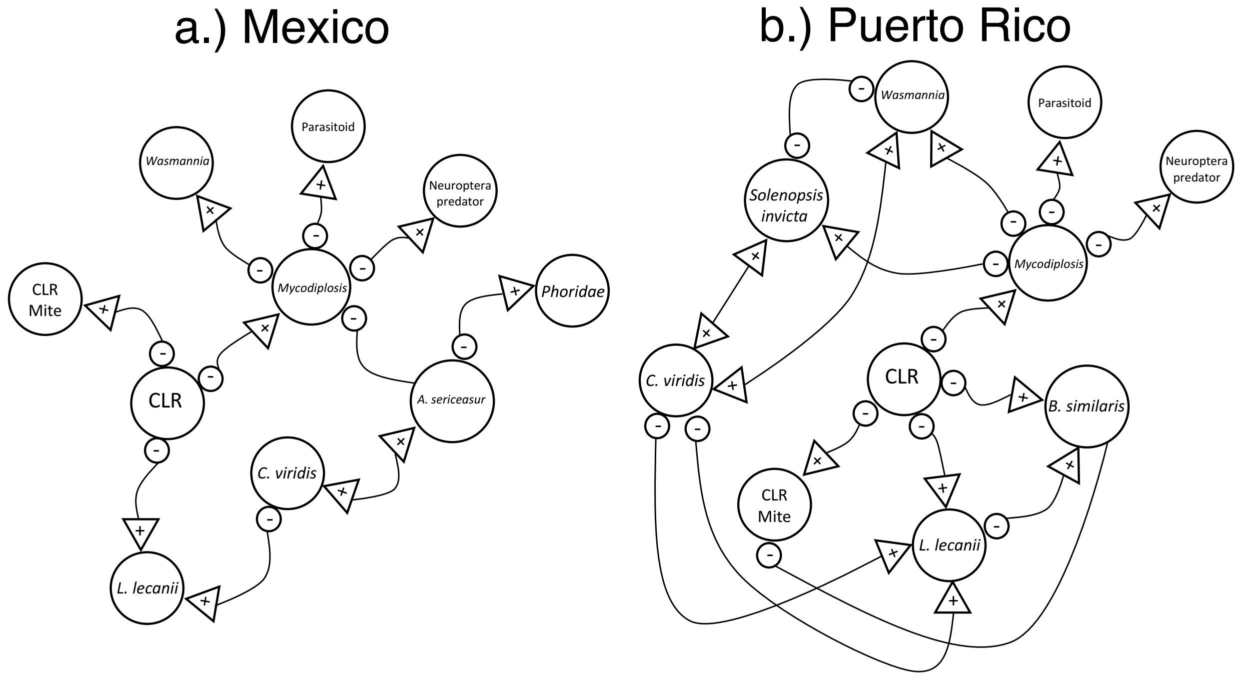
Case studies of ecological complexity and the coffee leaf rust

The regionally distinct ecological communities of Puerto Rico and Mexico

Almost all forms of agriculture involve the construction of a novel ecosystem to some extent (Perfecto and Vandermeer, 2015a). One of the most common ways to construct an agroecosystem, involves the transplanting of a plant or animal away from the context in which it evolved and placing it into a new ecological region. Coffee provides an example of one such system where the plants evolved in Eastern and Central Africa, and were subsequently transplanted for cultivation throughout the tropics and sub-tropics, where it resides in new ecological contexts. From an ecologist's perspective, any attempt to understand the dynamics of agroecosystems should be an attempt to understand the dynamics of how new interactions develop and play out through time in novel ecological settings. An appreciation of this is seen in both the ecological and agronomic literature, although cross fertilization between these two bodies of work is rare. The ecologist, Donald Strong, illustrated how quickly new interactions develop in agroecosystems through a series of papers in the 1970's which analyzed the accumulation of herbivores through time in several agroecosystems (Strong 1974; Strong et al. 1977; Strong 1979). He failed to find a signature of "time since introduction" of different crops on the number of herbivores reported feeding on them. Rather, the area in cultivation was the main predictor of the number of novel herbivores. These studies highlighted just how quickly agroecosystems can assemble themselves when introduced species (crops) interact with the surrounding biodiversity in which they are embedded. In addition to Strong's work, there is a growing understanding of how rapidly new interactions can form in ecological time (Agosta 2006; Agosta & Klemens 2008; Agosta et al. 2010; Nylin et al. 2018). We suggest that the dramatic differences in the dynamics of agroecosystems around the world may have more to do with the ecological context in which they are imbedded than is traditionally appreciated.

The apparent difference in the dynamics of the CLR in Mexico and Puerto Rico provides an example of the idiosyncratic dynamics of this pathogen in different parts of the world. These two locations were met with vastly different fates in recent times, where Mexico (along with other counties in Mesoamerica) experienced the epidemic of "the Great Rust" but Puerto Rico has been largely unscathed by island-wide outbreaks. This simple observation raises the obvious question of what is responsible for these vastly different outcomes? One may be inclined to focus on possible distinctiveness in abiotic conditions, searching for correlations in rainfall, humidity, and temperature to explain the apparent differences. While these factors have been extensively studied (Avelino et al. 2015), there is mixed evidence for their effect and no definitive smoking gun that explains why we see such drastic differences in the recent dynamics of the pathogen in one region but not the other. In fact, one recent study by Bebber et al. (2016) suggests that climate factors alone are insufficient to explain CLR dynamics. While we acknowledge that approaches that prioritize investigation of abiotic factors are important, we argue that a community ecological perspective which focuses on differences in the ecological communities of natural enemies between different regions may lend additional insight into the variable dynamics of CLR around the world.

Strong’s original analyses illustrated how distinct agroecosystems can be assembled depending the local ecological communities, tropical crops such as coffee tend to be cultivated in some of the most biodiverse regions of the world, suggesting that there is potential for a large number of novel interactions to arise quickly in areas of cultivation. There is now extensive documentation of the ecological communities in coffee agroecosystems in Mexico and Puerto Rico (Perfecto and Vandermeer, 2015; Vandermeer et al., 2019), including natural enemies of CLR. This documentation permits study and speculation on how these uniquely assembled ecological communities and interaction networks may be impacting regional dynamics of CLR (Figure 1.).


a.) Mexico

b.) Puerto Rico

Figure 6.1: The regionally distinct communities associated with the coffee leaf rust in Mexico and Puerto Rico. Links between organisms denote interactions, with triangles showing positive effects and circles negative effects. Note that interaction networks are constructed from personal observations by the authors in both field and laboratory settings.

In a comparative study between coffee farms in Puerto Rico and Southern Mexico it was found that the attack rates, (or the proportion of each natural enemy to CLR lesions on leaves), was 3.8% in Mexico and 32.2% in Puerto Rico for *Mycodiplosis sp.*, and for *L. lecanii*, 8.7% in Mexico and 61% in Puerto Rico (Hajian-Forooshani et al. 2016; 2022). Early work in Mexico, suggested that attack of *L. lecanii* on CLR may be mediated by indirect interactions with a dominant arboreal ant, *Azteca sericeasur* (Jackson et al., 2009; Jackson et al., 2012). Another coffee pest, the green coffee scale insect (*Coccus viridis*), has a mutualistic association with this arboreal ant and can reach high local population densities when under ant protection (Vandermeer at al. 2010). As with many other pathogens, when a host population becomes sufficiently large, epidemic outbreaks become more probable, and this is the case with the green coffee scale and *L. lecanii* (Vandermeer and Perfecto, 2019*)*. Studies in Mexico demonstrate that in sites where the *A. sericeasur* nests are present, *L. lecanii* attack on CLR is more common the following year, likely a consequence of *L. lecanii* building up on the green coffee scale populations and spilling over to attack CLR (Jackson et al. 2012a). Additionally, laboratory experiments suggest that *L. lecanii* can be dispersed by *A. seriseasur* (Jackson et al. 2012b). Thus, though various indirect and complex interactions, a native ant in Mesoamerica has a positive impact on a biological control of a pathogen which is presumably from eastern Africa. An additional complication is that although *A. sericeasur* has a positive impact on *L. lecanii* it seems to have a negative impact on the abundance of *M. hemileiae* (Hajian-Forooshani et al., 2016). It was found that coffee plants around trees where *A. sericeasur* was nesting had fewer *M. hemileiae* but interestingly no difference in the amount of CLR on plants. These results illustrate how the ecological contexts in which crops and their natural enemies are embedded influence them differentially and may have the potential to shape pathogen dynamics, such as those of CLR.

Coffee farms in both Mexico and Puerto Rico largely share the same suite of natural enemies, although there are some exceptions (see Hajian-Forooshani et al., 2020), yet the relative abundances of the various organisms are dramatically different. Years of personal observations in both systems from 2013-2021 suggests that *L. lecanii* and the CLR-dwelling mites *R. loxocheles* tend to be far more common in Puerto Rico than Mexico while *M. hemileiae* tends to be more common in Mexico. It is likely that these realized differences in abundances emerge from their interactions not only with their resource(s) (including CLR) but also from the plethora of interactions they take part in with the associated biodiversity within the coffee agroecosystems. From our experience, many interactions have been noted in the field although not yet formally reported in the literature which include parasitism of *M. hemileiae* by unidentified parasitoids in Mexico and Puerto Rico, predation of *M. hemileiae* by a neuropteran larvae in Mexico, and predation of *M. hemileiae* by a number of ants in Mexico and Puerto Rico. While the extent which these interactions impact the population dynamics of these potential biological control agents is currently unknown, it seems plausible that the accumulated impact of these diverse interactions could have consequences for the dynamics of CLR

Theoretical perspectives on space and environmental forces

Classic ecological models highlight how a consideration of space can fundamentally alter our understanding and intuition about the dynamics of ecological systems (Tilman & Kareiva 1997), and this is especially true for disease ecology where space can take a central role in governing disease dynamics. Relatively little has been done to understand the spatial ecology of CLR outside of understanding its modes of transmission, although there is a growing appreciation that space plays a central role in CLR dynamics (Rosas et al., 2021; de Carvalho et al., 2009). Given that coffee plants often have characteristic spatial arrangements and that several management factors are understood to interact with transmission (e.g. shade), focusing on the spatial ecology of the CLR can potentially lead to insights on how to better manage coffee agroecosystems with regard to the pathogen. Here we highlight some theoretical approaches to understanding the dynamics of CLR and highlight findings about the spatial ecology of CLR. We suggest that additional theoretical work on understanding the dynamics of CLR in space may be fruitful path forward to understand how the pathogen operates locally, within landscapes, and at a regional scale.

When considering CLR, some ecologists have abstracted the pathogen as operating at two distinct but interacting spatial scales. Perhaps most evidently, the pathogen spreads at a local scale from plant to plant within a given area, but in addition to this neighbor-to-neighbor spread, it can disperse large distances in wind currents. Avelino et al. (2012) highlighted how larger scale regional transmission can be related to management of surrounding landscape of coffee production. They found that the amount of pasture in the surrounding landscape was associated with higher CLR within farms. Exploring the often-non-intuitive implications of both the local and regional scale transmissions interacting has been a focus of recent theoretical explorations of CLR.

Vandermeer & Rohani (2014) used an understanding of the two scales of pathogen transmission to model the CLR. The basic idea behind their dynamical model is that there is an interaction between pathogen spore reservoirs at regional and local scales. CLR is modeled as building up within farms through the local transmission dynamics of rain splash and plant-to-plant contact, and as the reservoir of pathogen spores builds on a farm it feeds into the regional atmospheric environment's reservoir of spores which can be transmitted larger distances and "rain down" to infect other farms in the region. Using a modified patch-occupancy approach, they model both the portion of bushes infected within a farm and the proportion of farms infected within a region. Their results suggest three qualitative possibilities exist for the dynamics of the CLR which depend on the underlying parameters of the model which include: the bush-to-bush infection rate, the recovery rate of bushes, and the infection rate of farms. Depending on these parameters they find that the regional dynamics CLR can either be persistently absent, persistently epidemic, or a combination of absent and at intermediate infection levels depending on the initial conditions of the system. Furthermore, they explore how socioeconomic drivers that influence the number of farms within a region (e.g. the international market price of coffee) impact the overall dynamics of the CLR and find that evidence of tipping-point behavior regardless of different dispersal environments (i.e. high or low dispersal environments). This tipping-point or catastrophic transition behavior seems to robustly emerge from the interaction of the two scales of transmission as was illustrated by Vandermeer, Rohani and Perfecto (2015) who incorporated the additional effect of shade on modifying local dispersal of the CLR.

While the above studies employed a spatially implicit approach to understanding how multi-scale transmission impacts CLR dynamics, there have also been spatially explicit approaches to understanding CLR dynamics. Vandermeer et al. (2018) first used spatial networks to empirically infer the local transmission dynamics of CLR in Mexico. Hajian-Forooshani and Vandermeer (2021) employed spatial networks to explore the dynamic process of how spatial pattern is created in coffee agroecosystems and subsequently how that spatial pattern influences the pathogen dynamics. Beginning with the abstraction of a local area of coffee production with plants arranged in a approximate lattice formation, they allowed for stochastic death of plants, followed by imperfect replanting in a local neighborhood of the recently killed plant. The simple model of stochastic plant death and replanting created a range of spatial patterns that resembled the range of observed empirical spatial distributions of coffee plots on a farm in Mexico. They found that the empirical plots show a similar time-dependence of the spatial organization as observed in the model, where newly planted areas on the farm are better approximated by a lattice-like spatial distribution and older areas have more random-like distributions of plants. To understand the impact of different spatial patterning of plants on the dynamics of the CLR they modeled pathogen spread on the spatial patterns that emerged from the death and replanting model. By exploring a wide range of parameters combinations, they found that more lattice-like spatial patterns are susceptible to small changes in the spatial scale of CLR transmission, resulting in pathogen epidemics. It is suggested that these small changes in transmission scale can emerge from changes to management practices that interact with transmission, such as the amount of shade in a system.

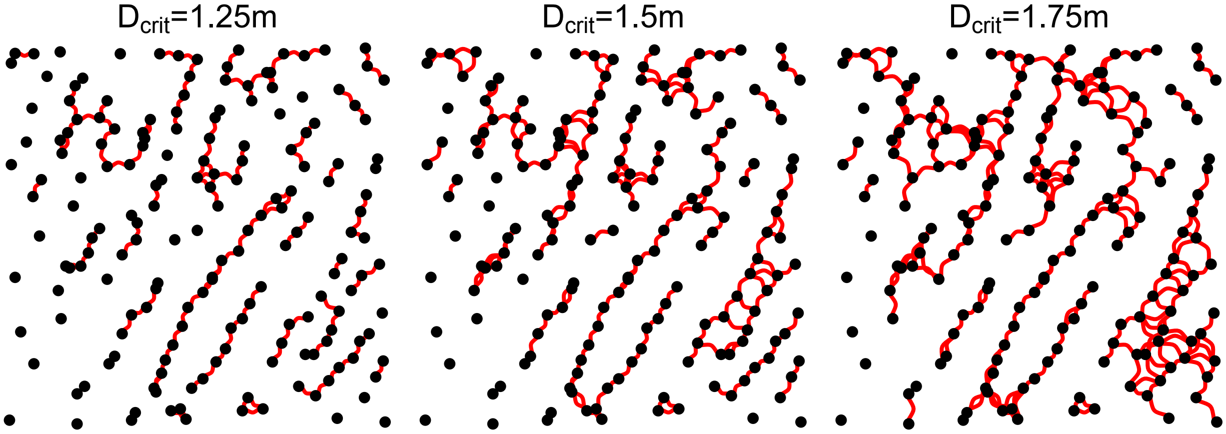


Figure 6.2: The network approach adopted by Vandermeer et al., (2018) and Hajian-Forooshani et al., (2021) to spatially explicitly model CLR. Black points show the distribution of coffee plants from a 20mx20m plot in southern Mexico. The red lines connecting the black points are stipulated by D_{crit} (denoting critical distance) and illustrate theoretical connections between plants, and thus tendency for local pathogen spread. This network approach has been used to estimate CLR transmission distance (D_{crit}) in empirical data (see Vandermeer et al. 2018 for details) and provides information such as the number of "outside infections" necessary to infect an area and the speed of pathogen spread across an area (see Hajian-Forooshani et al. 2021 for details).

Another recent spatially explicit modeling approach by Beasley et al., (2020) focused on the regional dynamics of CLR. They use a stochastic cellular automata approach to model the dynamics of CLR across heterogeneous landscapes. By incorporating different habitat types in the landscape to simulate the known impact of pasture land on CLR dynamics (Avellino et al. 2012), they explore how regional landscape composition interacts with the local dynamics of the pathogen. They found that the clustering of coffee plants at a local scale is one of the most important factors in the model, but that this interacts with the spatial distribution of deforestation in the landscape. Areas in the model where deforestation is more clustered resulted in more severe epidemics than when deforestation was more uniform across the landscape. This larger scale and spatially explicit approach to modeling the CLR highlights the importance of not only local dynamics but also how both coffee producing and non-producing areas together have implications for CLR.

Further reading

The scope of this chapter has been made intentionally narrow as to focus on what the authors consider to be potentially fruitful areas of research which they hope to bring attention to the larger community of coffee researchers as well as other agroecologists. Below we briefly recommend resources for more in-depth presentations on various aspects of CLR research and point readers in the direction of various researchers and research groups working with CLR which the authors find their approaches particularly informative.

Kushalappa and Eskes provided a comprehensive reference text on CLR with their 1989 monograph *Coffee Rust: Epidemiology, Resistance, and Management*. Various aspects of the biology of CLR can be found there as well as a wealth of information regarding control strategies among other topics. For a more recent and succinct treatment of CLR, readers should be aware of *Prevention and control of coffee leaf rust: Handbook of best practices for extension agents and facilitators* by Elias de Melo Virginio Filho and Carlos Astorga Domain (2019) from CATIE, which details more recent information regarding the ecology of the CLR (including some information on fungal mycoparasites) and best practices for management. For an excellent analysis of the history of the coffee rust see Stuart McCook's 2019 book *Coffee is Not Forever*. The ongoing work of Jacques Avelino and his research group has been cited throughout this chapter and his bibliography offers several insights in CLR's ecology. Ongoing work in Ethiopian coffee agroecosystems by Kristoffer Hylander and Ayco Tack's research groups at Stockholm University provide a unique ecological perspective on CLR in its native range. The authors feel that continued work by these two groups in Ethiopian coffee could particularly informative in developing a more ecological approach to understanding CLR.

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Chapter 7 Novel Community Assembly and the Control of a Fungal Pathogen in Coffee Agroecosystems

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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.

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, 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; Perfecto and Vandermeer, 2015). 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.

Methods

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 344m AMSL to 887m AMSL, while in the six sites in Mexico elevation ranges from 900m AMSL to 1150m 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 (Nelson, 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., 2012; 2012a; Vandermeer et al., 2009; 2014; Hajian-Forooshani, 2016; Gomez-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 loxocheles*) which is known to consume CLR spores and complete its lifecycle in patches of CLR spores (Oliveira et al., 2014). *R.*

loxocheles 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 similaris*, 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. similaris* 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.

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. loxocheles),* and the number of leaves containing gastropod feces with CLR spores (presumably from *B. similaris* 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, with 25 10x10m plots in Puerto Rico along with three 20x20 plots on a single farm, and six 20x20 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 300ha each in comparison to approximately 10ha 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.

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).

