Population level consequences of spatial networks: species coexistence and implications for invasive species.

by

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"Discovery is the ability to be puzzled by simple things"

- Noam Chomsky-
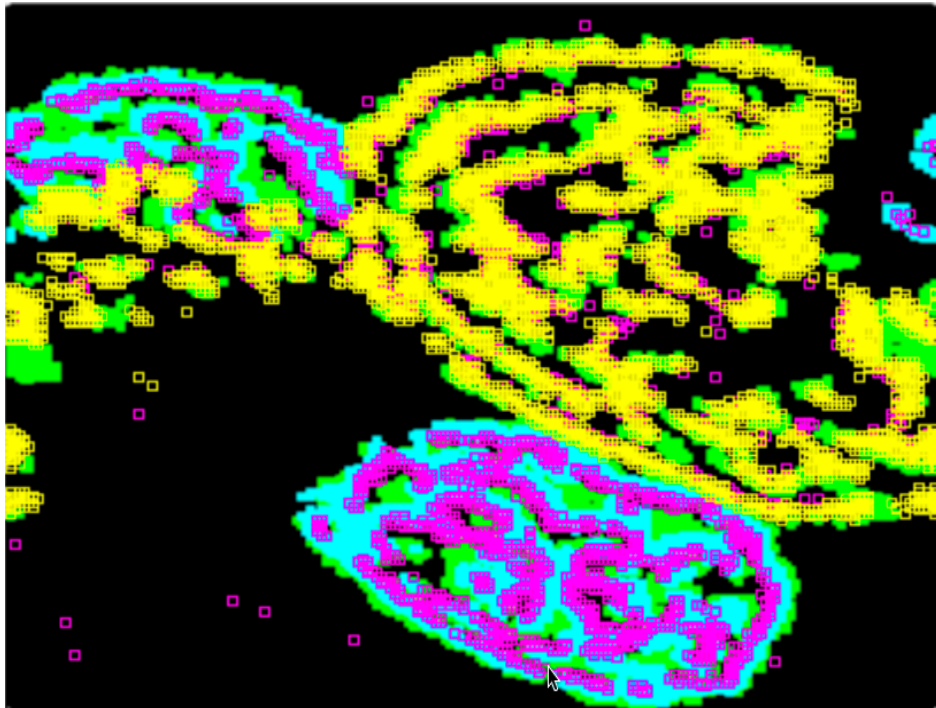
DEDICATION

To the custodians of the EEB Department.

To my custodian mother, this one is dedicated to you.

To my wife, for your unconditional support and love.

To my father, for teaching me to explore the world.

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pursue my educational goals and for this I am always grateful. My wife and best friend Diana has been my rock with her continual source of support and encouragement throughout this process. I especially cherish the moments when she accompanied me doing fieldwork on coffee farms in Mexico and Puerto Rico. She caught the "Wasmannia Blues". I am glad she did.

Preface

Ecologists seek to explain why so many species can coexist given intense competition for limited resources in environments (Hutchinson 1961). This long-standing question is rooted in the competitive exclusion principle, which states that two species competing for a limited resource cannot coexist (Gause 1932), and that the species better able to gain the resource will cause the inferior species to go extinct. When competition is strong, large differences in competitive ability will eliminate the inferior competitor, while small differences in competitive ability will result in coexistence (Gause 1932; Chesson 2000). The prediction that all inferior competitors will be eliminated has presented ecologists with an enigma since the rich diversity of species occurring in nature do not appear to abide by this principle, many species seemingly in strong competition with one another evidently coexisting (Hutchinson 1961). One approach to resolving this enigma was to consider species differences, differences in the ecological niche, that prevented inferior species from exclusion, laying the basis for our understanding of multi-species coexistence through the prevention of competitive exclusion (Macarthur and Levins 1967; Connell 1978; Levins 1979; Chesson 2000). Within this framework, if niche differences disfavor species that are common and favor those species that are rare then diversity can be maintained

The basic idea that species richness is the product of niche differences in the environment emanates from the classical Lotka-Voterra dynamics in which species coexistence is determined by competition coefficients (Macarthur and Levins 1967; May and Leonard 1975). In this scenario, two species competing weakly (i.e. small competition coefficients, thought to correspond to small niche overlap) leads to coexistence whereas strong competition results (i.e. large competition coefficients, thought to correspond to large niche overlap) in the competitive exclusion of one of the species (e.g., Gause's principle). The LV-framework has been expanded to multi-species communities (Levins 1968; May, 1972) with little difficulty. Much of this research has subsequently focused on small competition coefficients that allow for species coexistence, avoiding some of the complications that emerge with strong competition

(Huisman and Weissing 1999, 2001). We are left to ask what happens when competition coefficients are sufficiently large (i.e. > 1)? One useful construct was provided by Yodzis (1978), who placed competitive communities along a continuum ranging from dominance-controlled communities with small competition coefficients to founder-controlled communities with large competition coefficients. According to classical theory, species cannot coexist when competition coefficients are sufficient large, and the relevant question is simply which one will dominate. More recently theoreticians have pursued some of the complexities involved in founder-controlled communities(Armstrong and McGehee 1980; Huisman and Weissing 1999; Vandermeer 2011).

One potential mechanism for species coexistence in founder-controlled communities is intransitive competition. In recent years, there has been considerable interest in explaining species coexistence through the formation of intransitive networks beginning with the classic paper by May and Leonard (1975). Unlike transitive communities, whereby higher ranked species in the hierarchy always out-compete lower ranked species, intransitive communities contain groups of species that do not follow the fundamental rule of transitivity. For instance, we can envisage a three-species community structured in the following way: species A out-competes species B, species B out-competes species C, while species C out-competes species A, an intransitive loop. Although there are inevitable winners in all pairs-wise interactions,there is no single winner at the community level (e.g., Laird and Schamp 2006; Vandermeer and Yitbarek, 20??). To date, intransitive interactions have been found across a wide range of taxonomic groups, including plants (Soliveres et al. 2015), marine organisms (Buss and Jackson 1979), bacteria (Kerr et al. 2002), and lizards (Sinervo and Lively 1996). The general effect is that increasing intransitive loops tends to result in more species protected from competitive exclusion, thus leading to coexistence (Vandermeer 2011; Vandermeer and Yitbarek 2012).