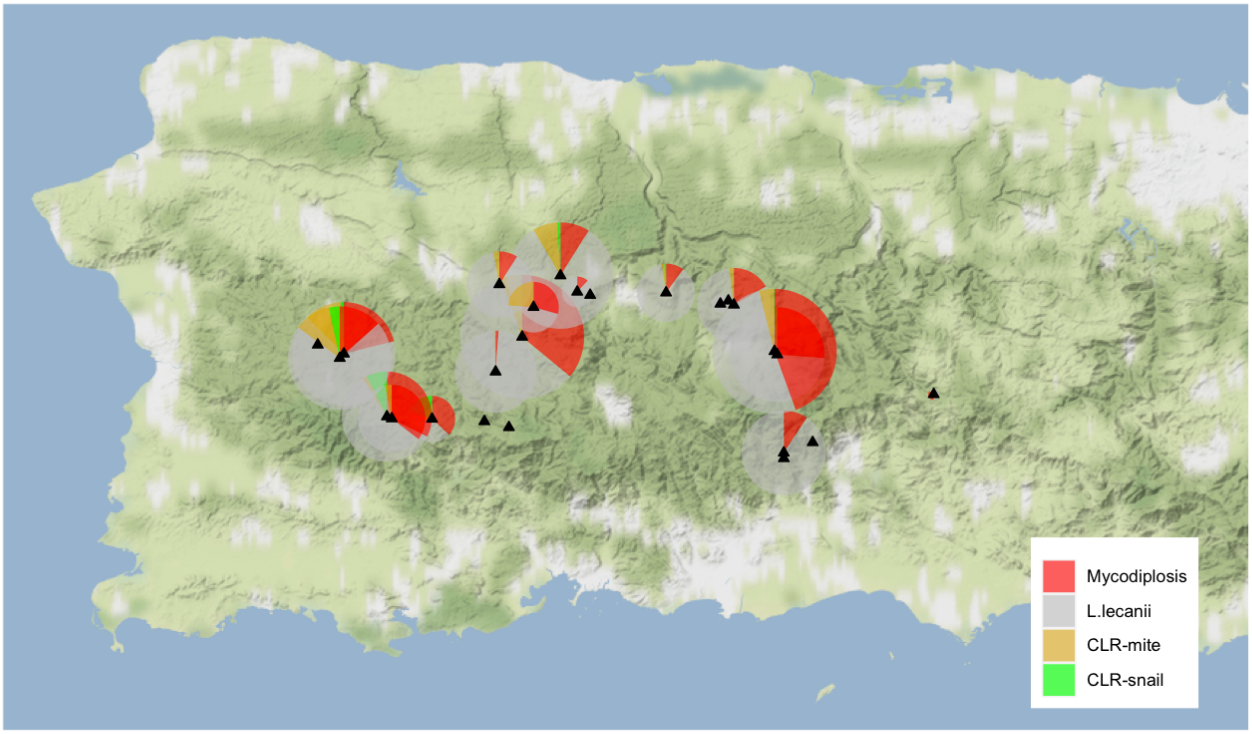

Figure 7.1: Abundance of coffee leaf rust (CLR) and the community of its main natural enemies, across the region in Puerto Rico, where the size of the circles is proportional to the average amount of CLR from a 12-month cycle of collected data. The fills of the circles represent the average composition of natural enemy communities throughout the 12-month cycles. Red – Mycodiplosis (M. hemileiae); grey – L. lecanii; gold – CLR-mite (R. loxocheles) and green – CLR-snail (B. similaris and other CLR consuming gastropods)

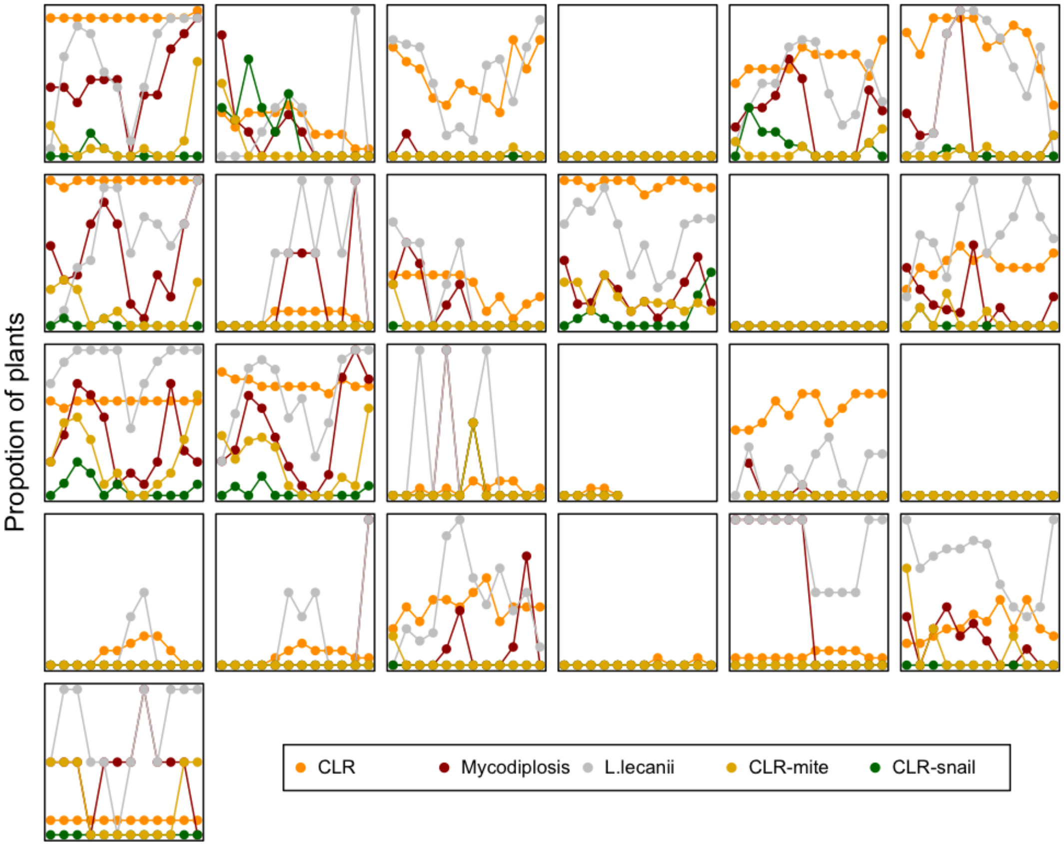

Figure 7.2: Distribution of the coffee leaf rust (CLR) and its community of natural enemies across 25 farms in Puerto Rico. On each of the 25 farms surveyed, 20 individual plants were monitored for a year. Each plot shows the proportion of the 20 plants infected with CLR and the proportion of CLR-infected plants with natural enemies present. The y-axis ranges from 0-1 and the x-axis represents each of the 12 months from the survey ranging from August 2018-July 2019.

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.

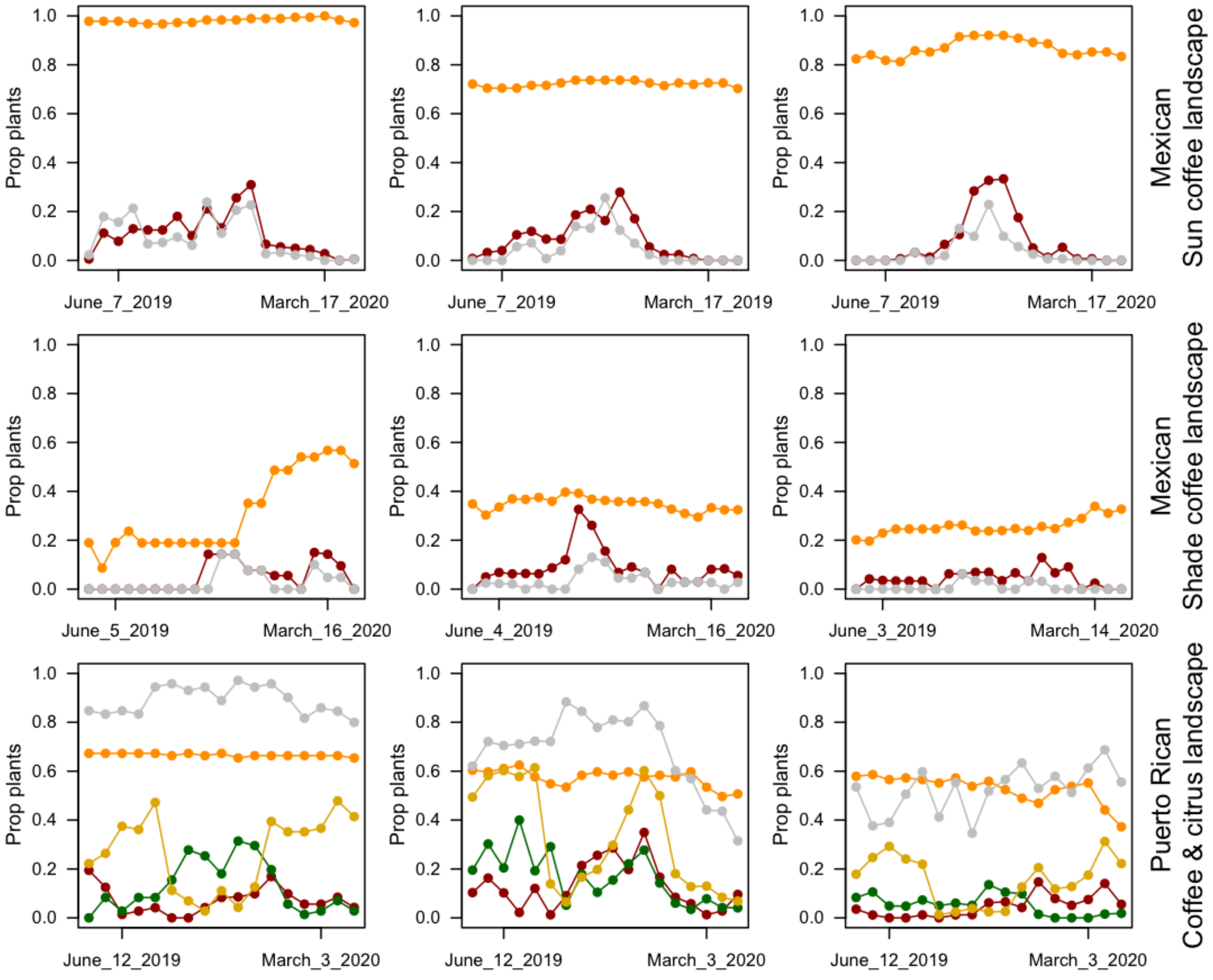

Figure 7.3: Data from fine scale surveys (20x20m plots surveyed biweekly) in Mexico and Puerto Rico. Each point represents the proportion of plants that have CLR (orange), Mycodiplosis hemiliea. (red), Asian tramp snail (green), the CLR-mites (gold), and L. lecanii (grey). Note that the farm in Puerto Rico was chosen (out of the 25 sampled) for this detailed study because it was the farm with the highest incidence of CLR.

An additional pattern is evident from the time series on the 20x20m 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 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.

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?

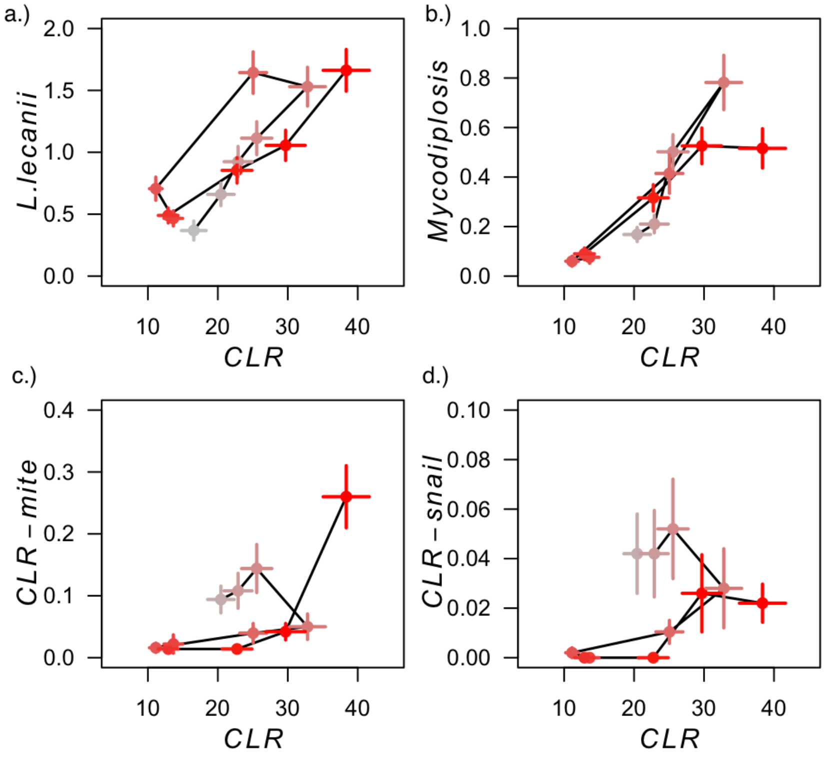

Figure 7.4: Consumer-resource phase diagrams of the coffee leaf rust (CLR) and its natural enemies throughout Puerto Rico. Each point represents a monthly mean across the 25 sampled farms and colors represent the progression of time, with grey being August 2018 and bright red July 2019. a.) is the mean 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. loxocheles), and d.) the mean number of leaves with CLR-snail (B. similaris) excrement. Note that panel a.) with CLR-L.lecanii exhibits a counter-clockwise oscillation as expected from a consumer-resource interaction.

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., 2012; 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 a 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 (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 exact 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.

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Supplementary Material

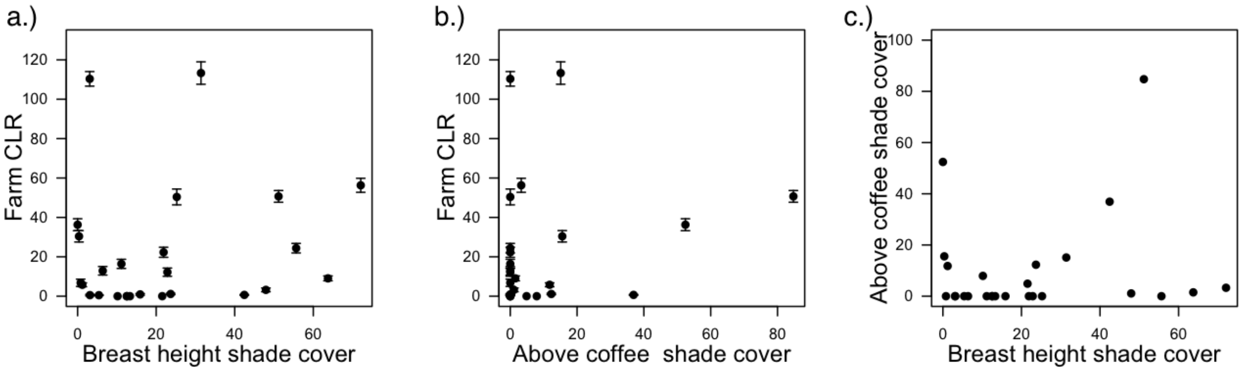

Figure 7.5: Relationship between shade measurements and amount of coffee leaf rust on a farm. Two different measures of shade were taken across the 25 farms used in the study. Panel a.) shows cover calculated with a spherical densiometer at breast height and b.) shade cover calculated above the coffee plants with a spherical densitometer. Both a.) and b.) show no significant linear relationship with the mean amount of coffee leaf rust found on the farms (a. p =0.457, b. p=0.300). c.) shows the relationship between both measures of shade cover on farms.

Chapter 8 The Role of Spatial Hierarchy in the Assembly and Structure of a Coffee Pathogen's Consumer Community

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Abstract

Spatial scale has long been a confounding factor in ecologists attempt to understand both ecosystem processes and community dynamics. Here we use a fungal pathogen and its community of four consumers in an attempt to understand how ecological communities respond to and interact within hierarchically nested patches in ecosystems. We employ three distinct hierarchical levels of analysis to understand the relevant scales for determining the dynamics of community assembly and organization in this system. By using two separate periods in the epidemic cycle of the pathogen, we capture the community assembly dynamics when the pathogen is at relatively low densities in the early infection period, then capture signatures of community interactions during the mid-infection period when the pathogen densities are higher and the community competes for their resource. We show how the community of consumers depletes the pathogen spores throughout the epidemic cycle representing an important dynamic feedback in the system where consumer activity modifies the patch distribution they consume.

Introduction

Spatial scale has long been a confounding factor for ecologists attempt to understand ecosystem and community processes and dynamics (Allen and Starr 1986, O'Neil et al 1986, Wiens 1989, Kotliar and Wiens 1992). Conflicting conclusions about the processes operative within ecological systems have been shown to be due at least in part to the various spatial scales in which they are under study, with both empirical (Levin 1992; Koliter and Weins 1992; Weins 1989) and theoretical examples (Viana and Chase 2019) highlighting the importance of taking a multi-scale approach in ecology, since organisms and processes may be scale dependent and even interact across scales (Johnson et al, 1992; Lin & Pennings 2017; Kotlier & Wiens 1990).

While there exist a variety of organizing metaphors for incorporating space (and therefore scale) into ecological theory, a discrete, patch-like framework for understanding the spatial organization of environments and the organisms which occupy them has been common in ecology and has arguably led to most of the dominant paradigms in the field (Levins 1969; Wilson 1992; Wiens et al. 1993; Leibold et al 2004; Leibold & Chase 2018). Although patch-like frameworks are common, a strict definition of what should be considered a patch in some systems isn't entirely clear. As noted by Weins (1976), what an ecologist considered a patch should necessarily be defined from the perspective of the organism which utilizes it. In ecological communities, which are composed of multiple interacting organisms, the question of patch definition then becomes even less clear. Additionally, the scale-dependent ecology of different organisms in communities complicate matters further.

The joint consideration of spatial scale and a patch-like framework has been abstracted as patches nested inside other patches in a hierarchical fashion (Kotlier and Wiens 1990). In the Kotliar and Wiens framework, the embedding of nested patches in others is referred to as "levels" and can be distributed across a range of continuous spatial scales. Understanding how communities respond to and interact across these levels and scale within this hierarchical patch framework is relatively poorly understood and not frequently addressed in the literature despite the various ecosystems and communities which naturally lend themselves to this framework. One such system that illustrates the hierarchical spatial organization of patches, is the structure of plants, where they can be abstracted discrete entities hierarchically embedded at multiple spatial scales, where discrete leaves are distributed within discrete plants which are distributed with an area in space.

Here we use a fungal pathogen that attacks plant leaves and its community of four consumers which have to navigate the heterogeneous pathogen distribution across hierarchical levels, to attempt to understand how ecological communities respond to and interact within hierarchically nested patches. Our model system of the coffee leaf rust (hereafter referred to as CLR), *Hemleia vastarix*, and its community of consumers in Puerto Rico is particularly well-suited to the study of the role of spatial scale and hierarchy in governing the dynamics of ecological communities due to the variety of natural histories encompassed within the community. The community is comprised of the Dipteran, *Mycodiplosis hemealiea*, whose larval stage is a specialist in CLR spores (Barnes 1939; Milne 1975), the parasitic fungus, *Lecanicillium lecanii*, a generalist fungal parasite that attacks both fungi and insects (Vandermeer et al, 2010; Jackson et al, 2012), the mite, *Ricoseius loxocheles* (referred to here as the CLR-mite), which consumers and completes its life-cycle in lesions of CLR but also utilizes other resources such as pollen (Flechtmann 1976; Oliveira et al., 2014; Ajilaet al., 2018), and finally a community of gastropods (including *Bradybaena similaris*) which are likely opportunistically consuming CLR (Hajian-Forooshani et al, 2020).

The interactions between the CLR and its associated community of consumers are necessarily realized at the scale of an individual leaf where the consumer ultimately encounters its resource. Although this is a truism of all consumer-resource interactions, the community of consumers is presented with the challenge of locating suitable patches in space. Given that the community of consumers described above represent a wide range of potential natural histories and physiological constraints, the ways in which they are able to locate their resources in space likely vary across the community with respect to both time and spatial scale. Factors influencing the consumer's ability to locate patches potentially include: duration of life-cycle, mobility throughout development, and diet breadth among other factors. For the community of CLR consumers the cues they use locate the CLR will likely be quite different considering they encompass four distinct Classes (*Gastropoda*, *Arachnida*, *Insecta*, *Sordariomycetes* (*Ascomycota*)), likely resulting in distinct scales of response to CLR patches.

Here we use three distinct hierarchical levels of analysis to understand the relevant scales for determining the dynamics of community assembly and organization in this system. By using two separate periods in the epidemic cycle of CLR, we capture the community assembly dynamics when the pathogen is at relatively low densities in the early infection period, then capture signatures of community interactions during the mid-infection period where CLR densities are higher and the community competes for its resource. Furthermore, we show how the community of consumers depletes the CLR spores throughout the cycle of the CLR representing an important dynamic feedback in the system where consumer activity modifies the patch distribution they consume.

Methods

Survey Methods

The study was conducted in the central coffee producing region of Puerto Rico, see Perfecto et al. (2019) for a description of the farms and coffee producing landscape. By talking to farmers at each of the 12 farms included in the study we identified regions within each farm that were impacted CLR. Once an area was located, plants were then haphazardly selected to be surveyed. The minimum distances between plants surveyed were five meters in each farm. Once a plant was selected via looking for multiple branches with lesions of the CLR, individual leaves were surveyed.

On each leaf the percentage of the leaf covered in CLR was estimated. Then the leaf was inspected for the presence of each of the community of natural enemies. The *Mycodiplosis* were found by visually scanning the leaf and recording the number of them present. Each lesion of the CLR on the leaf was inspected for the presence of mites. The number of lesions with mites (sometimes a single mite, other times a small group of mites and brood) was recorded. To survey CLR-gastropods, we noted the number of orange excrements, which has been shown experimentally to be a sign of gastropods consuming the CLR (Hajian-Forooshani et al. 2020). All surveys were conducted by a single individual to control any variation that may have existed in the quantification of leaf infection percentages.

Data was collected across two years which represented two distinct regimes of the infection cycle of the CLR. Our first surveys were conducted on five farms in late July 2017, and here we refer to this survey as taking place in the mid-infection period of the CLR dynamics in Puerto Rico. Our second survey was the subsequent year in 2018 and conducted in late-June on seven coffee farms. This second survey period is referred to as the early infection period. The differences in the distribution of CLR corresponding to the different time periods of infection can be seen below (Figure 1).

Statistical analysis

For the leaf scale analysis, we used the raw data of the percentage of leaf covered in CLR. For the plant scale analysis, we calculated the percentage of leaf infection for a given plant averaged over all plants sampled, and for the farm scale analysis we calculated the average percentage leaf infection across the farm (zack; this seems to imply that farm scale and plant scale are identical). Differences in the amount of infection across the three spatial scales were significantly different between the sampling periods with a Wilcoxon rank-sum test ($p < 0.05$).

To understand the colonization dynamics of the consumer community to the CLR we used binomial regressions to see how the presence/absence of a consumer responds to the varying amount of CLR infection across the three distinct hierarchical levels. The same approach with binomial regressions was used to infer how varying densities of consumers impacted each other's colonization dynamics, as well as for understanding how multiple consumers influence the probability of encountering spores across hierarchical levels.

In order to understand the probabilities of co-occurrence given the underlying distribution of our consumers in both survey time periods, we conducted randomizations of our data and calculated co-occurrence metrics. The randomizations were repeated 100 times and the 95% confidence intervals were calculated to compare to the observed co-occurrence dynamics of our consumers though time.

Results

Percentage infection:

Our two surveys periods present two distinct points in the infection dynamics of the CLR. The two distinct regimes in CLR infection can be seen in Figure 2, where the early infection distribution at the scale of the leaf shows a strong skewed distribution dominated by low levels of infection. This contrasts with the mid-infection frequency distribution at the leaf scale where a concentration of infection intensity of approximately 75% is apparent in the tail of the distribution. We found a significant increase in the infection intensity across leaf (W = 235862, p-value < 2.2e-16), plant; (W = 2318, p-value = 1.572e-06), and farm (W = 3, p-value = 0.01768) spatial scales, with an increase of approximately 12% in the average infection load across all three spatial scales. Conducting surveys at these two times provides a snap shot into not only the dynamics of community assembly, but also how the interactions amongst the community play out over the duration of the seasonal dynamics of the CLR.

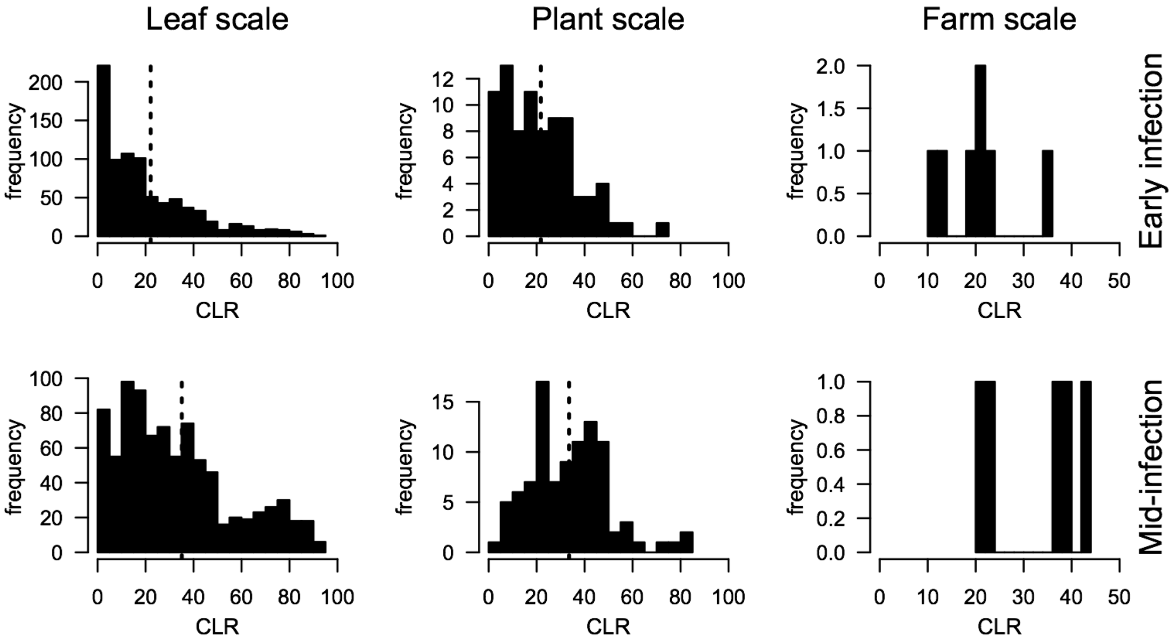

Figure 8.1: Shows the frequency distributions of percentage of infection on the leaf, plant, and farm scale for both survey periods and combined. Note the lower mean CLR at both leaf and plant scales for the early-infection period compared to the later-infection period. The dotted lines on the plant and leaf scale frequency distributions illustrates the mean values of CLR for the survey periods.

<u>*Consumer community response CLR density across scale*</u>

All CLR-consumers have significant positive responses to increasing CLR concentration at the leaf (Fig 2a) and plant (Fig 2b) plant scales during the early infection period, but not to the farm scale (supplementary materials). This ubiquitous positive response disappears during the mid-infection period, where the CLR-mites no longer respond at the (what) level and *Mycodiplosis* no longer responds at the leaf or plant level. In addition to simply affirming that the consumers respond to their resource, several notable patterns emerge from Figure 2 that lend insight into the ecology of the consumer community. First we note that *Mycodiplosis's* response to the CLR changes dramatically from early to mid-infection where it has significant responses at first but this effect disappears later. We suggest that this change in colonization across infection periods emerges from the basic natural history of the *Mycodiplosis* and its need to find it's resource early, while at relatively low density as compared to the other consumers in the community. We further note that *Mycodiplosis* responds most strongly in the community to low densities of CLR at the plant scale during the early infection period as evidenced by the relatively high y-intercept of the logistic regression (Fig 2b *Mycodiplosis* top panel). This suggests that *Mycodiplosis* is colonizing plants with relatively low average infection intensity, likely a result of it being a specialist on this resource and needing it to complete it life-cycle.

Regarding the colonization at low levels of resource across hierarchical levels, *L. lecanii* and CLR-mites share similar colonization dynamics at the plant scale, where they tend not to colonize plants with low infection in the early period but tend to do so more frequently in the mid-infection period, as is evidenced by the intercepts of the logistic regression (Fig2b). We also note an interesting pattern for *L. lecanii* at the leaf scale between early and mid-infection periods where we see *L. lecanii* is far more prone to colonize leaves with low CLR infection during the mid-infection period but not the early period. We propose that this is due in part to the local build-up of *L. lecanii* in the environment as the infection of CLR progresses throughout its epidemic cycle. Thus the higher concentration of *L. lecanii* in the environment allows it to colonize leaves with relatively low infection.

The CLR-gastropods show relatively consistent response across the early and late infection periods on the leaf and plant scales, where the probably of colonization increases as CLR infection increases. We suggest this may be due in part to the opportunistic utilization of CLR as a resource for gastropods and probably only utilize it as a food source when the pathogens density is sufficiently high.

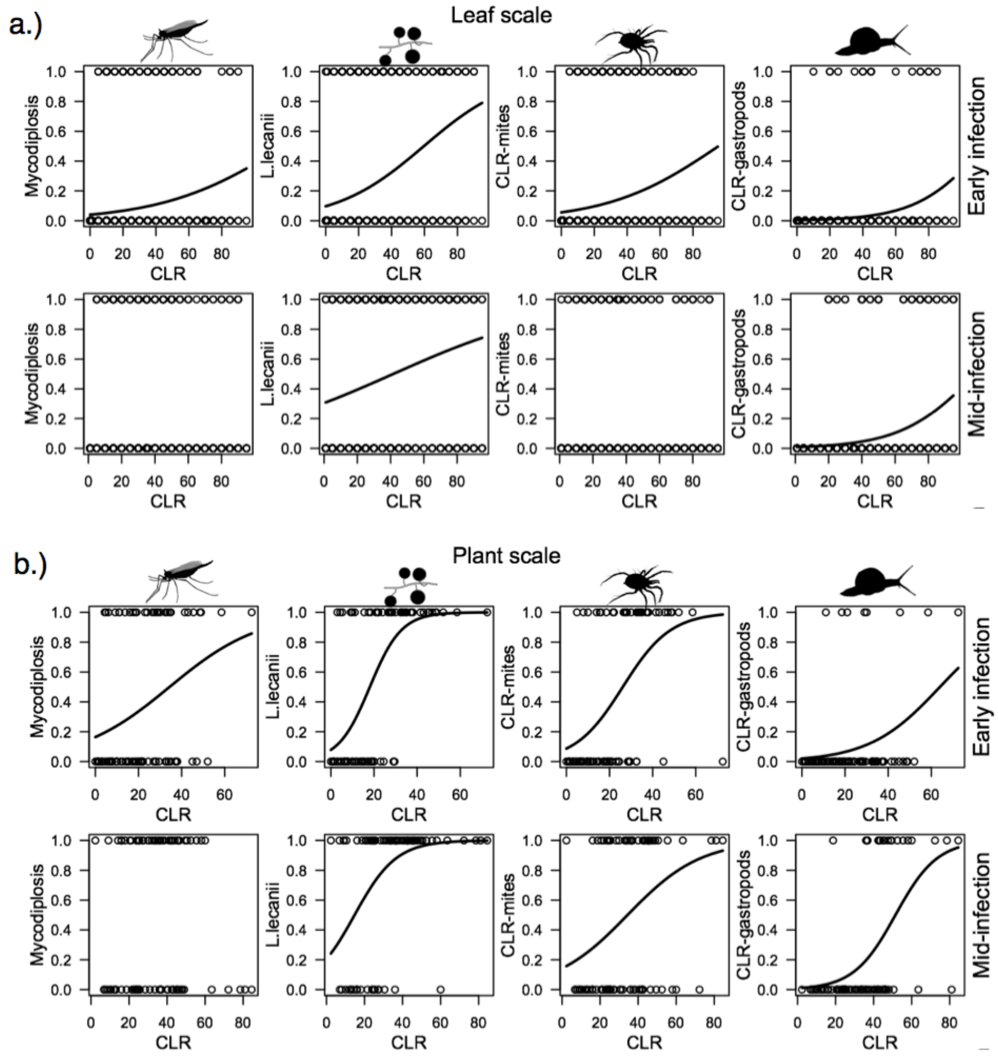

Figure 8.2: CLR consumer community's colonization dynamics in response a.) the percent of CLR on a coffee leaf and b.) the average % CLR leaf on the coffee plant. Black line shows

statistically significant logistic regressions. First row of a.) and b.) show the early infection period and the second row shows the mid-infection period.

Interspecific community interactions across resource dynamics

While in the above section we look to see how the consumer community responds to the amount of CLR at difference hierarchical levels, here we explore the relationships among the consumers. By focusing on how the colonization (presence) of natural enemies is moderated by the abundance of others in the community we can shed some light on how the interactions amongst the community play out through time as their resource increases. Here we comment on the significant interactions between members of the community and present the full pairwise analysis of natural enemies across all levels (leaves, plants, and farms) in the supplementary material.

First we note the colonization dynamics of the CLR-mite with respect to other members of the consumer community. We see no significant relationship with the colonization of CLR-mites with respect to the density of CLR-gastropods (see supplementary material), but such a relationship is evident with *Mycodiplosis* and *L. lecanii*. The CLR-mites show a higher probability of colonization at the leaf level as the density of *Mycodiplosis* on a leaf increases during the early infection period (Fig 4a). Interestingly this pattern is reversed during the mid-infection period where the probability of finding CLR-mites on the leaf decreases with increasing *Mycodiplosis* (Fig 4a). We suggest that these opposing effects of *Mycodiplosis* on the CLR-mite's colonization probabilities result from both natural enemies likely attempting to locate similar plants early in the dynamics of the CLR cycle, but as time passes competitive interactions structure the communities and competitive exclusion takes place. Note that the opposite effect of increasing CLR-mites driving a reduction in the probability of *Mycodiplosis* colonization is observed for the same period (see supplementary material). Regarding *L. lecanii's* impact on the colonization probability of CLR-mites, we see a consistent positive effect of increasing *L. lecanii* on CLR-mites (Fig. 4).

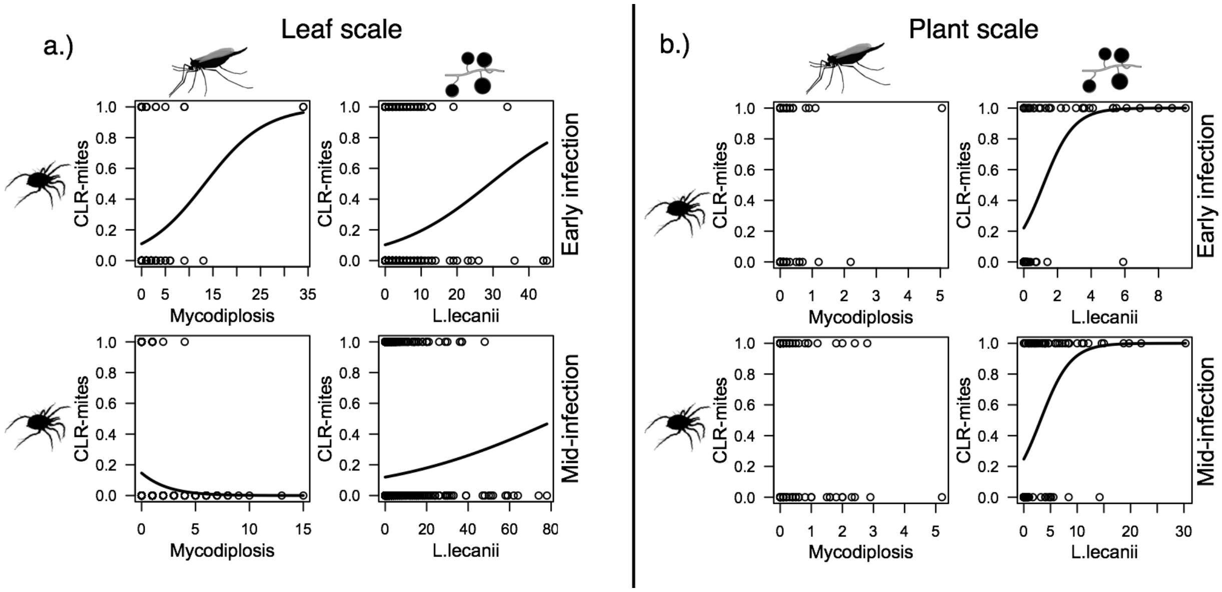

Figure 8.3: Colonization dynamics of CLR-mites in response to Mycodiplosis and L.lecanii densities on the leaf and plant scale. a.) shows CLR-mite responses to the leaf scale for early infection and mid-infection surveys. b.) shows CLR-mite responses to the plant scale for early and mid-infection surveys. Solid lines represent statistically significant logistic regressions.

The colonization dynamics of *L. lecanii* is related to the abundance of other consumers in the community. We find that the probability of colonization of *L.lecanii* consistently increases with increasing density of CLR-mites on both the leaf and plant scales (Fig. 5). This reciprocal effect of CLR-mites increasing the colonization probability of *L. lecanii* and *L. lecanii* increasing the colonization probability of CLR-mites seems to suggest some type of direct or indirect facultative interaction between these two consumers. The other significant effect we see is an increase in *L. lecanii,* resulting in a decreasing probability of *L. lecanii* presence during the mid-infection period. This negative association supports prior findings of antagonism between *L. lecanii* and CLR-gastropods (Hajian-Forooshani et al. 2020).

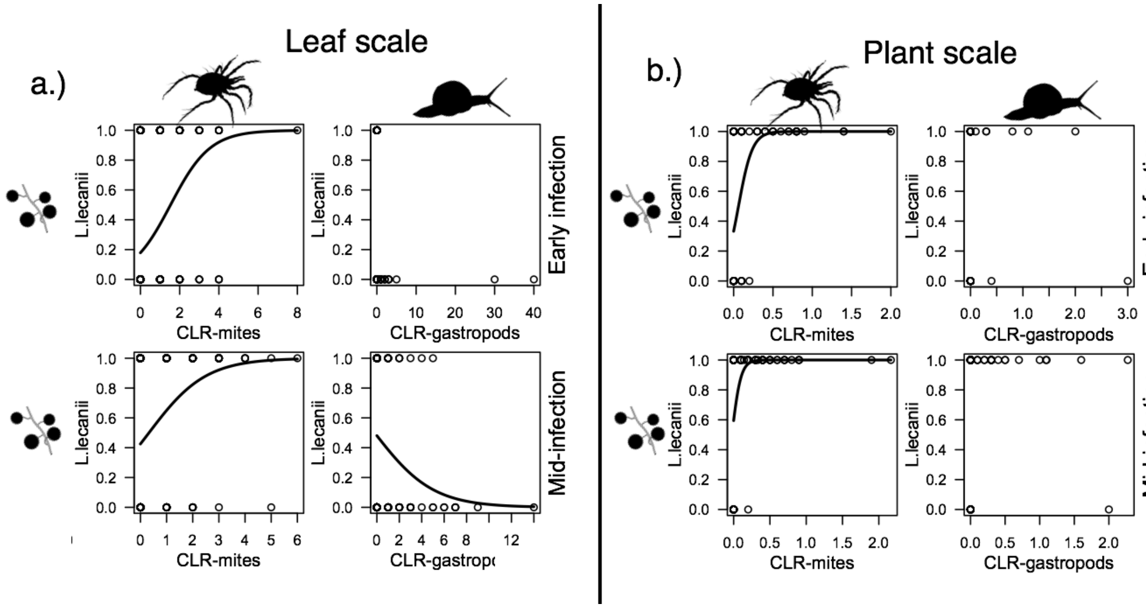

Figure 8.4: Colonization dynamics of L. lecanii in response to CLR-mites and CLR-gastropods densities on the leaf and plant scale. a.) shows L. lecanii responses to the leaf scale for early infection and mid-infection surveys. b.) shows L. lecanii responses to the plant scale for early and mid-infection surveys. Solid lines represent statistically significant logistic regressions

An analysis of co-occurrence patterns of the community highlights scale dependent patterns in how the consumers overlap with each other at distinct hierarchical levels through time (Fig 6). At the farm level, we only see significant deviations from the randomizations for co-occurrence of *Mycodiplosis* and CLR-gastropods, where in the early infection period they co-occur more frequently than is expected by change and in the mid-infection period they co-occur less frequently than expected by change.

At the plant and leaf levels, the co-occurrence dynamics become considerably more complicated with patterns at one hierarchical level flipping when considering the other. The general qualitative pattern that emerges is that consumers tend to co-occur more frequently than expected by chance at the plant scale and less frequently than chance at the leaf scale, with this pattern holding for *L.lecanii* and CLR-gastropods, CLR-mites and CLR-gastropods, *Mycodiplosis* and *L.lecanii* and *Mycodiplosis* CLR-mites (Fig 6.). One of the strongest consistent effects across hierarchical levels is that of *L. lecanii* and CLR-mites co-occurring more frequently than chance at the plant and leaf levels across both early and mid-infection periods.

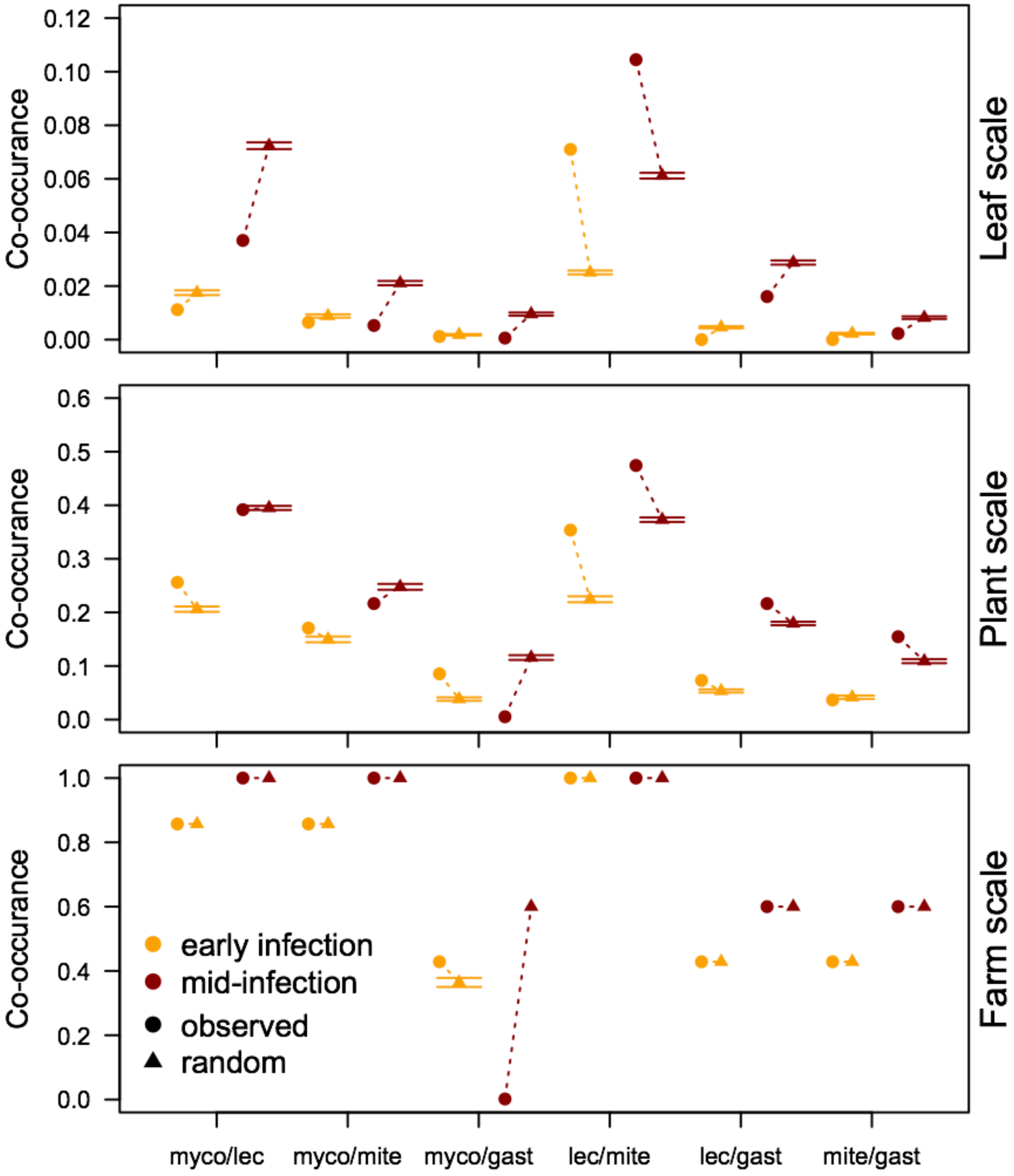

Figure 8.5: Shows the co-occurrence of consumers at three discrete hierarchical patch scales. Circles correspond to observed co-occurrence and the triangles to the co-occurrence

probabilities of 100 data randomizations. Errors bars represent 95% CI. Orange shows the early infection period and dark red the mid-infection period.