A long held assumption in classical competition theory is that communities are well-mixed system, with individuals panmictically dispersing. In the case of many sessile organisms (e.g. barnacles, plants, corals) the well-mixed assumption is evidently wrong, and mean field

approximations are useful but sometimes misleading. The inclusion of spatial structure in ecological models, where interactions occur at local scales, have shown that multi-species can coexist that otherwise would have gone extinct under panmictic conditions (Durrett and Levin 1998). Two separate spatial mechanisms have in recent years been identified in theoretical studies that can give rise to species coexistence. Several theoretical studies have described the formation of spatial mosaics as a result of local interactions that maintain a robust structure composed of discrete patchworks across long time period. (Bascompte and Solé 1995; Sherratt 2006). On the other hand, several studies have highlighted the formation of spiral wave patterns (Boerlijst et al. 1993; Kerr et al. 2006; Vandermeer and Yitbarek 2012) based on intransitive competitive networks (i.e. species A beats B, and species B beats C, but species C beats species A). While mosaic and spiral patterns have been described as separate phenomena in the literature, we construct a theoretical framework that combines both forms by interrogating competitive networks and its consequences for species coexistence. We quantify competitive networks along a continuum from symmetrical to asymmetrical competition, by using the covariance of the row and column sums of the competition matrix as a way to measure the relative degree of symmetrical versus assymetrical competition (Levins 1968). **In Chapter I**, we extend this theoretical framework by examining the effects of spatial mixing (ranging from small-world to random networks) on species coexistence. We show that under various levels of mixing species diversity declines more rapidly under asymmetrical competition.

To what extent these niche mechanisms play out in the natural world remains an open question. Biological invasions serve as a "natural" experiment across ecosystems to test various predictions about competition and community structure. Charles Elton (1958) was the first to provide a general theoretical framework to study ecological differences between native and exotic patterns of biodiversity. His biotic resistance hypothesis (Elton 1958), postulates that regions with high species richness are less prone to invasion because exotic species are less likely to find available niches as compared to regions with lower species richness. As a result, we expect a negative relationship between native and exotic species richness. Although the biotic

resistance hypothesis has been well studied in plant communities (Fridley et al. 2007), we lack such experimental tests for ant communities between native and introduced ranges. Exotic ants are known to negatively reduce the abundance and richness of native ant communities (Porter and Savignano 1990) presumably through competition since interspecific competition is assumed to be a major driving force structuring ant communities (Fellers 1987; Savolainen and Vepsäläinen 1988; Perfecto and Vandermeer 2011). In **Chapter II**, we investigate the invasion dynamics of the exotic ant *Wasmannia auropunctata*. We test the biotic resistance hypothesis by comparing the competitive interactions of *W. auropunctata* and local ant species between its native range of Mexico and introduced range in Puerto Rico. The results provide support for the biotic-resistance hypothesis in which native ant species in Mexico are able to resist *W. auropunctata,* reducing it to just another member of the ant community, not exhibiting any of the noxious characteristics of an invasive. This in stark contrast to the introduced range in Puerto Rico. However, this pattern depends strongly on temporal aspects of competition that seemingly affects the invasion process.

The discovery-dominance tradeoff has been described as a possible mechanism for species coexistence (Adler et al. 2007) where species traits are placed along an environmental gradient with some species excelling at discovery ability of resources while other species excel at dominance of resources, with minimal overlap in such traits resulting in separate niches. We expect that in regions with high species richness exotic ant species are less likely to penetrate the community structures, while in areas with lower species richness exotic ants are more likely to find available and un-occupied niches. It is important to understand how exotic ants are organized within local species assemblages in the native range in order to determine their success in the introduced range. To date, studies on exotic ant have primarily focused on the Argentine ant *L. humile* and the red-imported fire ant *S. invicta* in the introduced range (Lebrun and Feener 2007; Feener et al. 2008). To this end, **Chapter III** examines the ecological differences in resource discovery and recruitment by *W. auropunctata* within its native range (Mexico) and introduced range (Puerto Rico). We found that *W. auropunctata* was slower at discovering

resources in Puerto Rico, as compared to the native range of Mexico. This is in contrast to the widely held view that exotic ant species are dominant because of their rapid discovery abilities, suggesting that competitive traits such as resource discovery and recruitment are not necessarily indicative of invasive success.

Parasites are thought to play an important role in the spread and facilitation of invasive species into ecosystems with consequences for biodiversity and community structure (Tompkins et al. 2010). While much of this research has focused on how parasites influence direct interactions (i.e. competition and predation), indirect effects by parasites can strongly influence the structuring of ecological communities (Werner and Peacor 2003). Parasites can affect the outcome of competitive interactions between exotic and natives species through density-mediated indirect effects (DMII) and trait-mediated indirect effects (TMII) (Vandermeer et al. 2010; Hsieh and Perfecto 2012). However, the relative degree to which parasites indirectly influence the invasion process remains unexplored. In **Chapter IV**, we examined the effects of phorid flies on the competitive outcome between the arboreal ants *W. auropunctata* and native ant *L. iniquum* in Puerto Rico including a study of the searching efficiency of phorid flies in detecting *L. iniquum* nests. My results show that phorid fly parasitoids indirectly influence competitive interactions by attacking the host-ant *L. iniquum* and consequently providing an advantage to local spread of *W. auropuntata* populations in Puerto Rico. Furthermore, the spatial dynamics of arboreal ants shows that *L. iniquum* seeks protection from phorid fly parasitoids by moving their nests to *W. auropunctata* dominated patches.