Consumer community impact on CLR spores

During surveys of CLR and the consumer community, the presence or absence of spores on the leaves were noted. Given that all the consumers consume these spores, we are left with a record of lesions in which the spores have been removed, presumably through the action of the consumers in the community. An analysis of the presence/absence of the spores shows significant patterns that would be expected if there were impacts of the consumers in reducing the presence of spores aa the leaf and plant level (Fig 7). The consistent pattern, apart from the CLR-gastropods, is that in the early infection period the probability of finding spores on leaves was significantly higher when the natural enemies were present than when they were absent. This pattern then changes in the mid-infection period where the probability of finding spores on leaves is lower when the natural enemies are present. We interpret these results to mean that early in the cycle of the CLR natural enemies are attached to leaves with spores and by the mid-season the leaves have been cleared of spores, presumably due to the activity of these natural enemies.

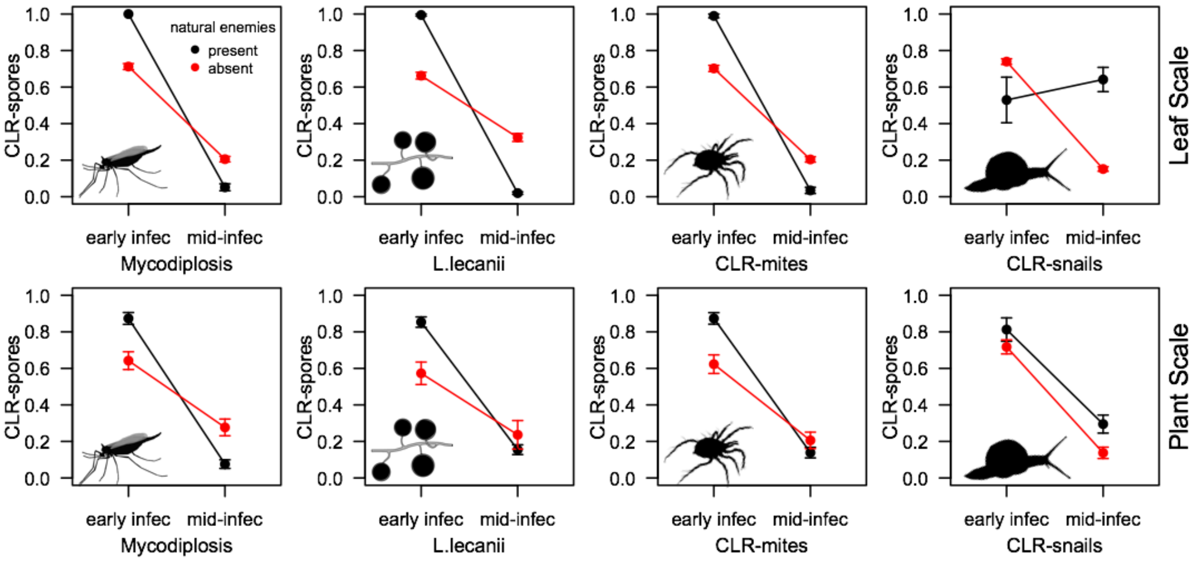

Figure 8.6: Show the change in average presence of CLR spores in the early infection and mid-infection periods. Black dots and lines show where the natural enemies were present and red dots and lines show where they were absent.

We see a similar pattern between the early infection and mid-infection period regarding spores and consumers when considering the co-occurrence of consumers at the leaf and plant scale (Fig. 8). The probability of finding spores at the leaf and plant scale increases with increasing consumer co-occurrence, and the probability of finding spores at both scales decreases at both scales for the mid-infection period.

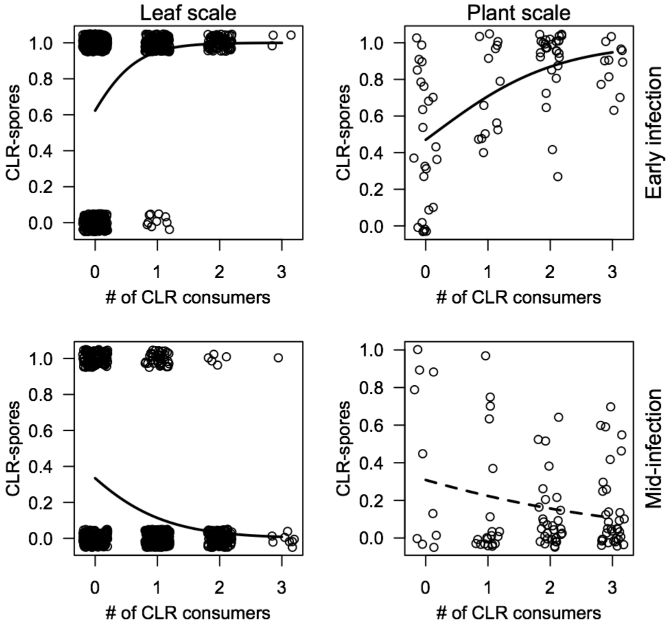

Figure 8.7: The impact of then number of consumers on the incidence of CLR spores at the leaf scale and plant scale. For plant scale analysis, average incidence of spores was used. Solid lines show significant binomial regressions and the dashed line shows marginally significant results (p<= 0.1)

Discussion

Here we used hierarchically distributed patches of a fungal pathogen to understand how a community of consumers responds to patch quality (amount of pathogen) across multiple hierarchical levels ranging from individual leaves to the dispersed farms which host the plants. We detect signatures of how the community interacts within this heterogeneous patch hierarchy and show scale-specific signals of antagonism and facilitation amongst various members of the community. We then asked about how this community feeds back to modify this underlying patch distribution through consumption of the pathogen's fungal spores and show that while they seem to consume the pathogen in isolation the effect is elevated when co-occurring, suggesting possible synergies amongst the community elements, as they engage in pathogen control.

Consumers response to hierarchical patch levels

During the early part of the CLR infection, community assembly is driven largely by the amount of CLR infection (i.e. patch quality) at the leaf and plant scale, where all members of the consumer community's colonization probabilities are positively associated with amount of CLR infection on a plant. This suggests that although assembly is realized at the scale of an individual leaf, the cue for resource detection also emerges at the scale of the plant. Notably almost no signature of response to the farm scale was detected in this analysis, apart from some co-occurrence patterns (see supplementary material for full farm scale analyses). Interestingly we detect qualitatively distinct dynamics for colonization between what we think to be specialist and more generalist consumers of CLR in this community, where specialists had higher probabilities of colonizing patches lower densities of CLR than the generalists (Fig 1).

The one clearly obligate consumer in the community, *Mycodiplosis*, only responds to the amount of CLR in the early infection period for both the leaf and plant scales (Fig. 2). Furthermore, we see that *Mycodiplosis* has the strongest response to relatively low densities of CLR at the plant scale for the early infection period (Fig 2). This suggests that when compared to the other consumers in the community, *Mycodiplosis* is locating and colonizing the plants at relatively low resource density, likely due in part to its specialist nature. We see similar dynamics at the leaf scale with the CLR-mites, where there is a positive effect of increasing CLR on colonization in the early infection period that disappears in the mid-infection period. Although questions remain about the natural history of these mites (see Ajila et al., 2018) their oviposition on lesions of CLR suggest a tight relationship between the CLR and their fitness, similar to *Mycodiplosis*.

The generalist fungal parasite, *L.lecanii*, which is known to be a mycoparasite as well as an entomoparasite, showed a consistent increase in colonization probability with increasing CLR at the leaf and plant scale, although there are some notable differences between early and mid-infection periods. As one would expect given the natural history of *L.lecanii*, the *L.lecanii* colonizes both leaves and plants at lower CLR densities in the mid-infection period compared to the early infection period. This is likely due to buildup of the fungal parasite in the environment over the course of the CLR dynamic, resulting in a more saturated environment as the epidemic cycle progresses. In addition to consistent colonization dynamics with increasing resource density, we also note a strong response of *L.lecanii* to the average CLR infection at the plant scale, where when the average leaf infection on a plant exceeds approximately 40% there is almost a 100% probability of finding *L.lecanii* on a plant. This pattern of consumer colonization at lower plant level patch quality is consistent not only in *L.lecanii* but with all other consumers apart from the CLR-gastropods. We suspect this lack of pattern with CLR-gastropods is due in large part to the opportunistic nature in which they utilize the CLR only when found in high quantities.

Community organization across scale

While the early infection period allows us to explore how the consumers navigate the heterogeneous patch hierarchy of their resource, the mid-infection period allow us to ask how the community organizes itself as time elapses and patches of their resource is more plentiful and of higher quality. We find some consistent effects that occur across the hierarchical levels, but also note scale dependency in the organization of the community. Analysis of co-occurrence patterns across the hierarchical patch levels shows that while some combinations of consumers occur more likely than expected by chance at the plant scale that they then occur less often than expected by chance at the leaf scale (Fig 6). This pattern is observed qualitatively with a large portion of the community and includes the co-occurrence combinations of, CLR-gastropods/CLR-mites, CLR-gastropods/*L.lecanii*, *Mycodiplosis*/*L.lecanii*, *Mycodiplosis*/CLR-mites and *Mycodiplosis*/CLR-gastropods at one or both of the survey periods. We interpret this scale dependence to at least be in part due to the joint response of multiple consumers to the plant scale and subsequent segregation amongst the leaves of plants.

In addition to the scale-dependent co-occurrence patterns observed in Figure 6, we also note the pattern of larger deviations from the random expectation of co-occurrence corresponds to the mid-infection period of CLR dynamics. This further suggests that while colonization is likely prioritized in the early period of the CLR increase, community organization plays out in large part during the mid-infection periods. Changes in direction of co-occurrence was also found to change from the early to mid-infection period, where for example *Mycodiplosis*/CLR-gastropods are found co-occurring more than expected at the farm and plant scale in the early infection but less than expected in the mid-infection period. Similar patterns are found for *Mycodiplosis*/CLR-mites *Mycodiplosis*/*L.lecanii* and CLR-mites/CLR-gastropods all at the plant scale (Fig 6).

In addition to the co-occurrence of members of the community, we also find signatures of consumers influencing the colonization dynamics of each other through time. Most notable is the consistent and reciprocal positive impact of CLR-mites and *L. lecanii* on each other, both in terms of colonization (Fig 4 & Fig 5) and co-occurrence (Fig 6) across the patch hierarchy, which suggests facilitation between these two members of the community. Given this clear and persistent pattern of apparent facilitation in our data, we hypothesize that *L.lecanii* may also serve as an alternative food source for the CLR-mites. The CLR-mites have been shown to complete their lifecycle in CLR but also other several pollen species (Ajila et al., 2018), showing a level of generalization in their diet breath and also an affinity for fungi, which makes *L.lecanii* a potential candidate resource. Furthermore, observations from the CLR-mites in our system as well as others (Oliveria et al., 2014) show that they frequently carry CLR-spores on their bodies and thus are likely dispersing it locally. We propose that CLR-mites may not be only consuming the *L.lecanii* but also dispersing across leaves as well as plants in this system. Such an interaction between the two consumers would explain the patterns found in our data.

Although there are consistent patterns suggesting consumers' effects on each other's colonization dynamics, there is also scale-dependence and signal shifts through time. For example, we find a positive effect of *Mycodiplosis* density on the colonization of CLR-mites during the early infection period at the leaf scale, but the opposite pattern in the mid-infection period. This pattern would be observed if both consumers prioritize similar patches early, when patch quality is relatively low followed by subsequent competitive exclusion as time progresses. Another pattern shift from early to mid-infection period is the impact of increasing CLR-gastropods on the incidence of *L.lecanii* at the leaf scale, where we see no effect in the early period of CLR dynamics but then increasing CLR-gastropods reducing the probability of *L.lecanii* incidence on leaves. This result confirms previous laboratory experiments that showed one of the known gastropods that consumers CLR, *Bradybaena similaris*, consumes *L.lecanii* in addition to CLR (Hajian-Forooshani et al., 2020).

Consumer feedbacks into patch quality and implications for biological control

One interesting aspect of the CLR system is that once leaves become infected and the characteristic spores have emerged creating a lesion of the leaf, the spores disappear from the leaf but the yellow-orange lesions remain. This allows us to detect the past action of the consumers in this system. Our analysis of CLR spore incidence shows that the presence of *Mycodiplosis*, CLR-mites, and *L.lecanii* is associated with higher probabilities of finding spores in the early infection period and with lower probabilities of finding spores in the mid-infection period (Fig 7). This suggests that the consumers are locating CLR patches, at both the leaf and plant scale, in the early infection and depleting them in the mid-infection period. Additionally, we find that as the number of consumers increase at the leaf scale, we find a higher probability of spore incidence during the early infection period and the opposite effect during the mid-infection period (Fig 8). This further illustrates how multiple consumers seem to be colonizing high quality patches in the early phase, and shows the implications for this with the elimination of spore load later during the mid-infection period. The same qualitative pattern holds at the plant scale, although not as strongly as at the leaf scale. This community of consumers has recently been noted for their potential role in providing autonomous biological control (Hajian-Forooshani et al., 2016; Hajian-Forooshani et al., 2020), and results from this analysis lend additional support to this hypothesis. Not only do we find evidence that suggest consumers are individually reducing the spore load of CLR at multiple spatial scales, but also that synergies with multiple consumers seem to exist in the system.

Conclusions

Here we link concepts in community assembly and consumer-resource dynamics with hierarchical patch distributions across scales to understand how a community of consumers navigate a hierarchical patch distribution to find their resource patches in space but also interact with each other and segregate themselves in space. This work highlights the importance of considering multiple spatial scales in understanding not only how communities assemble but how interspecific interactions structure communities across spatial scales and hierarchical levels. Furthermore, our system of the CLR is the most devastating pest of coffee around the world, and this work furthers our understanding of a natural enemy community that may have important implications for control of the CLR around the world. Understanding how this community assembles in space and time in other coffee agroecosystems where CLR is present is of potential importance to coffee producers concerned with the current and future status of the devastating pathogen.

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Chapter 9 Insights from Excrement: Invasive Gastropods Shift Diet to Consume the Coffee Leaf Rust and its Mycoparasite

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Background

Agroecosystems are almost always by definition composed of novel assemblages of organisms from various parts of the world (Perfecto and Vandermeer 2015). As ecologists, we have little ability to predict *a priori* how interactions within these novel assemblages will organize themselves and what their impacts will be within and adjacent to agricultural production. While it may be possible to make coarse predictions about well-studied organisms, as with natural enemy release in non-native ranges, it is less often the case that we are able to predict the development of novel interactions which result from host shifts in new ecological contexts (Agosta 2006; Nylin et al. 2018). This is an issue highlighted by the study of invasive species as well as the many disastrous attempts at classical biological control (Simberloff & Stiling 1996). Here we highlight this unpredictability of agroecosystems by reporting on a widely distributed invasive snail described as being an herbivore, apparently shifting its diet to consume a globally important fungal pathogen of coffee (McCook & Vandermeer 2015), the coffee leaf rust (CLR), *Hemliea vastatrix*. Both field observations and laboratory experiments show that the widespread invasive snail, *Bradybaena similaris*, along with other members of the gastropod community in Puerto Rico, are consuming CLR uredospores (here simply referred to as spores) (Fig. 1). Importantly, CLR lesions that produce these spores are characteristic of "mature" infections on leaves and are the transmissible stage of the pathogen (Talhinhas et al. 2017). Additionally, laboratory experiments show that *B. similaris* also consumes a known biological control agent of CLR, the mycoparasitic fungus, *Lecanicillium lecanii* (Vandermeer et al. 2009; Jackson et al. 2012).

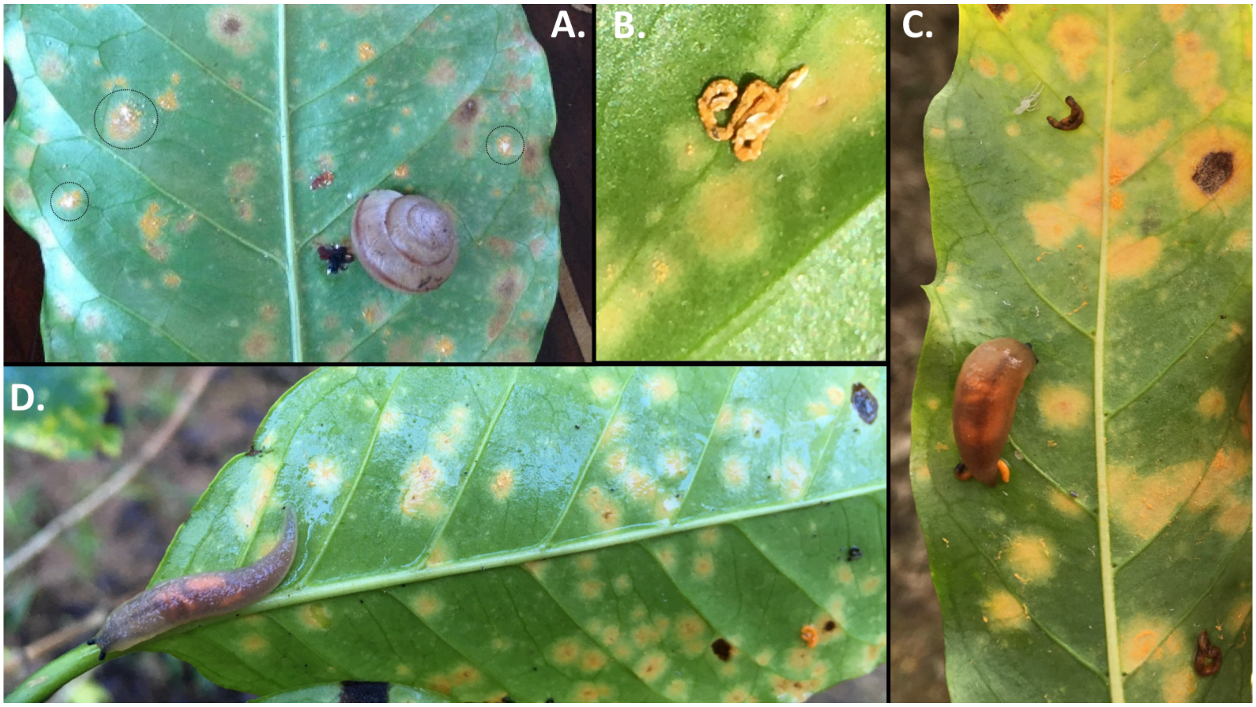

Figure 9.1: A.) B. similaris *on coffee leaf with CLR and small white patches of* L.lecanii *circled in black. Note that some CLR lesions have spores (bright orange and textured) and others do not (drab orange with smooth texture), B.) the characteristic orange excrement that led to the idea that gastropods could be consuming CLR, and C.) & D.) two unidentified gastropods with their guts full of what appear to be CLR spores in addition to the orange excrement on leaves from the field.*

Initial field observations in 2016 of brightly orange colored snail excrement on the undersurface of coffee leaves (Fig. 1, panels B and D) on various farms in the central mountainous region of Puerto Rico led to the insight that there may be a snail consuming spores of the coffee leaf rust. Later that summer, hundreds of the invasive *B. similaris* and a native Carribbean snail, *Bulimulus guadalupensis,* were found on the Estación Experimental Agrícola Adjuntas along with the characteristic orange excrement. To explore which of the snails was consuming CLR, both species were collected along with leaves containing CLR and preliminary experiments showed that after 24 hours *B. similaris* cleared the coffee leaves of CLR spores while *B. guadalupensi* failed to consume any CLR.

Laboratory Experiments

After the observations in 2016, we returned to collect *B. similaris* at the same location to conduct more extensive laboratory trials the following year. Given the high incidence of the mycoparasite *L. lecanii* growing on CLR lesions in the region, we sought to determine whether *B. similaris* consumes it in addition to CLR. Coffee leaves were collected from various farms in the region, and the percentage of a leaf covered in CLR lesions with spores was estimated along with the number of *L. lecanii* patches. A single coffee leaf and a single *B. similaris* were placed together in dark containers for 24 hours after which the percentage of CLR and number of *L. lecanii* patches were again quantified. After exposure to the snail for 24 hours there was an average reduction of 30 ± 4 percentage of CLR and 17.4 ± 3.8 in the number of *L. lecanii* patches (Fig. 2A). We also corroborated that the orange excrement we observed in the field is associated with the consumption of CLR spores (p-value =0.001, R^2=0.53, slope=-0.07 ± 0.017) and also its mycoparasite *L. lecanii* (p-value = 0.003, R^2=0.47, slope= -0.07 ± 0.02) (Fig. 2B). Additionally, laboratory results suggest density-independent consumption rates of the CLR by *B. similaris*. The linear regression is not significant when considering all the data (p-value =0.11, R^2=0.17, slope= -0.39 ± 0.23), but there is a clear trend in the data when removing the single point where *B. similaris* consumed no CLR at all (p-value = 0.01, R^2=0.40, slope= -0.52 ± 0.18)

(Fig. 2C). Furthermore, our experiments suggest that *B. similaris* consumes more CLR when a given leaf has more *L. lecanii* (Fig. 2D). Although this relationship is only significant when we remove an outlying point of very high number of *L. lecanii* patches (all data: p-value = 0.37, R^2=0.06, slope= -0.16 ± 0.18; outlier removed: p-value = 0.014, R^2=0.38, slope= -0.59 ± 0.21), it suggests that there may be non-linearities in how *B. similaris* consumes CLR when *L. lecanii* is present on a leaf. The exact mechanism driving this pattern is not clear due to the strong relationship between the amount of CLR on a leaf and the number of *L. lecanii* patches (p-value = 0.01, R^2=0.37, slope= -0.83 ± 0.29).

Our experiments and field observations confirm that the invasive *B. similaris* is one of the spore predators of CLR in Puerto Rico. Interestingly, even though *B. similaris* has been described as one of the most widely distributed invasive land snails, it has never been described as consuming other than plant material. In fact, there appears to be only one case in the literature of mollusks specifically consuming rust fungi, which found that the black slug, *Arion ater,* preferentially grazed on leaves infected by a rust fungus (Ramsell & Paul 1990). This is distinct from what we are observing in this system, as the gastropods do not seem to be consuming any plant material, but only the rust fungus and its mycoparasite. The irony of *B. similaris* consuming CLR in Puerto Rico is that it has been described as a severe agricultural pest of many crops in various regions around the world (Idris and Abdullah 1997). In fact, *B. similaris* has been shown to be resistant to a number of control methods implemented in agricultural systems.

Field observations

Following our experiments, our research team began to pay closer attention in surveys of CLR around the central mountainous region of Puerto Rico as part of ongoing research, and made note of other gastropods apparently consuming CLR spores (Fig. 1, panels C and D). It can be seen from these photos that they are on leaves that show spores having been cleared off portions of the leaves in addition to their guts being full of presumed bright orange CLR spores. Fig. 1C shows a snail in the process of defecating brightly colored orange excrement, and Fig. 1D shows orange excrement in the lower right hand portion of the photo. While these gastropods have not yet been identified, they do not bear resemblance to any of the known native gastropods.

These observations and experiments give rise to a number of interesting questions from both a scientific perspective and as having potentially important implications for the production of coffee. Further work is needed to understand the potential trade-offs *B. similaris* and other gastropods may provide to coffee agroecosystems given our understanding of other elements within the system. For example, *L. lecnaii* is a well-studied biological control agent of CLR (Vandermeer et al. 2009; Jackson et al. 2012; Hajian-Forooshani et al. 2016), and the effect of *B. similaris* (and potentially other gastropods) consuming it along with CLR needs to be understood especially in light of results suggestive of *B. similaris* consuming more CLR when *L. lecanii* is present. Related theoretical work suggests that when an herbivore is consumed by both a predator and a pathogen which exhibit intraguild predation, the intraguild predation (i.e. the predator eating prey infected with the pathogen) can be a stabilizing force that could prevent the outbreak of the herbivore (Ong and Vandermeer 2015). In short, there are non-obvious but potentially consequential implications which stem from these observations. The work summarized here provides evidence that the orange excrement observed in the field is indeed representative of consumption of CLR (Fig 2B).

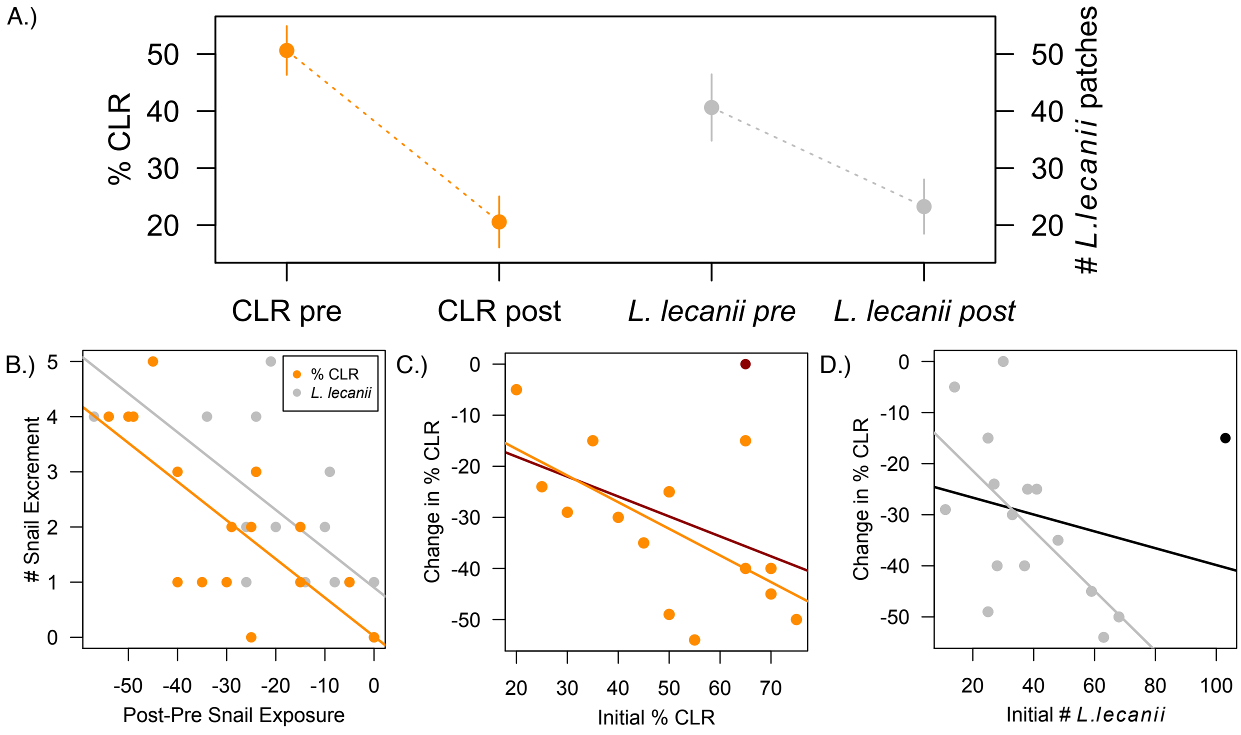

Figure 9.2: 2017 laboratory experiments exposing leaves with CLR and L. lecanii *to* B. similaris *for 24 hours. A.) Percentage of CLR spores and the number of* L. lecanii *patches on a leaf pre and post exposure to* B. similaris. *B.) The number of snail excrement associated with the change in both the % CLR and the number of* L. lecanii *patches. C.) The change in CLR and the initial amount of CLR on a leaf. The dark red line shows the regression including all points and the orange line excludes the one outlying point where no CLR was consumed. D.) The change in CLR associated with the initial number of* L. lecanii *patches on a leaf. The black point indicates the particularly high density outlier. The grey regression line includes all points; the black regression line excludes the outlier.*

Conclusions

CLR is the most economically significant pest in coffee around the world, and has been introduced in nearly every coffee producing country worldwide. Here we present what is, to our knowledge, the first case of gastropods feeding on CLR, thus shedding light on a potentially important element of autonomous biological control in coffee agroecosystems (Vandermeer et al. 2010). This work highlights how the ecological theater in which interactions play out turns an agricultural pest in one system to a biological control agent in another. The extent to which *B. similaris* consumes CLR in its native regions, or other introduced regions of the world where coffee is cultivated, is currently unknown. Undoubtedly part of the unpredictability of agroecosystems results from the particular combinations of native and introduced biodiversity, and we suggest that understanding the ecology of these systems will provide key insights in how to manage them. In many agroecosystems technocentric approaches are becoming the norm, where efforts to control supersede efforts to understand the basic ecology. It is our hope that more agronomists start making observations like the ones presented here and that more ecologists leverage their perspectives to help find solutions to issues confronting farmers in agroecosystems around the globe.

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Chapter 10 Cascading Interactions from Ants Influence Landscape-Scale Pathogen Dynamics in a Coffee Agroecosystem

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Abstract

1.) Complex interactions are a key feature of many ecological systems, both "natural" and human influenced. Understanding the implications of complex and indirect interactions on the dynamics of ecological systems is especially important when considering agroecosystems where questions of population regulation via top-down control is often a primary concern.

2.) Here we explore how the large-scale dynamics of the coffee leaf rust (CLR), caused by the fungal pathogen of coffee, *Hemileia vastatrix*, are influenced by cascading interactions from a dominant ant, *Azteca seriaceacur,* in a coffee agroecosystem. Prior work has shown an indirect negative impact of *Azteca* on CLR, mediated through a generalist natural enemy of CLR, *Lecanicillium lecanii* and a positive impact of Azteca an the specialist natural enemy of CLR, *Mycodiplosis hemileia* (referred to here as the CLR-midge).

3.) We utilize over seven-years of CLR survey data from a 45ha plot, in an organic coffee farm in Chiapas Mexico. Across the 45ha plot we use sites with and without Azteca nests present to understand how Azteca influences CLR dynamics. We also utilize laboratory experiments to understand the impact of *Azteca* on a specialist natural enemy of the CLR-midge.

4.) Results from the survey data show that sites with *Azteca* nests tend to have higher amounts of CLR seasonally, the opposite of what was predicted given what was known about the indirection relationship between *Azteca* and CLR mediated through *L. lecanii.* Our laboratory experiments found a negative impact of *Azteca* on the CLR-midge, thus offering a potential explanation of large-scale positive effect of *Azteca* on the CLR via *Azteca* reducing the top-down control by CLR-midges.

5.) Understanding the dynamics of predominately top-down controlled systems such as pests and pathogens in agriculture within the context of the contingencies of the communities in which control agents are embedded, presents a challenge for both farmers and ecologists alike. Here we provide evidence for a trophic cascade that results in the release of the most important pathogen of coffee, highlighting that it is not enough to only understand the consumer-resource dynamics of such systems but how they fit into the community.

Introduction

Understanding the forces that structure population dynamics has a long history in ecology and has taken many forms (Andrewartha & Birch 1954; Hariston et al. 1960; Murdoch 1966; Turchin 1995; Hixon et al. 2002). In an attempt to understand the dynamics of any particular population, the question has often been framed as understanding if it is structured via “top-down” or “bottom-up” forces, referring to the adjacent trophic levels within a given community. While there are well known examples that caricature each class of population regulation, a more nuanced understanding has emerged suggesting that often it can be a combination of both mechanisms in concert (Hunter & Price 1992; Meserve et al. 2003). It is appreciated that an attempt to truly understand the dynamics of populations will most likely necessitate looking at it from a community context where more complex interaction structures can emerge, such as trait-mediated indirect interactions (Werner & Peacor 2003) or indirect interactions such as trophic cascades (Estes et al. 1998; Knight et al. 2005). Questions about what structures population dynamics are not only of interest from a theoretical standpoint, but also have practical implications for how humans construct and modify ecosystems around the world.

One such constructed ecosystem is the agroecosystem, the question of population regulation looms large when considering pests of the crops and becomes a question of practical significance. One of the peculiarities of the agroecosystem is that consumers (insects, pathogens, etc.) of crops are infrequently controlled from the bottom-up (although one might argue that phytochemical defenses pose some class of bottom-up control), and when they are, the agroecosystem itself is effectively collapsed through depletion of the crop itself. Thus, a practical option in agroecosystems is to facilitate or simulate control from above. The application of pesticides can be thought of as the simulation of top-down control, where the intention of pesticide application is to effectively do the job of natural enemies. The facilitation of top-down regulation is often referred to as biological control and exists in a number of forms, from classical biological control, where species are intentionally introduced into the system, to what some call autonomous biological control where the community interactions in the agroecosystem provide regulation without direct intervention (Murdoch et al. 1985; Vandermeer et al. 2010; Vandermeer et al. 2019). This latter approach seeks to allow these usually highly managed systems to self-regulate by taking advantage of the community of natural enemies and the network of interactions in which they are imbedded (Vandermeer et al. 2010; Cruz-Rodríguez 2016). Utilizing naturally occurring interactions for pest control usually entails conserving biodiversity within the agroecosystem, which can simultaneously maximize both biodiversity and ecosystem services.

One often-cited example that illustrates the complex interaction networks in agroecosystems is that of ant-hemipteran mutualisms wherein the apparent negative effect on the plant (from ants protecting the herbivorous hemipterans) is ultimately compensated by the indirect negative effects that ants bring to other (often more harmful) herbivores in the system (Wang et al. 2021). A well-studied and yet more complicated indirect variant on this classic system, the relationship between an ant (*A. seriaceacur)* and one of its hemipteran mutualists (*Coccus viridis),* is remarkable for its indirect effect on the fungal pathogen, the coffee leaf rust (CLR) (*Hemileia vastatrix*). The scale (*C. viridis*) itself, when at very high local population densities falls victim to the fungal parasite *L. lecanii*, which is also a pathogen of CLR. The importance of *L. lecanii* as a natural enemy of CLR has long been established, and its complex ecology has been studied in detail (Jackson et al. 2009; Vandermeer et al. 2009; Jackson et al. 2012a; Jackson et al. 2012b; Jackson et al, 2014). Those studies have demonstrated the pathway of interactions between *L. lecanii*, *C. viridis* and *A. cericeasur* that effectuate a top-down control on CLR in Mexico coffee agroecosystems. A number of complexities emerge as being operative in the system such as spatial pattern formation (Vandermeer et al., 2008) and time-lags (Vandermeer and Perfecto, 2019), suggesting a whole system approach to unravel the complexity of top-down control in these complex systems will be necessary.

Recent studies on the community ecology of CLR has shed light on a community of natural of enemies whose ecology and impact on the dynamics of CLR are not well understood (Hajian-Forooshani & Vandermeer (accepted book chapter)). A less understood, but potentially important, natural enemy of CLR is the midge *M. hemileia*, (referred to as CLR-midge) (Barnes 1939) (Figure 1). While this midge is known to consume CLR spores, relative little is known about its biology and overall impact it might have on the dynamics of the coffee rust. Earlier accounts in its presumed native rage where coffee is endemic dismissed its potential for impacting the dynamics of CLR, although recorded observations noted its ability to clear leaves of the CLR spores when their densities are high (Miline 1975). In contrast to *L. lecanii*, field survey data show that CLR-midges are negatively associated with areas where *Azteca* forages (Hajian-Forooshani et al. 2016). The two proposed mechanisms for this observed pattern were either *Azteca* directly removing and or consuming CLR-midges, as it is known to do with a number of other insects on coffee plants, or a trait-mediated indirect interaction where *Azteca* disrupts oviposition behavior of the CLR-midge adults. The contrasting impact of *Azteca* on these two natural enemies, positive on *L. lecanii* and negative on CLR-midges, creates a situation where the net effect of *Azteca*'s interactions could go in either direction depending on the details of the natural enemies impact on the CLR dynamics.

Here we attempt to understand how *Azteca's* interactions within the coffee agroecosystem cascade down to CLR and ask if it has an impact on CLR dynamics at the landscape scale. Given prior research in the system we hypothesized that *Azteca* would have a negative indirect impact on the CLR. Although several correlational studies documented the indirect effect of *Azteca* on CLR mediated through *L. lecanii* prior to the "great rust" of 2012 (Vandermeer et al., 2009; Jackson et al., 2012), there has been no work on this dynamic subsequent to the rust epidemic. Furthermore, there have not been any studies exploring how a seemingly positive impact on one natural enemy (*L.lecanii*) and negative impact on another (CLR-midge) scales up to the dynamics of CLR. Here we present results from a seven-year systematic survey of CLR on 128 sampling sites over a 45ha permanent plot in a Mexico coffee agroecosystem. Naturally, some sites are centered on trees that contained nests of *Azteca* while others do not, creating a situation where we can evaluate the net impact of *Azteca* on the dynamics of the CLR across the coffee landscape. We also present results from laboratory experiments designed to understand the effect of *Azteca* on the CLR-midge and help explain our results from the 45ha plot surveys.

Methods

Field surveys

All field surveys were conducted on a 45 ha plot within an organic coffee farm in Mexico (see Vandermeer et al. 2006; Vandermeer et al. 2010; Vandermeer et al. 2019 for details of study system). Each hectare was subdivided into four 25X25 hectare sub plots. Eliminating all the plots along the edges of the 45-ha plot left a total of 128 sites (a quarter of hectare plots) that were used to monitored the CLR and its natural enemies from 2013 to 2020. At each of the 128 sites, a focal shade tree was selected that was located closest to the center of the plot, and the nearest five coffee bushes were surveyed. Each month, the total number of leaves on each of the plants was estimated, and the number of leaves with coffee rust were counted. Each focal tree was examined for nests of *A. sericeasur*, and classified as an *Azteca* or a not-*Azteca* tree. If an ant nest was present in the focal tree, there is a high probability that the surrounding coffee bushes were being tended by the ant (Perfecto & Vandermere 2006; Vandermeer & Perfecto 2019).

Field Survey Analysis

Generalized linear mixed effect models were used to test for Azteca's impact on the amount of CLR throughout our time series data. Using the presence of Azteca as a categorical variable, the survey month, year, as well as quadrat of the sampling were all used as random effects in the model with a Poisson distribution. A non-parametric bootstrap test for differences in the amount of CLR infect at sites with and without *Azteca* nests was used to look for significant differences throughout the time series. For each survey period, the data was split into sites that contained *Azteca* nests and sites that did not. The observed difference in the means was calculated then the data was resampled with replacement while maintaining the sample sizes for the groups and the resampled random differences between the groups was calculated 10000 times. The p-values were calculated by comparing the resampled differences with the observed differences for each sampling month.

Laboratory experiment

Coffee leaves infected with coffee leaf rust and CLR-midge larvae were haphazardly collected within the 45Ha plot avoiding the plants used for the CLR surveys. In the laboratory, the number of CLR-midge on the leaves was quantified under a dissection scope. When two leaves had equal numbers of CLR-midge they were randomly designated for control and ant-exposure treatment. If we were unable to find two leaves with the same number of CLR-midge naturally occurring on leaves, some larvae were removed to have equal quantities. Preliminary observation in the laboratory highlighted the difficulty of manipulating CLR-midge larvae on leaves, and in particular, any attempts to add to larvae to leaves resulted in the larvae rapidly moving off the leaf. Due to this, we were only able to take CLR-midge larvae off of leaves.

To contain the *Azteca* ants in the laboratory, an approximately 10x10cm piece of *Azteca* carton nest was placed in to a 50x30x20cm plastic container with Tanglefoot surrounding the top edge and inter-perimeter. Prior to all experimental treatments the ants were given 24 hours to acclimate to the container. After the initial acclimation period, a coffee leaf with CLR-midges was placed in the container with the ants, and another coffee leaf with the same number of CLR-midges was placed outside of the container. A total of 56 paired trials were run from June 26-July 8, 2017.

Laboratory experiment

To understand if the presence of Azteca has an impact on the number of CLR-midge on leaves in our experiment we compared the two treatments in our experiment. First, we used a bootstrapping procedure to calculate the probability of observing the difference in means between the control and ant exposed treatment. In short, all data was pooled together and 56 data points were drawn at random without replacement from the total of 112 points (56 from control and 56 from ant treatment) and the difference in means was calculated. This procedure was repeated 10,000 times and the probability of observing our measured difference in means (or a greater difference) was calculated. We also used the Wilcoxon Rank-Sum to compare the two groups as well.

In our experiment, we also used varying densities of CLR-midges on leaves to understand if there is a density dependent effect from Azteca on the CLR-midge. To look for density dependence of the impact of Azteca on CLR-midges we conducted linear regressions using the difference of the proportional change in CLR-midges between control and treatment and their initial density. Details of this analysis as well as the results can be found in the supplementary material. All code was written and statistical tests performed in R 4.1.1.