Lastly, we examined to what extent competitive network structure occur in real-world ecosystems. In **Chapter V**, we examined competitive network structures among arboreal twig nesting ant species at local and regional spatial scales across a 50-ha coffee farm. The study related the competition networks of twig nesting ants in the lab to their relative abundances in the field by determining the rankings of twig nesting ants at the community level solely from the structure of a competitive interaction network. We found that dominance rank of ant species was not correlated with relative abundance across the entire coffee farm; however, transitive

networks were correlated with increases in relative abundance at the local scale compared with relative abundances at the regional scale. However, intransitive competition networks did occur in 13 % of all cases despite our relatively small species pool. This seems to suggest that nested intransitive networks appear to exist among a particular subset of species.

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Abstract

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Chair: John H. Vandermeer

Spatial mixing and species coexistence. Previous theoretical work (Vandermeer and Yitbarek 2012) showed that the self-organization of spatial patterns serve as an important mechanism for species coexistence. In this work, we developed a theoretical framework of inter-specific competition that generated two distinct spatial patterns: mosaics and spiral waves. The spatial patterns in the model depended on the covariance of the competition matrix. In chapter I, we extended this theoretical framework by examining the effects of spatial mixing (i.e. dispersal) on species extinctions. We show that the rate of species extinctions was more pronounced under a negative covariance as local species were being rapidly replaced by distant species in the spatial model.

Priority effects: late arrival by an exotic ant. Chapter two examines the role of priority effects by the exotic ant *W. auropunctata* invasion in Mexico and Puerto Rico. We investigate the ecological differences in resource discovery and recruitment by *W. auropunctata* within its native range (Mexico) and introduced range (Puerto Rico). We found that *W. auropunctata* was slower at discovering resources in Puerto Rico, as compared to its native range of Mexico. This is in contrast with the widely held view that exotic ant species are dominant because of their fast discovery abilities, suggesting that competitive traits such as resource discovery and recruitment are not necessarily indicative of invasive success.

Biotic resistance limits invasiveness. In chapter three, we investigated the invasion dynamics of the little fire ant *Wasmannia auropunctata*. We studied competitive interactions between *W. auropunctata* and native ants in Mexico and Puerto Rico. We conducted experiments over short-term and long-term time intervals in both the field and laboratory to determine relative

differences in number of workers found at baits, time to resource discovery, and recruitment time to resources. We showed that *W. auropunctata* is a relatively rare ant species in a highly diverse region of Mexico, but is locally dominant due to its population structure. Meanwhile, in Puerto Rico, *W. auropunctata* is a dominant ant species in a mostly depauperate region. Our results provide support for the biotic-resistance hypothesis in which native ant species in Mexico are able to resist *W. auropunctata* as compared to the introduced range of Puerto Rico. However, this pattern depends strongly on the temporal aspect of invasion. We propose that temporal considerations are necessary when determining the competitive abilities of native and exotic ants.

Trait-mediated indirect effects by parasitoids. In chapter four, we examined the effects of phorid flies on the competitive outcome between the arboreal ants *W. auropunctata* and native ant *L. iniquum*. Furthermore, we investigate the searching efficiency of phorid flies in detecting *L. iniquum* nests. We found that the presence of phorid fly significantly reduced recruitment of *L. iniquum* workers to baits through induced behavioral changes thereby increasing the ability of *W. auropunctata* to acquire resources. In addition, we found that phorid arrival time in isolated patches of *L. iniquum* patches was faster as compared to *L. iniquum* nests located within *W. auropunctata* patches. Our results show that phorid fly parasitoids indirectly influence competitive interactions by attacking the host-ant *L. iniquum* and consequently providing an advantage to local spread of *W. auropuntata* populations in Puerto Rico. However, the spatial dynamics of arboreal ants shows that *L. iniquum* seeks protection from phorid fly parasitoids by moving their nests to *W. auropunctata* dominated patches.

Competitive network structure and twig-nesting ant abundances. In chapter five, we examined competitive networks among twig nesting ant species at local and regional spatial scales across a 50-ha coffee farm. The study related the competition networks of twig nesting ants in the lab to their relative abundances in the field by determining the rankings of twig nesting ants at the community level solely from the structure of a competitive interaction network. We found that dominance rank of ant species was not correlated with relative abundance across the entire coffee farm; however, transitive networks were correlated with

increases in relative abundance at the local scale compared with relative abundances at the regional scale

CHAPTER I

REDUCTION OF SPECIES COEXISTENCE THROUGH MIXING
IN A SPATIAL COMPETITION MODEL

Abstract

Many ecological systems exhibit self-organized spatial patterns due to local interactions. Such patterns can promote species diversity and therefore serve as an important mechanism for biodiversity maintenance. Previous work has shown that when species interactions occurred at local spatial scales, species diversity was greatest when robust mosaic spatial patterns formed. Also, intransitive interactions led to the emergence of spiral patterns, frequently resulting in multispecies coexistence. In some instances, intransitive interactions reduced species diversity as the consequence of competitive hierarchies. Here we extend and broaden this line of investigation and examine the role of global competition along a continuum ranging from spatial mosaics to spiral patterns. While previous models have predicted that species diversity is reduced when interactions occur over larger spatial scales, our model considers the stochastic effects of mixing on species diversity, in the context of various network structures as measured by the covariance of row and column sums of the competition matrix. We find that diversity is rapidly lost when dispersal and interactions occurs over relatively small spatial scales (i.e. small amounts mixing). This pattern of diversity loss is more pronounced under negative and zero covariance levels, while species diversity is maintained under a positive covariance.

Introduction

Persistence of species that seem to be occupying the same niche is enigmatic since, according to the venerated ecological idea of the competitive exclusion principle, no two species can occupy the same niche (Gause 1934), suggesting that the process of competition should result in a continued reduction of biodiversity over the long run when groups of species appear to be occupying similar niches (i.e., in the case of founder-controlled communities, those with very high rates of competition). Nevertheless many communities of multiple coexisting species have been reported on a restricted resource base (or niche base) despite Gause's axiom. Numerous mechanisms have been proposed to demonstrate that diverse communities of species can coexist together (Chesson 2000; Hubbell 2001), despite high levels of competition. One potential mechanism, demonstrated both theoretically and empirically for biodiversity maintenance, is based on intransitive competition (May and Leonard 1975; Sinervo and Lively 1996; Kerr et al. 2002). It has been theoretically shown that intransitive competition in a competitive network can maintain large number of coexisting species (Huisman and Weissing 1999; Huisman and Weissing 2001; Laird and Schamp 2008; Schreiber and Killingback 2013). However, the outcomes of competitive interactions, based on measurements of competitive network structures, are often represented as pairs of species interactions, not accounting for the fact that competitive outcomes in a community are the consequences of the network structure itself. Furthermore, theoretical studies on intransitive competition in a spatial context have focused on one end of the competitive network spectrum, asymmetrical or unbalanced competitive interactions, but without considering symmetrical or balanced competitive interactions that have been reported to form remarkable mosaic structures in spatial models (Vandermeer 2011; Vandermeer and Yitbarek 2012). We can generally frame competitive interactions in terms of a network composed of vertices (species) that are connected by edges (analogous to competition coefficients in Lotka-Volterra systems). Rather than casting competitive outcomes solely as a subset of interactions whereby two individuals interact along vertices of a graph, we contend that individual interactions take place within a wider set of "community" interactions ranging along a continuum of balanced and unbalanced competitive interactions. Thus, for example, if species j has a generally large effect on all the other species in the community (which is to say $\sum \alpha_{i_j}$ is

large) and the effect of all the other species in the community on species j is also large (which is to say $\sum \alpha_{j_i}$ is also large), we refer to this as a balanced state. Contrarily if species j has a generally small effect on all the other species in the community (which is to say $\sum \alpha_{i_j}$ is small) but the effect of all the other species in the community on species j remains large (which is to say $\sum \alpha_{j_i}$ is remains large), we refer to this as an unbalanced state (fig 1).

Our approach thus formulates species interactions as a statistical community concept (Vandermeer 2011; Vandermeer 2012). We take the convention (Goldberg and Landa 1991) of referring to the column sums of the competition matrix (i.e. $\sum \alpha_{i_j}$) as the "effect" competition and the row sums of the competition matrix (i.e., $\sum \alpha_{j_i}$) as the "response" competition. Thus, when effect and response competition are positively correlated we have balanced competition but when effect and response competition are negatively correlated we have unbalanced competition. We previously developed a spatial model to simulate interspecific competitive interactions that examined the degree to which the formation of spatial patterns related to the number of coexisting species in the community, depending on balanced and unbalanced interactions (Vandermeer and Yitbarek 2012). Our results showed that balanced competition resulted in the formation of robust mosaic spatial patterns harboring the greatest number of species. When simulating unbalanced competitive interactions our results showed the frequent occurrences of multiple intransitive interactions as in the classical rock-paper-scissor game, often outcompeting the remaining species in the lattice. However, in some cases unbalanced competitive interactions resulted in a strict competitive hierarchy, with the most superior species dominating the community (Vandermeer and Yitbarek 2012). While our theoretical framework showed important differences between balanced and unbalanced competitive interactions, our results only held true for local spatial interactions based on a cellular automata model. In the present communication, we continue to explore the relationship between balanced and unbalanced competition as it relates to the number of species, but here we consider the stochastic effects of varying levels of mixing.

Our hypothesis is that scenarios of balanced competition maintain a high degree of species richness under local competition (unmixed systems) and to a lesser degree for global competition (mixed systems) where species go extinct much more rapidly as neighboring competitors are replaced by competitors migrating from far away. We expect species richness to

decline rapidly under unbalanced competition for both local and global competition as dominant species out-compete subdominant species in a well-mixed system (contrary to the case in an unmixed system). Using a cellular automata model we explore global competitive interactions in space.

The Theoretical Background

The outcome of inter-specific competition is usually modeled according to the basic dynamics of the Lotka-Volterra equations whereby the different arrangements of competition coefficients in the community matrix determine the final winner during competitive battles. From previous work (Vandermeer 2012), we extend this framework into discrete time and space including both the competitive effect/response interactions and local density dependency for each species. We generally speak of a good effect competitor when the species in question is considered to be good at "offense" generally (e.g., efficiently consuming a resource) while a good response competitor is good at "defense" (e.g., able to survive under conditions of reduced availability of a key resource). In either case, in our model a species offense and/or defense is weighted by its population density. We subsequently compute "total competition" by taking the ratio of the competitive effect and competitive response, in which the species with the highest total competition coefficient becomes the winner for that particular point in the lattice. The degree to which interactions represent either balanced or unbalanced interactions have been noted as an important component in determining species diversity (Vandermeer 2012). One way to measure the relative degree of balanced versus unbalanced competition is to consider the covariance of the competition matrix, a framework originally suggested in a different context by Levins (Levins 1979). The row sums and column sums of the competition matrix will be either positively correlated (in the case of balanced competition) or negatively correlated (in the case of unbalanced competition), with the corresponding covariance of the rows sums and columns sums either positive (balanced) or negative (unbalanced). The covariance then measures the effect of species i on all other species in the community in relation to the effect of all the other species in the community on species i, the latter of which is the "response" of species i. Our previous work (Vandermeer and Yitbarek 2012) showed that when only local spatial interactions are considered, a positive covariance results in the greatest number of species in the communities while a negative covariance results in the fewest number of species. In addition, a negative

covariance frequently generated intransitive loops that were also implicated in determining the number of species in the community (Vandermeer 2012). We extend our original model, which had been strictly based on local interactions, by incorporating well-mixed interactions and determine how the covariance of the competition matrix (both balanced and unbalanced competition) relates to the total number of species in the community. Furthermore, we evaluate the effect of mixing on the time to extinction and species survivorship.