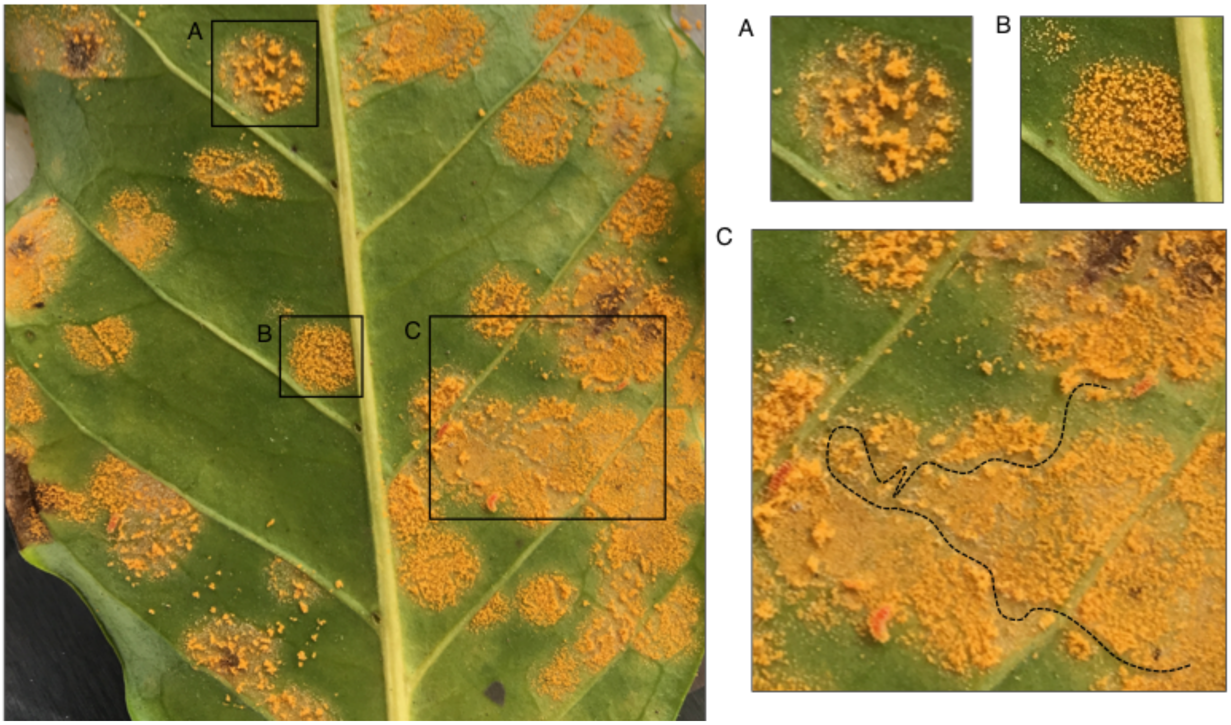

Figure 10.1 Illustrates the impact the CLR-midge has on the distribution of spores on a leaf after approximately 24-hours of feeding in the laboratory setting. Inset B.) shows a typical lesion of CLR having not been foraged on by the larvae. A.) Shows the state of a lesion after CLR-midge larvae have fed on it. Note that the spores are seemingly reduced in density as well as more clumped together. This is presumably due to the larvae pushing spores around as it feeds, but also possibly part of the excrement from the larvae. C.) shows three CLR-midge larvae feeding on a region of the leaf. Note in the early stages of feeding on an area the foraging trails are apparent and one is outlined with the dotted line there.

Results

Results from the more than 7-year survey of the CLR on a 45ha plot suggest that sites which centered on *Azteca* ant nests tend to have more severe infections than sites without the ants (GLMM; estimate =-0.04± 0.003. p <0.0001) (Fig. 2). The dynamics of the CLR are seasonal and thus inherently oscillatory in nature as seen in the data from figure 2. Interestingly the effect of *Azteca* on the dynamics of the CLR is also seasonal, where we see a positive effect of *Azteca* on CLR during the crescendo of the seasonal cycle. This pattern is relatively robust and is observable on six of the eight rising phases of the CLR cycle (Fig. 2). Additionally, a pattern of *Azteca* having negative association with the CLR also exists in the data and tends to occur in the declining phase of the CLR seasonal cycle.

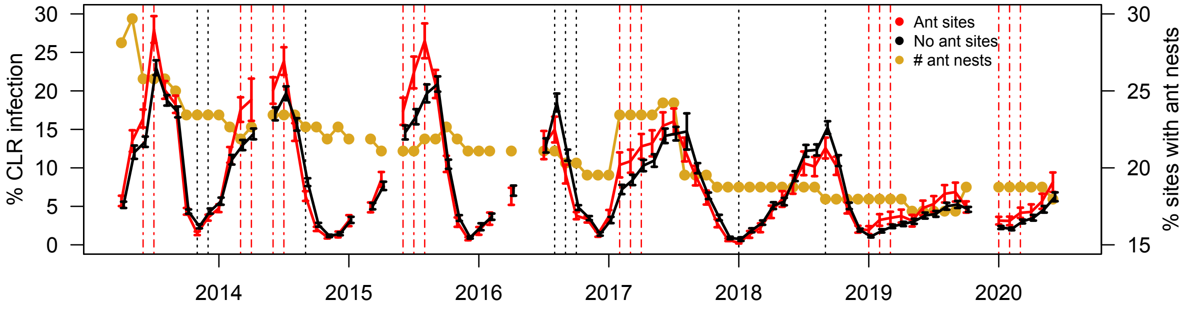

Figure 10.2: Results from the seven-year sampling of the coffee rust on a 45ha plot show the pattern of higher intensity of infection at sites which are centered on Azteca nests. Red points are sites centered on a tree with an Azteca ant nest and black points are sites without ant nests. The yellow points show the proportion of sites (out of the 128) that are centered on an Azteca nest. The vertical dashed lines show survey dates where there is a significant difference between Azteca and non-Azteca sites. Red dashed lines mean there was significantly higher % CLR infection on Azteca sites when compared to non-Azteca sites and black dashed lines suggest the opposite.

Experiments on the CLR-midge were preceded by extensive observations on the natural history of the midge. As illustrated in figure 1, lesions of CLR where the larvae had not yet visited were characteristically uniform with uredinia scattered across the entire lesion. After the CLR-midge larvae attack, the spores are typically at lower density and present a more clustered appearance, mainly from the midge having created feeding routes as it proceeded through the lesion. Frequently it is evident where a feeding trail has been laid (Fig. 1c). The probability of observing the difference in mean change in CLR-midges on leaves between our control and ant treatment was significant (p=0.0013) through the bootstrap procedure described above, which was also supported by a the Wilcoxon rank sum test (W= 2027, p=0.00735) (Fig. 3). The mean change in CLR-midges for the control was -1.07 and -4.80 for the ant treatment, showing more than a 4 times reduction in the number of CLR-midges on a leaf after 24 hours in the presence of the ants.

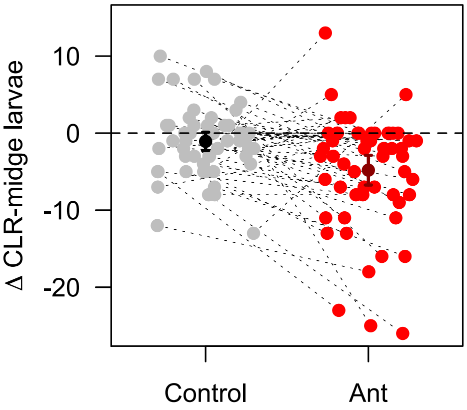

Figure 10.3: Shows the change in CLR-midge larvae in the control and ant treatments after 24 hours. Lighter colors in the background show the individual paired trial points connected by dotted lines and darker points in the foreground show the means and 95% confidence intervals.

Discussion

Here we present results from experiments with long-term and large-scale data that suggest that a top-down trophic-cascade has the potential to influence the most economically significant fungal pathogen in coffee agroecosystems. Contrary to our initial expectations, the general 7-year pattern of CLR does not reveal a top down control of CLR from the *Azteca* which was hypothesized to be operative though indirect interactions with *L.lecanii*. Indeed, the effect seems to be the reverse, with *Azteca* positively associated with the CLR (Fig. 2). Although we do not have direct measurements of the CLR-midges to accompany the 45ha survey data, the negative association between the CLR-midges and *Azteca* has been established in the field in this same system (Hajian-Forooshani et al. 2016) as well as in the laboratory as presented here (Fig. 3). It is, we propose, likely that *Aztecas'* negative effect on the CLR-midge in the laboratory translates into the field and explains the positive seasonal relationship between *Azteca* and CLR.

Understanding the consequences of this positive impact of *Azteca* on CLR is complicated by the community context of natural enemies of CLR, and in particular both *L. lecanii* and CLR-midge. *Azteca* is known to have several facultative mutualistic associations with different hemipterans in the coffee agroecosystem in Mexico (Jackson et al. 2012a; Livingston et al. 2014; Rivera-Salinas et al. 2018; Vandermeer & Perfecto 2019). In areas where *Azteca* tends green coffee scales, local populations of *L. lecanii* build up dramatically, and it has been shown that *L. lecanii* can effectively spill over at these sites resulting in greater attack on the CLR (Jackson et al. 2012a). Effectively *Azteca* has a positive impact on *L. lecanii* mediated thorough hemipterans which has been shown as an indirect negative association between *Azteca* and the CLR (Jackson et al. 2012a). Here, an emerging image of the complicated and indirect ways *Azteca* impacts the natural enemies is coming to light, where it has a positive association with one natural enemy, *L.*

lecanii, and a negative association with another, the CLR-midge. Our results here suggest the relative importance of the understudied CLR-midge in comparison to *L. lecanii* in terms of providing control of the CLR. If the indirect negative association between *Azteca* and CLR was mediated though *L. lecanii*, the expectation would be the opposite of the pattern observed in Figure 2. Clearly this long-term data shows that, while the *Azteca*-mediated *L. lecanii* control of the rust may be operative under certain circumstances, it does not scale up to the larger spatial scales that data was collected. One possible explanation for the apparent discrepancy between the results presented here and the prior studies (Vandermeer et al. 2009; Jackson et al. 2012a), is that the densities of both *L. lecanii* and coffee hemipterans have been noticeably lower since the onset of the CLR epidemic in 2012 (Personal observations of the authors).

Interestingly, the positive effect of *Azteca* on the CLR was largely constrained to the increasing periods of the CLR's seasonal oscillations. Again, if *Azteca* was promoting local densities of *L. lecanii*, we would expect precisely the opposite result, where sites with *Azteca* would have slower growth and overall less CLR. Contrarily we suggest that *Azteca's* disruption of CLR consumption by the CLR-midge can explain our observed results. Our laboratory experiments show that the presence of the *Azteca* ant significantly reduces the CLR-midge larvae densities on coffee leaves. These results correspond to earlier published results showing a negative association with the CLR-midges and this *Azteca* ant in the field (Hajian-Forooshani et al. 2016), and suggest that this relationship likely comes from a direct interaction between the two organisms. While relatively little is known about the natural history of the CLR-midge, we know that there is unsurprisingly a positive correlation between it and what is presumably its only resource, the CLR (Hajian-Forooshani et al. 2016; other paper from Mexico). Additionally, we know that in this region the populations of the CLR-midge peak right about the same time as the CLR does (Fig. S2. Supplementary material). The fact that CLR-midge population growth corresponds with the seasonal increase in CLR helps make sense of the punctuated impact of *Azteca* on CLR as seen across the 45ha plot data. If top-down control of CLR from the CLR-midge is greatest during this seasonal increasing phase in CLR, it makes sense that this is precisely when we would expect to see an indirect effect of *Azteca*.

Although this effect of *Azteca* on the CLR-midge is apparent in the field (Hajian-Forooshani et al. 2016) and lab (Fig. 2), the exact mechanism that causes the reduction in CLR-midges in the presence of the ant is not completely understood. One possibility is that *Azteca* is actively foraging and removing larvae from the coffee leaves. It is well established that when *Azteca* is foraging on coffee it can remove different insects from the coffee plants and can thus have either a consumptive or non-consumptive effect (Jiménez-Soto et al. 2013). The other possibility is that the CLR-midge larvae are leaving the leaf due to being disrupted by *Azteca's* foraging. As mentioned above, observations in the laboratory suggest that when the CLR-midge are disturbed or moved on a leaf they will often flee the leaf. The extent of their mobility in the field is largely unknown currently and even though they can crawl off of leaves and around containers in the laboratory, it is not clear if they may be moving from leaf to leaf on coffee plants in the field. Whether the decrease is due to active removal by *Azteca* or by the CLR-midge actively leaving the leaf in the presence of *Azteca*, the effect is more pronounced where there are more CLR-midges on the leaf. This density dependent change in the number of the CLR-midges only in the presence of the ants suggests that the most likely explanation has to do with foraging behavior of the ant. Effectively a high density of CLR-midges would reduce the encounter time and result in increased recruitment and subsequent removal of larvae from the leaves.

A plausible alternative hypothesis for the observed patterns in the time series of figure 2. could be that the *Azteca* ants spread the fungal pathogen on coffee plants around their nest. Given that other insects have been shown to carry spores on their bodies and have been suggested as long-distance vectors (Crowe 1963), it is not outside the realm of possibility that these ants could contribute to the local spread of the pathogen. If *Azteca* were directly responsible for this observed pattern of higher pathogen at sites where they are present by spreading it on plants, one would expect that this pattern would be approximately consistent throughout the time series.

Understanding the dynamics of predominately top-down controlled systems such as pests in agriculture within the context of the contingences of the communities in which control agents are embedded, presents a challenge for both farmers and ecologists alike. Here we provide evidence for a trophic cascade that results in the release of the most important pathogen of coffee, highlighting that it is not enough to only understand the consumer-resource dynamics of such systems but how they fit into the community. While the appearance of this trophic cascade is seemingly only operative when the natural enemy of the system is at relatively high densities, the effect was most pronounced during the height of the epidemic which is precisely when effective top-down control is most critical for coffee farmers. Given that coffee agroecosystems such as the one studied here are replicated similarly around the world with many of the same organisms transplanted into the regionally specific ecologies of their regions, opportunities for natural experiments to gain understanding of how similar trophic motifs interact in different ecological communities can provide a useful tool for ecologists to further our understanding of population regulation.

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Authors contributions: Z H-F, IP, JV all conceived of the study jointly. Z H-F conducted the experiment and analysis; Z H-F wrote the first draft of the manuscript and all authors contributed critically to subsequent drafts. IP and JV acquired funding for this study.

Data Availability Statement: Data used in the manuscript will be made freely available with DOI upon publication and code for analysis will be available on github.com/ZHAJIANF

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Supplementary Material

Exploring the data for a density dependence effect of Azteca on CLR-midge

The laboratory experiment was conducted using a range of initial densities of CLR-midge that were matched on the control and Azteca-exposed treatment. Data were analyzed in attempt to detected any signature of a density-dependent effect of *Azteca* on the CLR-midges. To do this, we looked at the change in the number of CLR-midges on leaves on both treatments after 24 hours divided by the initial number of CLR-midges to control for densities. Figure S1. Shows the fractional change in CLR-midge for paired control and Azteca-treatment data.

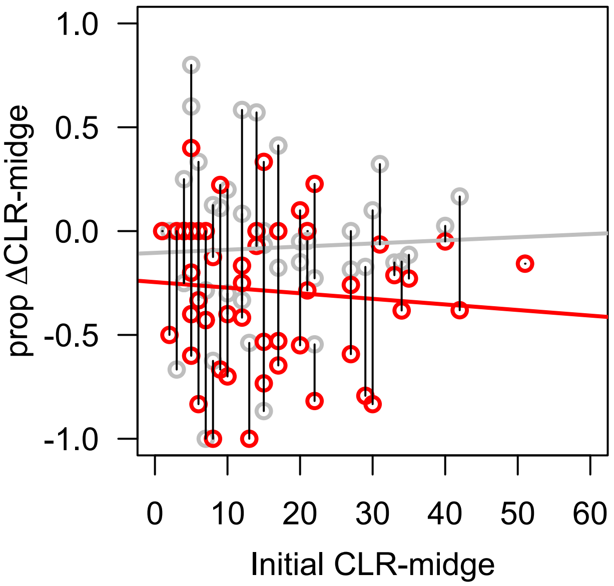

Figure 10.4: Shows the fractional change in CLR-midge for control and Azteca-treatment against the initial number of CLR-midge. Red points are the Azteca-treatment and grey points are the control treatment. Black lines connecting points show the paired treatments. Grey and red lines show the linear regressions of each treatment.

Given the data was paired, we looked at the absolute value of the difference between the controls and Azteca-treatment. No significant effect was found with a linear regression (m=-

0.005 ± -0.003, p=0.117, $R^2 = 0.027$), suggesting the initial density of CLR-midges on the leaf do not interact with the effect of *Azteca* (Figure S2.)

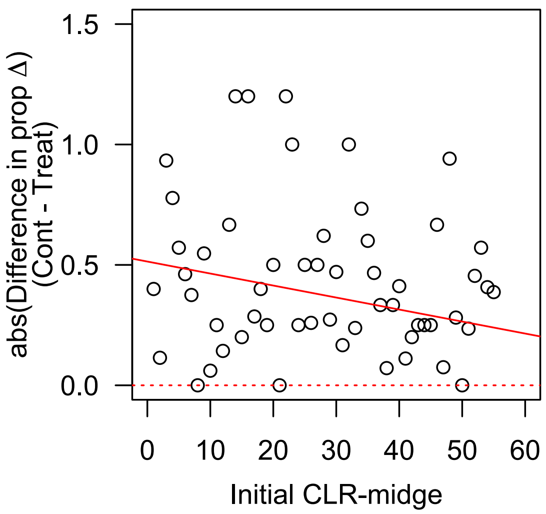

Figure 10.5: Shows the absolute value for the difference between control and Azteca-treamtnet change in CLR-midge to look for an effect of density dependence in Azteca's removal of CLR-midges.

<u>The population dynamics of CLR-midge in relation to CLR in Mexico</u>

Smaller scale surveys were conducted on three 20mx20m plots to understand the dynamics of the natural enemies *L.lecanii* and the CLR-midge. The number of leaves with CLR, *L. lecanii* and CLR-midges were surveyed every other week on each plant that fell within the 20mx20m area of the plots. We suggest that the data from the 20x20m plot surveys lend clues as to why we see a seasonal impact of *Azteca* on CLR dynamics. Note in Figure 2 that populations of the CLR-midge strongly track the seasonal dynamic of the CLR and peak just prior. This suggests that the population growth of the CLR-midge is greatest leading up to the peak of CLR, and thus its ability to provide top-down pressure on the pathogen will be greatest in the phase of the CLR cycle. Given the previously reported negative association between Azteca and CLR-midge, it is possible the results from the 45ha survey can be explained by Azteca distributing top-down control by CLR-midges.

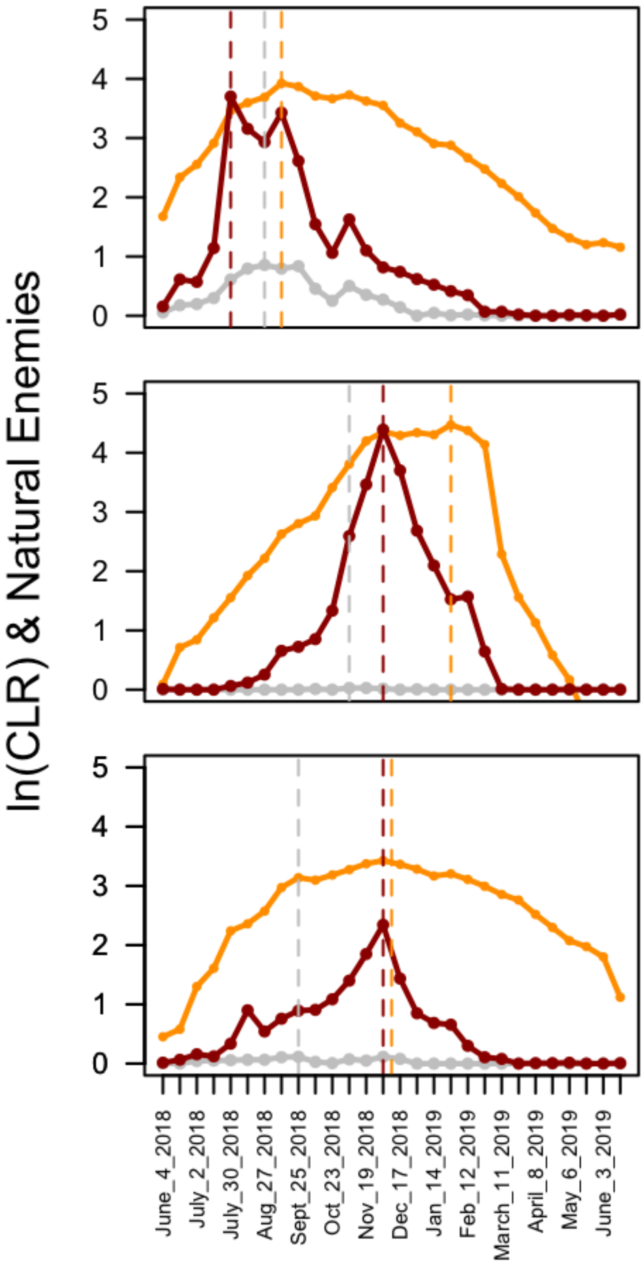

Figure 10.6: Data from the three 20x20m plots showing the average number of leaves on the leaves with CLR (orange), CLR-midge (red), and L.lecanii (grey) for a year cycle of CLR infection. The vertical dashed lines correspond to the time of peak infection for each organism.

Each panel of the plot shows the dynamics of a different 20x20m plot on the same farm. Note that Azteca nests were not present in any of the plots here

Chapter 11 Citrus Intercropping Structures the Interaction Network of Autonomous Biological Control in Puerto Rican Coffee Agroecosystems

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Abstract

In agroecosystems, the question of population regulation is of particular interest for practitioners of agriculture when considering pests and pathogens. Understanding the forces that shape the dynamics of pest regulation is of importance, especially in regard to management practices that may influence ecological processes. Here we explore how the management of inter-cropping citrus with coffee rewires complex networks of ecological interactions which include invasive ants, their mutualists, and pathogens. We show, through large scale surveys across the coffee producing region of Puerto Rico, that the inter-cropping of citrus influences the ant communities found on coffee farms as well as the density of their *Hemipteran* mutualist partners. We also find that the fungal pathogen of coffee, the coffee leaf rust (CLR), experiences higher levels of attach by a parasitic fungi, *L.lecanii*, when citrus is present. Using fine scale surveys of ants, *Hemipterans* and coffee leaf rust we show supporting evidence for the supporting hypotheses that citrus promote elevated hemipteran densities on coffee which in turn results in higher levels

of parasitism of *L.lecaniii* on coffee leaf rust through an indirect network of interactions. These findings have potentially significant implications for the management of the coffee leaf rust.