The Model

We compute the competitive effect of a species i at a point (m,n) in the lattice as:

$$E_i(m,n) = \sum_{x=m-1}^{m+1} \sum_{y=n-1}^{n+1} N_i(x,y) \sum_{j=1}^{S} N_j(x,y)\alpha_{j_i}$$

where $N_i(x,y)$ is a binary variable representing the population density of species i at point x,y and the α_{j_i} parameter denotes the strength of competition effect of species i on species j. Similarly we compute the competitive response of species i at point (m,n) as,

$$R_i(m,n) = \sum_{x=m-1}^{m+1} \sum_{y=n-1}^{n+1} \sum_{j=1}^{S} N_j(x,y)\alpha_{i_j}$$

We finally compute the total competition of species i by taking the ratio of the effect/response:

$$C_1(m,n) = \frac{E_i(m,n)}{R_i(m,n)}$$

where μ is a stochastic variable ranging between zero and 1. Thus, we compute the total competition for each lattice point (m,n) and the species with the largest $C_i(m,n)$ is the winner at that particular lattice point. The total competition is subsequently computed for all the lattice points (100x100 cells). When $C_i = C_j$ at a lattice point we select the winner at random. The covariance of the competition matrix is the covariance of the row sums and column sums (Vandermeer and Yitbarek 2012).

$$cov_{ij} = \sum_{i=1}^{12} [(\alpha_{._j} - \overline{\alpha})(\alpha_{i_.} - \overline{\alpha})]$$

Modeling Global Competition

Global competition occurs when the system is well mixed, that is, when the spatial structure from one iteration is only a part of the input to the next iteration. Specifically, the mixing means that rather than subjecting the occupant of a lattice point to the competitive effect only of the individuals in the surrounding eight lattice points in the Moore neighborhood, individuals from random positions on the total lattice replace one or more of the individuals in the surrounding Moore neighborhood. This "mixing" creates a situation in which the individual at any particular lattice point is subjected to some element of the set of individuals over the entire lattice, thus the appellation global competition. We simulated species interactions for global competition by varying parameters for both positive and negative covariances. We then randomly replaced some of the 8 neighbors surrounding a cell with an occupant from a random cell in the entire lattice. The number of random replacements varied from 1 to 8 neighbors, representing a degree of mixing from small to large. All updating of cell status was done synchronously after the total competition was computed for each cell. The model was run for 300 time steps, 50 replications each run, on a 100 x 100 lattice with periodic boundaries. We explored the behavior of the model by adjusting the covariance of the competition matrix from a highly negative covariance to a highly positive covariance. To do so, we set aij parameter values from a uniform distribution ranging from 0 to 1. For the positive covariance, we set the values above the diagonal equal to the values below the diagonal. For the negative covariance, we stipulated $a_{i_j} = 1 - a_{j_i}$. Finally, we added stochasticity to the symmetry of the original matrix from a uniform random distribution $\{1.0, 1.2\}$.

Results

We investigated species richness and time to extinction for communities at various levels of mixing for balanced (positive covariance) and unbalanced (negative covariance) competition. The general expectation for well-mixed communities is that species richness should quickly decline as more individuals selected randomly from the entire matrix displace local individuals. As expected, our model results in species richness declining over time, but at different rates depending on whether competition is balanced or unbalanced and the competitive network structure. We observed that species richness began to decline rapidly under balanced competition but was even more pronounced under unbalanced competition (fig 1.1). In the case of balanced

competition, species richness declines rapidly under partial mixing. This pattern is consistent when we look at the time to extinction. The extinction rate (as measured by time to the first extinction event) occurred significantly faster when competition was unbalanced (negative covariance) whereas in highly balanced competitive communities (positive covariance) time to first extinctions is higher, meaning that the extinctions occurred at a much slower rate (fig 1.2).

An alternative approach to modeling population level consequences of spatial network structure is to impose heterogeneity in the dispersal of individuals. Whereas the well-mixed approach assumes a very high dispersal rate of individuals at each iteration of the model, coexistence patterns can differ when corresponding to weakly mixed communities (i.e. involving lower dispersal rates). While our simulation results show that well-mixed communities undergo rapid extinction rates, it's less clear what the coexistence criteria is for weakly mixed communities. Therefore, we were interested to what extent weakly mixed communities promoted coexistence. To do so, we related the network structure of the community to the covariance of the matrix. It has previously been noted, that the extent to which a community is either symmetrical (balanced) or asymmetrical (unbalanced) serves as an important indicator of the number of species in a given community. The relationship between the covariance and species diversity has been explored in previous work (Vandermeer and Yitbarek 2012).

Here we extend this approach by examining the relationship between covariance and species diversity in the case of weakly mixed communities with varying dispersal rates. We explored mixing levels of 1 substitution in greater detail (i.e., one cell randomly chosen from the entire lattice and a random cell in the Moore neighborhood replaced with it), because the overall mixing was effectively large, even though this was our lowest level of mixing. The 10,000 cells each had one neighbor randomly changed each cycle through the model, and consequently our "low" level of mixing was effectively not very low. To study the effects of yet lower levels of mixing, we modified the one replacement scenario with a probability of one replacement. That is, at each iteration, we randomly sampled a single cell in the lattice with some probability. Thus the Moore neighborhood of a particular cell was modified with that cell, meaning that we could adjust the level of "mixing" (d) to range from one substitution 100% of the time, to one substitution 0% of the time, where we refer to d as the dispersal rate. Examining the number of species as a function of the covariance, with varying dispersal rates we obtain the following

patterns as illustrated in Fig 1.3. We find that when d is zero, with 1-substituion, we still maintain a large number of species in the community as indicated by the positive relationship between covariance of the competition and species diversity. As we increase the dispersal rate beyond 0.1, we see the slope of this positive relationship between covariance and species diversity decreasing. The rapid decline of species diversity under a negative covariance seems to indicate that increases in dispersal rate eliminate intransitive loops. This becomes particularly evident when assessing species diversity with dispersal rates ranging between 0.4-1.0. In some cases communities consist of triplet species, in which cases intransitive loops eliminate remaining species, while in the majority of cases 1 dominant species takes over due to the formation of a competitive hierarchy. The relationship between the positive covariance and species diversity appears to be more transient (fig 1.33). Overall, the pattern for the positive covariance shows a gradual decline in species richness with increasing d. However, a closer look at the pattern suggests that the transient nature of species richness depends on the covariance values. The range in covariance values between 0.4 and 1.3 has the highest number of species. At low dispersal rates, species form intransitive loops at the lower bound of covariance values, but as d increases we find that species richness declines rapid. At covariance values above 1.3, we observe a similar trend in that species richness declines rapidly with increasing dispersal rates. However, the zone between 0.4 and 1.3 exemplifies a transient state that alternates between mosaic pattern structures consisting of 10-12 species or spiral patterns in the form of triplets that reduce species richness. These alternate stable states appear to be consistent across a range of d values and may prevent species from going extinct.

The changes in spatial pattern formation in communities ranging from weakly mixed (i.e. low dispersal rates) to well mixed (i.e. high dispersal rates) are illustrated in Fig 1.4. In the absence of mixing, we generate mosaic patterns for the positive covariance and spiral patterns for the negative covariance. As we model interactions with 1-replacement under low dispersal (10%) we find that the general pattern still coincides with high species diversity. However, as we increase the dispersal rate to 1, the mosaic pattern structure is maintained albeit at a lower level of species richness, while the strong spiral patterns are reduced to only 3 species in the system. As we increase the level of mixing to 3-replacements in the Moore neighborhood under high dispersal rates, we find that the mosaic and spiral patterns completely disappear with all species going extinct (fig 1.4).

The generalization that species diversity is maintained with increasing covariance values still holds true at low levels of mixing (i.e. 1-replacements). However, as the dispersal rate increases the linear pattern changes to an abrupt transition with extinctions at low and high covariance values. Meanwhile, species richness is still maintained at a critical covariance zone between 0.4 and 1.3 with patterns consisting of both spiral and mosaic patterns. As we increase the mixing level (i.e. 2 and 3-replacments) extinctions are more prevalence across all covariance values and species richness rapidly declines as illustrated by monoculture patchworks (fig 1.4-d). Alternative spatial patterns can emerge with intermediate level of competitive balance (i.e. covariance near zero). In the strictly local scenario (i.e. in the absence of dispersal), with intermediate levels of competitive balance, we observed the formation of both mosaic and spiral patterns depending on initial conditions (fig 1.3a). However, alternative spatial patterns emerge at extremely low d values.

As shown in fig 1.5, we find that fixed mosaic patterns merge with spiral patterns, in which spirals are embedded within the fixed mosaic patchwork. At low d values of 0.01 and 0.05, distinct patterns emerge of 4 species consisting of one triplet and one dominant species (fig 1.5). This pattern appears to be transient phenomena as we expect the dominant species to eventually take over community. A closer look at Fig 1.6, reveals that this transient pattern is taking place at the intermediate level of competitive balance near the zero covariance. At low covariance values, extinctions are high but triplets of 3 species can still be maintained. At high covariance values, mosaic pattern maintain species richness. However, it's at the intermediate level of balanced competition that we see a sudden drop in species richness. It appears that in the absence of stabilizing forces, such as mosaic and spirals, species go completely extinct (fig 1.6). This is to say, that the spatial network structure in the form of mosaic or spiral patterns provides a mechanism for species coexistence, but that in its absence communities are likely to go extinct.

Discussion

Our study investigated the degree to which species that ordinarily persist over a long period of time when spatially constrained, will also persist when well mixed, which is to say, when the strict cellular automata assumption of only local dispersal is relaxed. While it has been

well-established (Durrett and Levin 1998; Kerr et al. 2002) that well-mixed communities will more quickly reach species extinctions than unmixed communities, we were primarily interested in understanding the time course for these extinctions, specifically, how long it would take for the first few extinctions to occur in the system, and the degree to which the overall competitive structure, as measured by the relative degree of balanced versus unbalanced competitive structure, matters. While much attention regarding well-mixed communities has focused on competition that involves either unbalanced or balanced competition, our study investigates the role of both balanced and unbalanced competitive interactions in determining the degree to which communities can coexist. Using the covariance of the community matrix as our measure for symmetrical (balanced) and asymmetrical (unbalanced) competition, in earlier work we found that with only local dispersal (from the Moore neighborhood) aggregation and dissipation of mosaic patches are strongly implicated in the coexistence of species, as shown elsewhere (Durrett and Levin 1998; Kerr et al. 2002). With mixing (dispersal from the entire lattice) we find that species extinctions generally decline, as would be expected since a completely random model results in a single species surviving on the lattice (since all competition is strong, competitive coexistence at a local level is not possible). Under balanced competition extinction rates gradually increased for the first few replacements, after which all the subsequent extinctions occurred much faster when more sights in the Moore neighborhood were replaced. Under unbalanced competition, extinction rate rapidly increases after the first replacement and continues to increase at an even more rapid rate as more neighbors are being replaced.