Introduction

Attempts to understand the operative forces that structure ecological populations have a long and varied history in ecology (Andrewartha & Birch 1954; Hairston et al. 1960; Murdoch 1966; Turchin 1995; Hixon et al. 2002). In agroecosystems, the question of population regulation is of particular interest for practitioners of agriculture when considering pests and pathogens. While population regulation may take many forms, there is growing interest in leveraging ecological processes to provision the ecosystem service of biological control. By taking advantage of the community of natural enemies and the network of interactions with agroecosystems, it has been proposed that pests and pathogens may be regulated without frequent intervention (Murdoch et al. 1985; Lewis et al. 1997; Vandermeer et al. 2010; 2019; Cruz-Rodríguez 2016).

Here we aim to understand how the assembly of novel ecological communities within agroecosystems impact the dynamics of ecological processes and the subsequent provisioning of the ecosystem services of biological control. We use the coffee agroecosystem and a widespread and devastating pathogen of coffee, the coffee leaf rust (CLR), *Hemileia vastrix* as a model system in Puerto Rico. In coffee agroecosystems, the potential for autonomous top-down control of what is the most economically devastating pest of coffee, the CLR, has become a point of theoretical and practical inquiry since it reached epidemic status in Central America in 2013 (Hajian-Forooshani et al. 2016; 2020; Vandermeer et al. 2019). Understanding the ecological factors operative in some regions of coffee production where the CLR pathogen is kept under control versus others where it is at epidemic status, has practical implications for coffee producers around the world.

While there are multiple natural enemies of the CLR whose community ecology is relatively poorly understood at this point, work done to date suggests that communities of fungal mycoparasites may be important for controlling the CLR in various regions of production (Carrión and Rico-Gray 1987; Jackson et al., 2012; Hajian-Forooshani et al., 2016; James et al., 2017; Zewdie et al., 2021). In particular 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), where it was found to have higher attack rates on CLR. *L. lecanii* is both mycoparasitic as well as an entomopathogenic fungus which attacks a wide range of insects, but notably sap-feeding *Hemipterans* such as scale insects (Jackson et al. 2012). It has been demonstrated that *L. lecanii*'s attack of 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., 2012).

An important component of the interaction network which leads *L.lecanii* to attack CLR, at least in Mexico (Jackson et al., 2012; Vandermeer 2010), is the presence and tending of *Hemipterans* by ants in the agroecosystem. Jackson et al., (2012) found that the dominant arboreal ant, *Azteca serisur,* helps build populations of the green coffee scale (GCS), *Coccus viridis*, which then create local concentrations of *L.lecanii* in space that are negatively associated with CLR. Given that GCS (and Hemipterans more generally), *L.lecanii* and CLR and present in many coffee producing regions around the world in conjunction with *Hempiteran* tending ants, the possibility for a similar type of interaction network to exist elsewhere is plausible. One such region includes Puerto Rico, where throughout the coffee producing region of Puerto Rico, scale insects, and in particular, the green coffee scale (GCS) (*Coccus viridis*), is widespread (Perfecto et al. 2018). It occurs not only on coffee plants, but is also a common pest of citrus, which is widely cultivated and intercropped with coffee (Smith et al., 2004).

The community of ants throughout the coffee producing region of Puerto Rico has recently come under study by Perfecto and Vandermeer (2020), who discovered that three invasive ant species on the island, *Wasmannia auropunctata*, *Solenopsis invicita*, and *Monomorium floricola* (hereby just referenced as their genus names) are the most dominant in coffee farms surveyed. While signatures of competition (especially between *Wasmannia* and *Solenopsis*) were detected in structuring the ant communities realized distributions, management factors were also found to be associated with variable distribution of these important invasive species. In particular, it was found that *Wasmannia* was more abundant on shaded coffee farms, while *Solenopsis* more abundant on farms with little shade. One unexplored aspect of this system is how the widespread cultivation of citrus may impact the distribution of these ants, given that citrus is a shade providing tree in these agroecosystems and potentially harbors communities *Hemipterans* that may serve as an important resource for both *Solenopsis* and *Wasmannia*. Furthermore, the possible higher incidence of *Hemipterans* may result in higher levels of *L.lecanii* locally on farms resulting in more parasitism of CLR by *L.lecanii*, setting the stage for an important cascade of ecological interactions that could have implications for this important pathogen of coffee.

Here, our central hypothesis is that the community of natural enemies, and especially fungal mycoparasites, which include *Lecanicillium lecanii*, are the main controlling agents that keep the CLR pathogen at relatively benign levels in regions such as Puerto Rico. Additionally, we hypothesize that the widespread cultivation of citrus with coffee in Puerto Rico promotes the community of fungal parasites that control the CLR by harboring populations of *Hemipterans* which are alternate hosts for fungal parasites such as *L.lecanii.* Here we explore these interactions across the coffee producing region of Puerto Rico and further seek to understand how the dominant invasive ants across the region may shape this interaction network.

Methods

26 farm analysis

Monthly surveys were conducted on the 26 farms to monitor populations of GCS, CLR and attack of CLR by *L.lecanii*. Each farm had a 10x10m meter plot where 20 coffee plants were monitored each month. Data presented here for GCS, CLR, *L.lecanii* use the average values per plant across a whole year of surveying each month from Aug 2018-July 2019. Ant surveys were conducted on the same farms using the same coffee plants for the pests. A detailed description of the farms used in the study as well as the methodology of the ant survey can be found in Perfecto and Vandermeer (2020).

To understand the potential impact of citrus-coffee intercrop management on the community of ants, we conducted ordination in the form of non-metric multidimensional scaling analysis (NMDS). Both Bray-Curtis and Jaccard dissimilarity weights were used for the data. Bray-Curtis to understand compositional changes that include abundance and Jaccard to look at the presence and absence of species on the farms. We tested for significance differences between citrus-coffee farms and coffee farms with analysis of similarity (ANOSIM) statistical test implemented from the vegan package in R.

Citrus farm survey

To understand how the populations of Hemipterans correspond to ant community, we measured the number of out of 10 randomly branches on each plant coffee for incidence of green coffee scale, helmet scales, and mealy bugs. The presence or absence on a branch was noted and the number of branches with each Hemipteran was used in our analysis. For surveys of the coffee leaf rust, five leaves representing the most heavily infected with CLR on the plants were selected haphazardly on each plant. The percentage of the leaf covered in CLR was estimated along with the percentage of CLR covered with *L.lecanii*.

Results

Landscape dynamics of CLR community and the influence of coffee-citrus intercropping

A more general analysis of the same dataset can be found in Perfecto & Vandermeer (2020), and for our purposes we will focus on how the dominant ant community relates to the intercropping of coffee and citrus and the CLR. Throughout the coffee producing landscape where surveys were conducted, we had ten farms where citrus was intercropped with coffee, and sixteen farms where only coffee was grown. Broadly we find evidence to support the hypothesis that the management of citrus in coffee farms in the region influences the ant community dynamics in the system. We see a marginal significance in the divergence in the ant communities though ordination analysis using the Bray-Curtis dissimilarity measurements ($p = 0.055$) (Fig. 1), but no significance difference was noted when using the Jaccard dissimilarity ($p=0.43$). These results taken together suggests that while the identities of the ant species present on the communities is not significantly difference on coffee-citrus intercrops versus coffee monocrops (Jaccard), that the relative abundances of the species (Bray-Curtis) trend toward diverging based on this management factor (Fig 1).

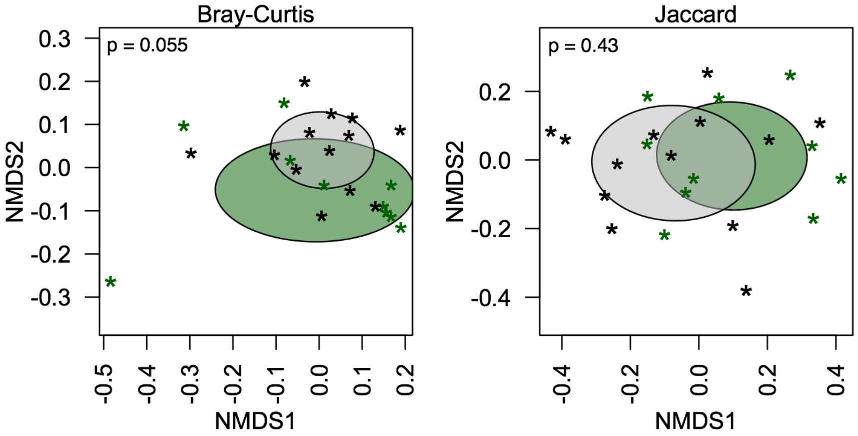

Figure 11.1: Non-metric multidimensional scaling analysis of ant communities across the 25 coffee farms surveyed in Puerto Rico. Left panel shows ordination with Bray-Curtis dissimilarity (p=0.055) and right panel with Jaccard dissimilarity (p=0.43).

While we note a trend towards differences in the composition of the ant communities across the landscape with respect to management of citrus, we do not see any difference in the average number of species or the average abundance of the ant community based on citrus management (Fig 2). These results taken together with the ordination suggests that very targeted, and possibly species specific differences in the ant communities are realized when farms are managed for citrus-coffee intercrops.

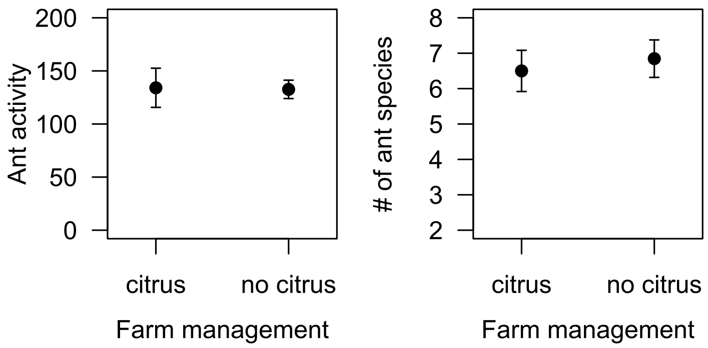

Figure 11.2: Shows no impact of citrus-coffee inter-crop management on the ant abundance (number of baits occupied) across the 25 farms and no impact on the number of ant species found on the farms.

When considering the three most dominant ants on coffee farms surveyed in the region, *Wasmannia*, *Solenopsis*, and *Monomorium* (see Perfecto and Vandermeer 2020), we find significant impacts of coffee-citrus intercrop management on the dominance of the ants. The largest effect is with *Wasmannia*, where they occupy on average approximately 4 times as many baits on citrus-coffee intercrop farms than farms that solely grow coffee (Fig 3). For *Monomorium* we find a significant difference between citrus-coffee intercrop and coffee monocrop but in the opposite direction as *Wasmannia*, where they tend to be more abundant on monocropped coffee farms. As for *Solenopsis*, we see no effect of the citrus-intercrop on their dominance of those farms.

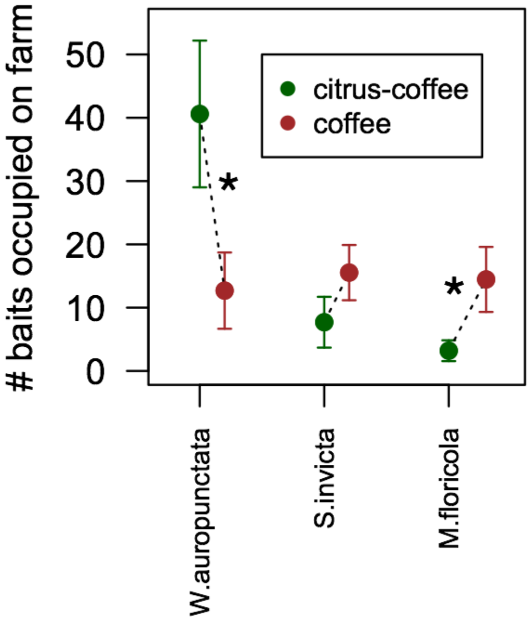

Figure 11.3: shows the relative dominance (as measure by the # of baits occupied on average for a farm) Wasmannia auropunctata, Solenopsis invicta, and Monomorium floricola

In addition to the citrus-coffee intercrop influencing the structure of the ant community, we also note differences in the CLR, GCS and attack of CLR by *L.lecanii*. First we note that citrus-coffee farms have significantly less CLR infection than farms with solely coffee (Fig 4a). In addition to the lower quantities of CLR, we also find higher attack rates of *L.lecanii* on CLR on citrus-coffee farms. Although this effect is relatively small (approximately 3% difference in attack rate), it is statistically significant. Finally, we also note a statistically significant difference in the amount of GCS, where they are more abundant on citrus-coffee farms than only coffee farms.

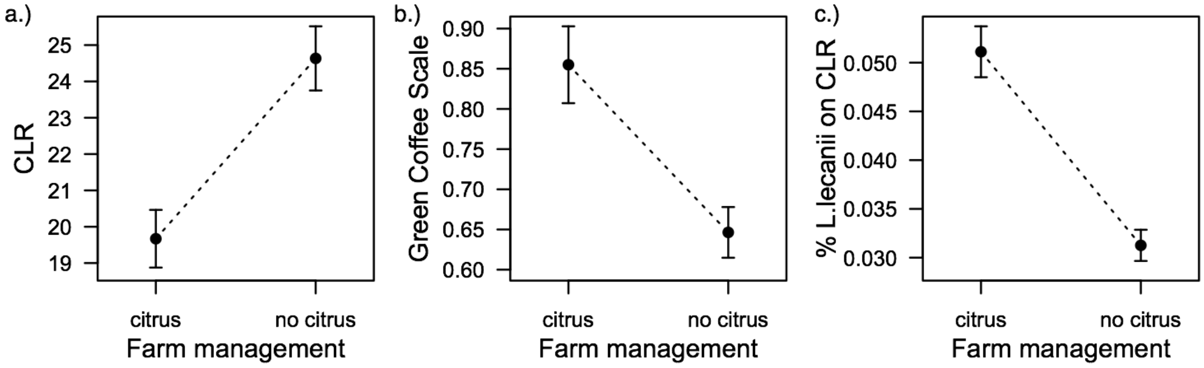

Figure 11.4: relationship between citrus-coffee intercrop and a.) the average amount of CLR on those farms, b.) the amount of green coffee scale on coffee plants, and c.) the % of CLR leaves attacked by the mycoparasite *L.lecanii* . p-values < 0.05 for all plots

Local dynamics of CLR community and dominant ants

Our surveys of the spatial distribution of the ant community, scale insect community and CLR community suggests evidence for influence of ants on the dynamics of the CLR through a network of direct and indirect interactions. Figures 5 and 6 together suggest differential overlap between the two most dominant ants on the plot, *Wasmannia* and *Solenopsis*, with regards to the GCS and CLR. Notably, *Monomorium*, who is one of the most dominant ants in the region, is not very common on this plot. Analysis of *Monomorium* can be found in supplementary material. The realized spatial distribution of *Wasmannia* and *Solenopsis* has been hypothesized to be driven largely by interspecific competition between three dominant ant species in this region (see Perfecto and Vandermeer 2020). We note that *Wasmannia* is largely constrained to the left-hand side of the plot in a largely clustered distribution (Fig 5) while *Solenopsis* more homogeneously across the plot (Fig 6). We find the relatively strong relationship between the distribution of

Wasmannia and GCS, while no such relationships exists with *Solenopsis* and GCS. Furthermore, we note strong overlap with the distribution of *Wasmannia* and the distribution of *L.lecanii*, both on GCS and CLR (Fig 5). We see similar patterns with regards to *L.lecanii* on both CLR and GCS and *Solenopsis* (Fig 6), where dense concentrations of *Solenopsis* are associated with high amounts of *L.lecanii* on CLR and GCS, although this pattern is more varied due to their dominance across the plot.

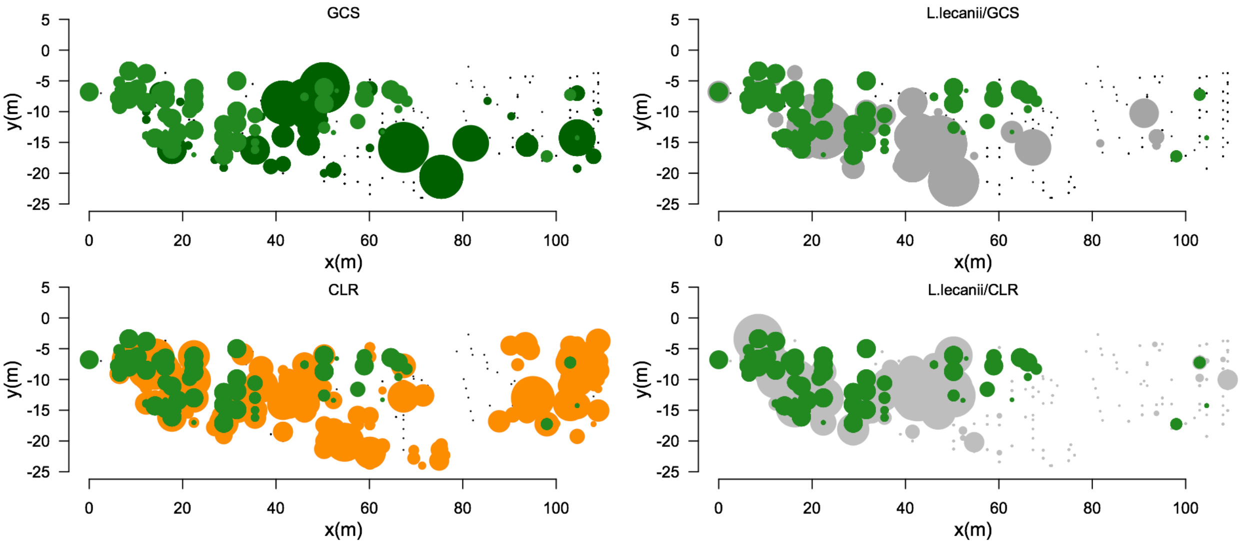

Figure 11.5: The spatial distribution of CLR and GCS both without (left panels) and with (right panels) L.lecanii parasitism in relationship to the spatial distribution of Wasmannia. The spatial distribution of Wasmannia is in light green, while GCS is in dark green, CLR is in orange, L.lecanii on GCS is in dark grey and L.lecanii on CLR is in lighter grey.

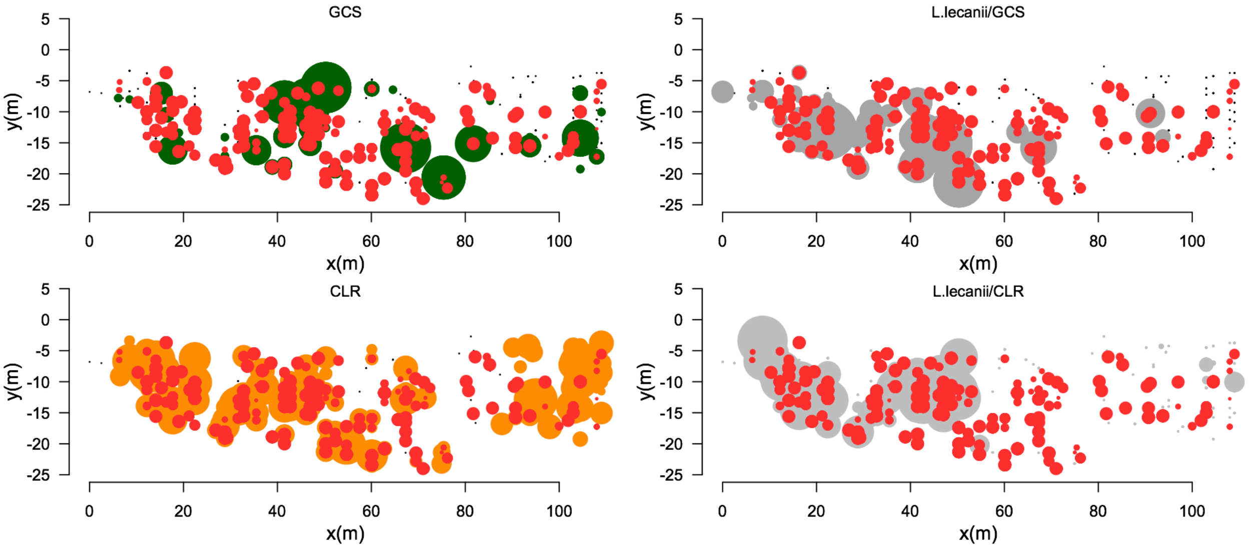

Figure 11.6: The spatial distribution of CLR and GCS both without (left panels) and with (right panels) L.lecanii parasitism in relationship to the spatial distribution of Solenopsis. The spatial distribution of Solenopsis is in red, while GCS is in dark green, CLR is in orange, L.lecanii on GCS is in dark grey and L.lecanii on CLR is in lighter grey.

The spatial distributions from the plots above translate into statistically significant relationships between these two dominant ants and *Hemipteran*-CLR community. First, we find a significant increase in the amount of GCS attacked by *L.lecanii* as the dominance of *Solenopsis* (Estimate: 0.23 +- 0.049, p< 0.001) and *Wasmannia* (Estimate: 0.23 +- 0.052, p< 0.001) increase (Fig. 7). Showing, somewhat unsurprisingly that as the ants become more abundant on a plant, they increase the populations the GCS and thus the GCS's pathogen becomes more abundant. Next, we find no relationships between increasing dominance of *Solenopsis* and attack of *L.lecanii* on CLR. In contrast, we note a significant increase in the average amount of L.lecanii parasitism of CLR as the dominance of Wasmannia increases on coffee plants (Fig. 8).