While previous research (Vandermeer and Yitbarek 2012) has shown that local competitive interactions, when competition is balanced, maintains species diversity for many generations through the formation of rigid spatial mosaics, it is probably more likely that species interactions in nature occur somewhere between local and global mixes. Our results for the 1st generation of extinctions under balanced competition show a gradual decline for the first few replacements and remain steady for the remaining replacements. We reach what seems to be a critical point at 3 species replacements when most of the species are still maintained in the systems for up to 50 generations, after which extinctions occur far more rapidly. On the contrary, in the unbalanced case, extinctions occur almost instantaneously as the system becomes effectively more random. The rate of initial species extinctions as a result of partial mixing thus

allows us to outline scenarios under which species can still coexist, albeit for only very few replacements.

Our general spatial theory posits that when interactions take place locally, involving strong competitive interactions, two distinct mechanisms allow large number of species to coexist which can be either through the formation of fixed mosaics or spiral structures such as intransitive loops. The basic difference between these two mechanisms is directly related to competitive network structure as measured by the covariance of the community matrix. In the case of unbalanced competition (i.e. negative covariance), the probability of an individual that occupies a cell and becomes part of an intransitive interaction with its nearest local neighbor resulting in spiral structures is relatively high. This pattern, however, was violated when we introduced mixing in the form of long-distance dispersal, which drove the system towards a random system thereby reducing the probability of generating intransitive interactions. In our model, we found that local replacement by only 1 individual with a dispersal probability of 40 % led to the rapid extinction of species in the community (fig 1.3). In the balanced competition scenario (i.e. positive covariance), the probability for the formation of fixed mosaic structures is similarly high with a greater chance of encountering conspecific neighbors in the local Moore neighborhood. However, as we mix the system with random replacements of 1-individual in the Moore neighborhood, we see a gradual decline in species richness as the probability of dispersal increases. In this case, the random replacement of a cell by a migrant is less likely to be a conspecific meaning that the fixed mosaic pattern gradually dissipates with higher rates of dispersal (fig 1.3). This trend becomes even more apparent when we increase the levels of mixing (fig 1.4). The formation of fixed mosaic patterns persists when mixing levels involves 2 replacements under high dispersal rates (100%). However, this pattern rapidly disappears by the time mixing reaches 3 replacements under high dispersal rates (100%). In a similar vein, we find that spiral structures are retained in the system up to 2-replacements after which a monoculture pattern emerges. Thus, small amounts of mixing coupled leads to the rapid loss of species richness.

While our model has primarily interrogated two extreme forms of competitive network structures (i.e. symmetrical versus asymmetrical interactions) a more interesting feature emerges at intermediate levels of competitive balances where the covariance of the community matrix is near zero. At the two extremes of competitive balances we detected spatial patterns that either

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consisted of fixed mosaic or spiral structures. However, at intermediate levels of mixing we detected patterns that merged these two patterns together. Depending on initial conditions, we obtained spiral like structures that were seemingly contained within a fixed mosaic (fig 1.5). Although alternative patterns are to be expected depending on initial conditions, these special cases emerged under extremely low dispersal rates. As a consequence of intermediate levels of competitive balance, the system reaches a critical point that rapidly leads to species extinctions (fig 1.6). In the absence of mosaic or spiral patterns, there does not exist any other spatial mechanisms that can rescue species from extinction.

Our results on the effects of spatial structure and mixing on species coexistence are in general agreement with other cellular automata models (Durrett and Levin 1998; Frean and Abraham 2001; Kerr et al. 2002; Laird and Schamp 2008; Rojas-Echenique and Allesina 2011). The general conclusion of these studies is that three-species can be maintained when interactions are localized and intransitive interactions resulting in cyclical competitive replacement lead to biodiversity maintenance. Recent extensions (Szabó et al. 2004; Laird and Schamp 2015) have included graph-theoretical approaches where intransitive competitive interactions take place on a continuum of small-world networks ranging from spatially structured to regular random graphs. In these scenarios, species coexistence is still maintained on the spatial end of the continuum but dissipates and leads to species extinctions beyond a critical point as it nears the random end of the network (Laird and Schamp 2015). Our results are in agreement with these findings in that long-range dispersal leads to rapid species extinctions in well-mixed cases. However, our work additionally examines alternative competitive interactions, such as symmetrical competition, in which the outcome of an individual competitive interaction is uncertain.

While we have examined the effect of spatial structure on a two-dimensional lattice, our work can be extended to alternative spatial configurations. For example, metacommunities composed of local populations coupled through dispersal can be used to examine the effects of spatial heterogeneity on species coexistence. Recently work (Schreiber and Killingback 2013) applying metacommunity theory to intransitive competitive interactions has found that weakly-mixed communities can still persist as long as the dispersal rate does not reach a critical dispersal threshold beyond which the community is extinction prone. This suggests that both lattice based and general metacommunity models can be used to empirically test under what conditions weakly mixed communities can still persist and maintain species coexistence. This becomes

more important as social-ecological systems are becoming increasingly coupled by long-range dispersal.

The general spatial model that we have introduced here complements existing approaches that examined effects of spatial structuring and competition on species coexistence. The obvious case is when intransitive competition maintains species coexistence when operating in space. Coexistence is the consequence of spiral pattern structures that cyclically invade competitors, while coexistence levels off as the level of mixing increases. However, intransitive spatial networks are only one end of the spectrum. We find that alternative patterns can emerge as we move along a continuum of spatial network structures as measured by the covariance. To this end, we show that various network structures ranging from intermediate to balanced levels of competition can maintain coexistence. By combining varying mixing levels and dispersal rates in a spatial framework, we have sought to understand under what conditions multiple species assemblage can persist.