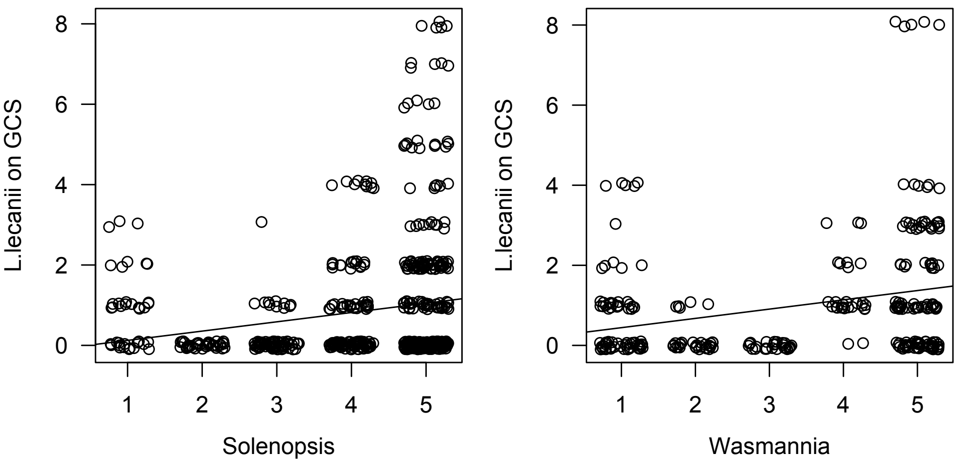

Figure 11.7: The abundance of Solenopsis and Wasmannia and their relation to the parasitism of GCS with L.lecanii. Note significant increase in L.lecanii on GCS as the number of baits occupied by Solenopsis and Wasmannia increases. Note that points are randomly perturbed on the x and y axes to better illustrate the underlying distribution of the data on the plot.

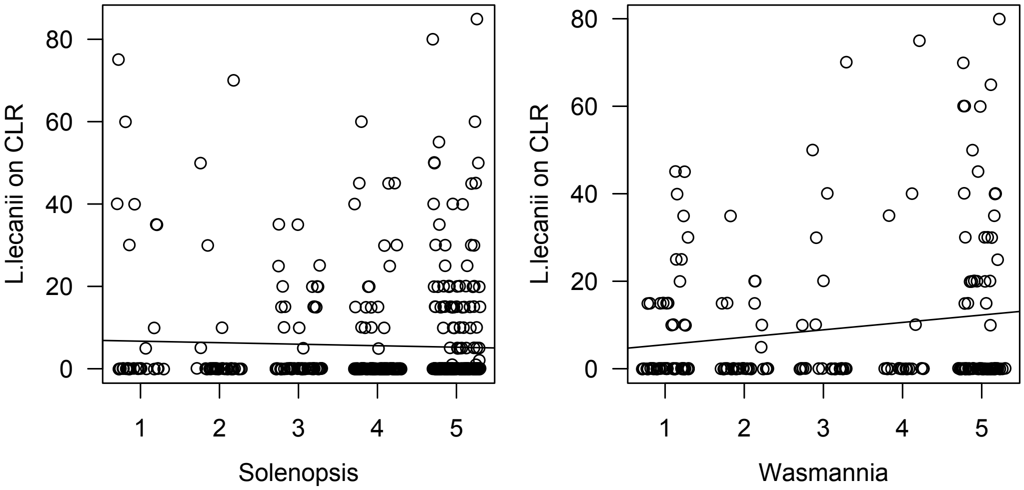

Figure 11.8: Relationship between increasing dominance of (a) Solenopsis and (b) Wasmannia and how the parasitism of CLR is related. No significant relationship between an increase in Solenopsis and L.lecanii on CLR (p = 0.45), while a significant positive effect of Wasmannia on L.lecanii parasitism of CLR is seen (p= 0.0149). Note that points are randomly perturbed on the x and y axes to better illustrate the underlying distribution of data on the plot.

We found strong evidence for non-linear relationships between the dominance of both *Solenopsis* and *Wasmannia* and the *Hemipteran* communities (Fig 9). In particular, we see that at low dominance of both ants that there is no difference in amount of healthy and infected *Hemipterans* on a coffee plant. When either ant is at intermediate dominance (2-3 baits occupied out of the 5 placed on the plant) we see significantly more healthy Hemipterans than Hemipterans infected with *L.lecanii*. Interestingly, when either ant becomes more dominant (more than 3 baits out of 5 occupied on the coffee plant) then we see the relationship flip and there are significantly more *Hemipterans* infected with *L.lecanii* than uninfected. This non-linearity in ant abundance with the parasitism of *L.lecanii* on scales suggests density dependent dynamics that have been suggested elsewhere with relationship to ants and similar hemipteran communities (Vandermeer & Perfecto 2019).

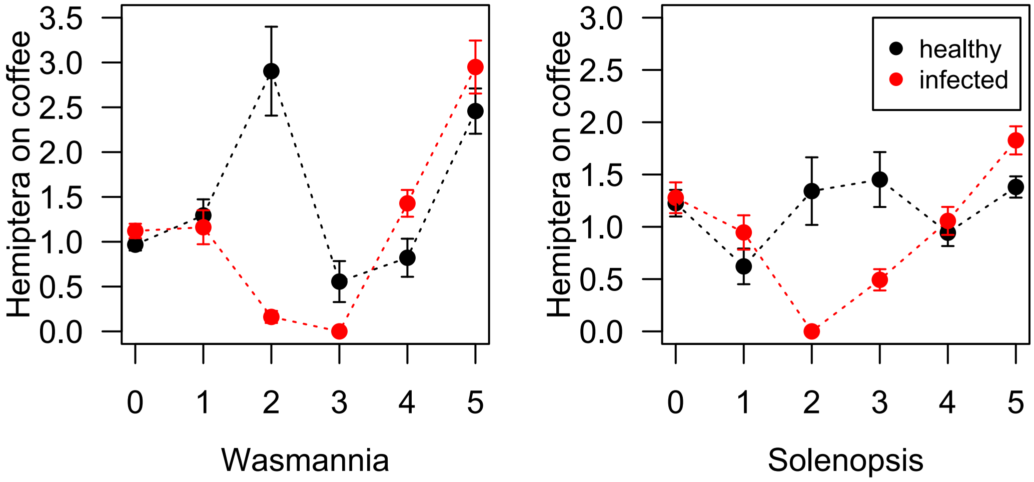

Figure 11.9: The average incidence of healthy and infected hemipterans on coffee as they related to the dominance of Wasmannia and Solenopsis. Black points and lines represent healthy hemipterans and red infected by L.lecanii.

Given the positive significant impact of both *Solenopsis* and *Wasmannia* on the amount of GCS infected with *L.lecanii* in conjunction with significant effect of increasing *Wasmannia* dominance on the attack of *L.lecanii* on CLR, we tested to see if there was a relationships between the amount of *L.lecanii* on GCS and *L.lecanii* on CLR on coffee plants. We discovered that there is indeed significant positive relationship between increasing GCS with *L.lecanii* and CLR with *L.lecanii*.

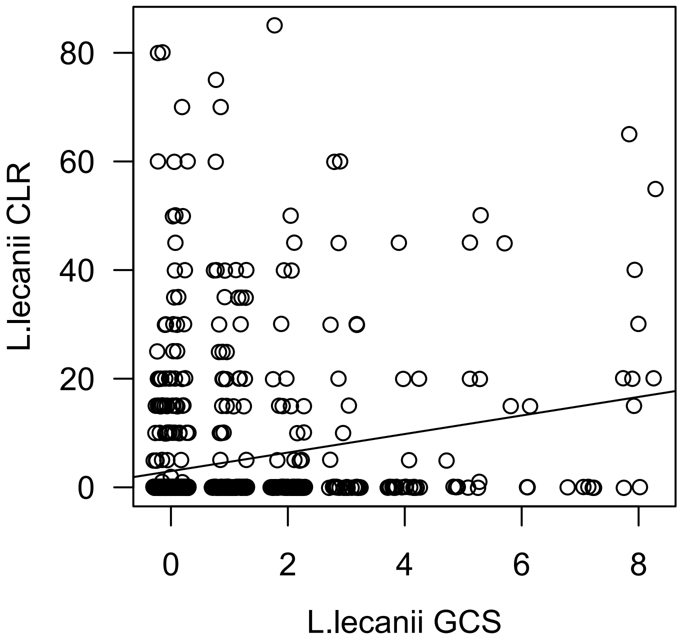

Figure 11.10: Relationship between increasing GCS infected with L.lecanii on a coffee plant and percentage of L.lecanii covering CLR on coffee leaves. Note significant linear increase in L.lecanii on CLR as L.lecanii infected GCS increase (p<0.001).

Discussion

There is an emerging understanding that diverse and regionally specific communities of natural enemies of CLR are present in different regions of coffee production (Hajian-Forooshani & Vandermeer 2016). Prior work in coffee agroecosystems in Puerto Rico and Mexico has shown how the composition of the communities differ between regions (Hajian-Forooshani et al. 2020), and, even when members of the natural enemy communities overlap, their population dynamics differ dramatically between regions (Hajian-Forooshani et al. 2016). Our analysis here lends support to the hypothesis that this observed difference in natural enemy communities is at least in some part linked to both the management of the agroecosystems but also the local ecological communities in which the natural enemy – CLR subsystem is embedded.

Here we build on prior analysis by Perfecto and Vandermeer (2020) of the ant communities within the coffee producing region of Puerto Rico. We find support for the idea that citrus is at least in part contributing to the structure of the competitive ant communities throughout the farms surveyed. While changes in species identity do not seem evident, the relative dominance of the common ants in the region changes in accordance to whether the farm is inter-cropping citrus with coffee (Fig 1). While this shift in the ant communities do not emerge from the overall number of species and the overall ant abundance (Fig 2), we find evidence for species specific impacts of the citrus-coffee intercrop. In particular, we find strong evidence that the most dominant ants throughout the region being influenced by this management factor.

More than other ants in the community, *Wasmannia* is strongly associated with the cultivation of citrus on coffee farms, where they tend to be approximately 4x more abundant on citrus-coffee intercrops than on coffee monocrop farms (Fig 3). Given prior results suggesting that *Wasmannia* is more dominant on more shaded farms (Perfecto and Vandermeer 2020), the relationships with citrus further supports this trend. In contrast, to *Wasmannia* we find that *Monomorium* was less abundant on citrus-coffee intercrops than coffee only farms, and no significant effect of *Solenopsis* abundance (Fig 3). While the distribution of *Solenospsis*-dominated verses *Wasmannia*-dominated farms has been previously noted (Perfecto and Vandermeer 2020), as well as their competitive interactions, the precise competitive mechanisms which result in the observed data remained unknown. We suggest that one potential mechanism to explain these results is that the presence of citrus alters the competitive interactions between *Solenopsis* and *Wasmannia*. We hypothesize that the widespread incidence of *Hemipterans* in citrus offers an important resource for *Wasmannia* on intercropped farms that allow them to thrive and become more abundant. While *Solenopsis* does forage on and nest near citrus (personal observations), they predominantly forage and are competitively dominant on the ground where they build their nests. This is in contrast to Wasmannia which actively nests and forages both on the ground and arboreally (Yitbarek et al. 2017)

Our analysis suggests that the underlying dynamics of the ant community across the landscape interacts with the management of citrus and forces the CLR-GCS-*L.lecanii* dynamics throughout the region. With respect to GCS populations across the landscape, we find that coffee farms which are intercropped with citrus have significant more GCS on coffee plants. Additionally, we find higher proportion of CLR leaves with *L.lecanii* and overall less CLR on these citrus intercropped farms (Fig 4) These results taken together are consistent with the hypothesis that citrus promotes populations of GCS who then increase the density of the CLR mycoparasites, such as *L.lecanii*, that spill over and result in the control of CLR. Importantly we propose that the promotion of GCS populations at the landscape scale is driven by the ant community and in particular the action of *Wasmannia* who is found in higher abundance, along with their mutualists, GCS, on citrus-coffee intercropped farms.

While analysis of the 26 farms give us a course picture into the general dynamics of how this subset of the ecological community interactions with intercrop management, our detailed surveys of the ant community and *Hemipteran* community on a single citrus farm lends insight into the mechanisms driving the large-scale patterns described above. First we note a strong signal of spatial overlap between the distribution of *Wasmannia* on the plot and the incidence of *L.lecanii* attack both on GCS and CLR (Fig 5 and 6). This manifests as significant relationships with both dominant ants on the farm, *Wasmannia* and *Solenopsis* having significant relationships with the amount of uninfected GCS found on coffee plants. Although the signal is stronger for *Wasmannia* than *Solenopsis*, it is apparent for both species (Fig 7). While we generally see a signal of increase, the pattern is more nuanced when considering the average amount of healthy and infected hemipteran populations at the plant level. Interestingly, we find that the relationship between ant dominance of a coffee plant and the amount of healthy and *L.lecanii* infected GCS is strikingly non-linear in nature (Fig 9). We see clear signal of the basic ecology of the host-pathogen system being forced by the dominant ants in the agroecosystem. The lack of difference between healthy and infected GCS when ants are low densities show the baseline of GCS-*L.lecanii* interaction, but when the dominant ants become more abundant we see healthy scales are more abundant than *L.lecanii* infected scales. Interestingly we find that this patter reverses for both species when they become highly dominant on a single plant (at least 4 baits occupied by the ant) (Fig 9). This represents the basic ecology of host-pathogen systems that has been noted between ants, *Hemipterans* and *L.lecanii* in other systems (Vandermeer and Perfecto 2019), where a critical population threshold leads to the sudden onset of a disease outbreak.

Given the clear signal for the interaction between *Solenopsis* and *Wasmannia* driving *L.lecanii* outbreaks in *Hemipteran* populations, the question is now if and to what extent this *L.lecanii* outbreak on GCS in coffee plants leads to higher parasitism of *L.lecanii* on CLR. We find that increasing amounts of GCS with *L.lecanii* on coffee plants is associated with increasing amount of CLR parasitized with *L.lecanii* (Fig 10). This provides supporting evidence for the hypothesis that *L.lecanii* "spills-over" from infected *Hemipteran* populations to CLR, consistent with other ant-hemipteran-*L.lecanii*-CLR systems (Jackson et al., 2012). Interestingly we find no signal of plants dominated by *Solenopsis* translating to having higher amounts of *L.lecanii* on CLR, but we do find a significant relationship between *Wasmannia* and CLR parasitism by *L.lecanii* (Fig 8). Although both dominant ant species are associated with higher amounts of GCS, the cascading effect which results in more *L.lecanii* on CLR is only apparent for

Wasmannia, possibly due to in part to the higher absolute densities of the healthy and infected GCS on *Wasmannia* dominated plants (Fig 9).

Intercropping is known to provide synergies in agroecosystems such as facilitation (Li et al., 2014) and natural enemy attraction (Cook et al., 2007). Here we show how through a series of direct and indirect interactions that's citrus-intercrop facilitates the attack of an important fungal pathogen by mycoparasites. Citrus harbors *Hemipteran* communities which we suggest promotes dominant ants whom create a positive feedback through their mutualistic association leading to high *Hemipteran* populations not only on citrus but also on the coffee grown alongside it. This elevated *Hemipteran* population subsequently leads to higher amounts of their mycoparasites which also attack the fungal pathogen of coffee, CLR. This demonstration of how management of an intercrop forces feedbacks within the interaction networks of ecological communities in agroecosystems leading to pest control can serve as a template for uncovering similar complex interaction networks within agroecosystems.

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Conclusions

In Chapter 1, we addressed the issue of how ecological interactions result in the creation of dynamic spatial patterns in ecosystems. By developing a mechanistic framework based on the demographics of both consumer and resource in the system, we demonstrated the feedback of how interactions create spatial pattern and how spatial pattern structures ecological interactions in our system of an arboreal ant and its parasitoid which occur on a coffee farm in southern Mexico. Importantly, this chapter provides a framework for the study of consumer-resource induced spatial patterns, something which has empirically been lagging behind work on intraspecific mechanisms (Rietkerk and Van de Koppel 2008). It is our hope that this mechanistic approach, based on the demography, sheds light on the mechanism of pattern formation in other ecosystems. Chapter 2 builds on Chapter 1 by asking how a dynamic spatial pattern constrains basic ecological interactions in space and through time. By using the idea of a pilot pattern (Vandermeer and Jackson 2018), we explore a coupled-map lattice of the Nicholson-Bailey system where the host has high-quality patches of resource interspersed in a matrix of low-quality resources. We ask how the dynamics of this heterogeneous resource background structures the host-parasitoid dynamics in the system, showing how the speed of change in environmental heterogeneity constrains the interactions.

Next in Chapter 3, we ask how spatial structure emerges in agroecosystems, as well as how that spatial structure may influence processes which are constrained to it. Using the coffee leaf rust system as inspiration, we develop a spatial model to recreate the distribution of coffee plants in coffee agroecosystems and then show the planting arrangement can influence the dynamics of pathogens in the system. We find that under certain conditions, small changes in the underlying spatial distribution of the hosts can cause large catastrophic shifts in the pathogen dynamics. Chapter 4 asks how migration in metacommunities influences community structure. Although there exist a variety of experiments in laboratory microcosms and theoretical explorations, we approach this questions by using a system of intermediate complexity in the form of the leaf litter arthropod community found in a coffee agroecosystem in Mexico. We experimentally manipulate the system and show that migration differentially structures different trophic levels of the community.

Chapter 5 continues the theme of community organization and asks how various couplings of multiple predator-prey systems influence the synchrony dynamics of communities as well as if multiple models of communities may correspond to each other. Given that a multitude of ecological communities exhibit overlap in resource consumption (cross-feeding) as well as resource competition, we showed how community dynamics modeled by Lotka-Volterra system can be approximated by the Kuramoto model when the focus of investigation is understanding the dynamics of synchrony (Vandermeer 2004; Vandermeer 2006). This work provides an alternative way to conceptualize ecological communities, where dynamics take front and center in opposition to questions of coexistence and stability (Vandermeer et al., 2021).

Following some theoretical explorations of community structure, the dissertation turns towards the empirical system of the coffee leaf rust (CLR) and explores the community ecology of the pathogen along with its community of natural enemies. Chapter 6 offers an overview of our empirical study system, exploring some of the history of the pathogen and reframing much of the agronomical focus which has dominated research on the pathogen towards a community ecological perspective. We synthesized the literature on the natural history and ecology of the system and point towards future research directions that will both further our understanding of ecological systems as well as the important fungal pathogen.

With an introduction of ecological community associated with the coffee leaf rust, Chapter 7 explored regional differences in the CLR communities in Mexico and Puerto Rico. The notable differences in the regions are that in Mexico the pathogen had recently been at epidemic status, while it has never been so in Puerto Rico. We found that Puerto Rico harbors a more diverse community of natural enemies than Mexico and suggest that the novel assemble of natural enemies in Puerto Rico may in part contribute to the benign nature of the pathogen on the island. Following-up on the dynamics of the CLR community in Puerto Rico, Chapter 8 explored how the community assembles and organizes itself through time in the CLR seasonal cycle. We found that different members of the natural enemy community had drastically different responses, with evidence of both facilitative and antagonistic interactions operative within the community. Importantly, we also note evidence that supports the hypothesis that members of the natural enemy community reduce the spore loads of CLR. Chapter 9 continues to explore antagonistic interactions within the natural enemy community and find evidence of intraguild predation in the community.

In Chapter 10, we link the pattern forming consumer-resource system to the system of the CLR. We demonstrated that the dominant spatially clustered ant, *Azteca*, has an indirect positive impact on the CLR, increasing the pathogen load on plants where present. We demonstrate that while there are conflicting indirect effects from *Azteca* on two natural enemies, *L.lecanii* and *Mycodiplosis*, that the direct negative effect of *Azteca* on *Mycodiplosis* is possibly the causative agent of the observed effect. Finally, in Chapter 11, we continue to explore how dominant ants interact with the community of the CLR, but this time in Puerto Rico. We find support for the hypothesis that the intercropping of citrus in coffee agroecosystems in Puerto Rico promotes the abundance of *Wasmannia*, an important invasive ant on the island, and thus leads to a cascade of interactions which results in the mycoparasite, *L.lecanii*, attacking CLR more frequently on citrus-coffee intercropped farms.

Taken together this dissertation offers several case studies of how heterogeneity emerges in ecological systems and how that heterogeneity alters community structure and subsequent provisioning of ecosystem services such as biological control. I feel confident that the empirical portions of this dissertation could have very well been written with the focus being on a community other than the ones described here. The general concepts and processes presented here for this system should be operative in a variety of other ecological communities embedded in a variety of agroecosystems. It is my hope that these basic questions about the emergence and consequences of spatial heterogeneity in ecosystems are seen not as only an academic curiosity, but also appreciated for their potential importance in our understanding of agroecosystems. The heterogeneity in and around agroecosystems has the potential to interact with issues which are currently of great concern such as the loss and preservation of biodiversity as well as the emergence and suppression of pests and pathogens around the world (Perfecto et al., 1996; Vandermeer et al., 2019). Fully leveraging ecology in all its complexity and nuance to better understand and manage agroecosystems is a struggle I am looking forward to continue engaging with and hope this dissertation positively contributes to in some way, however insignificantly.

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