Positive Covariance
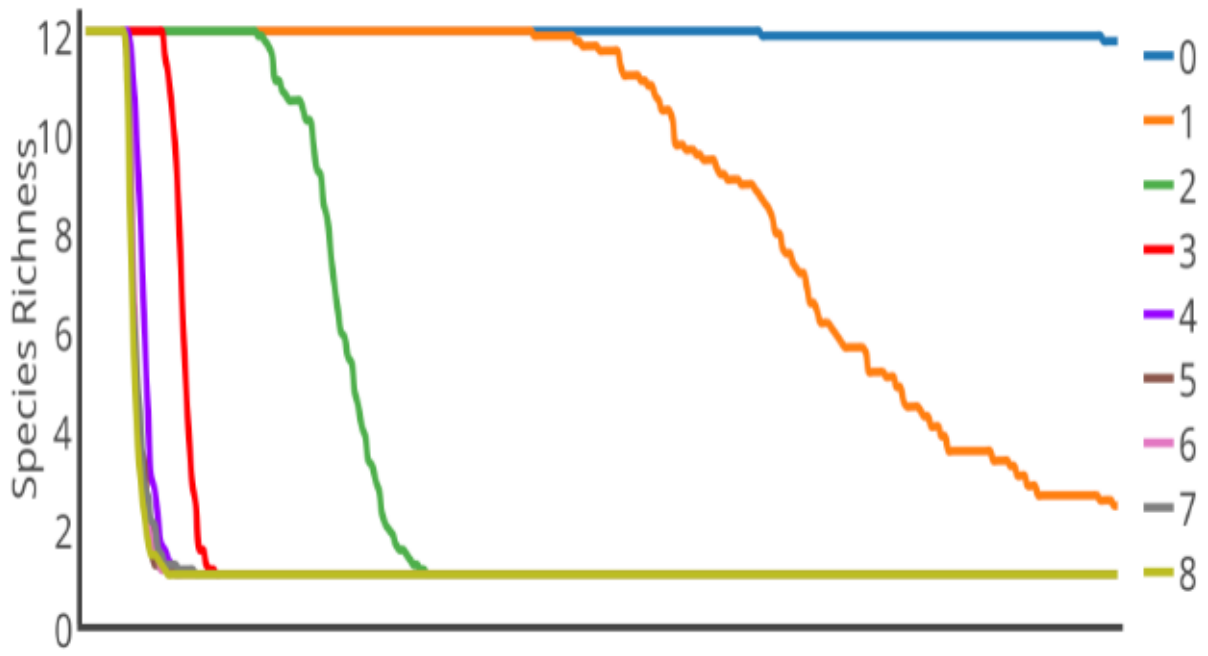
Negative covariance
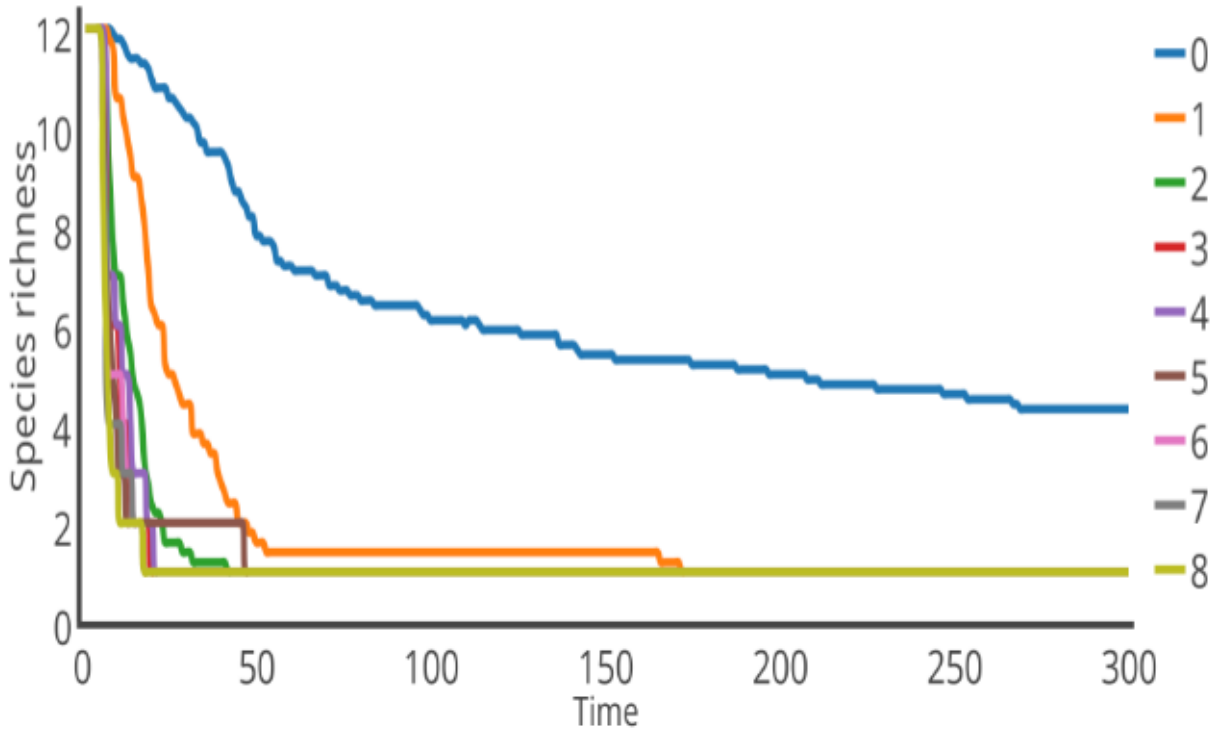
Fig 1.1 Time series of species richness over 300 time steps. Different colors represent degrees of spatial mixing in the Moore Neighborhood ranging from zero (no-mixing) to eight (full-mixing). Each colored line shows final species richness after 50 iterations for both positive and negative covariance values. As levels of mixing increases, species richness declines over time. In the case of negative covariance, small levels of mixing resulted in rapid declines in species richness.
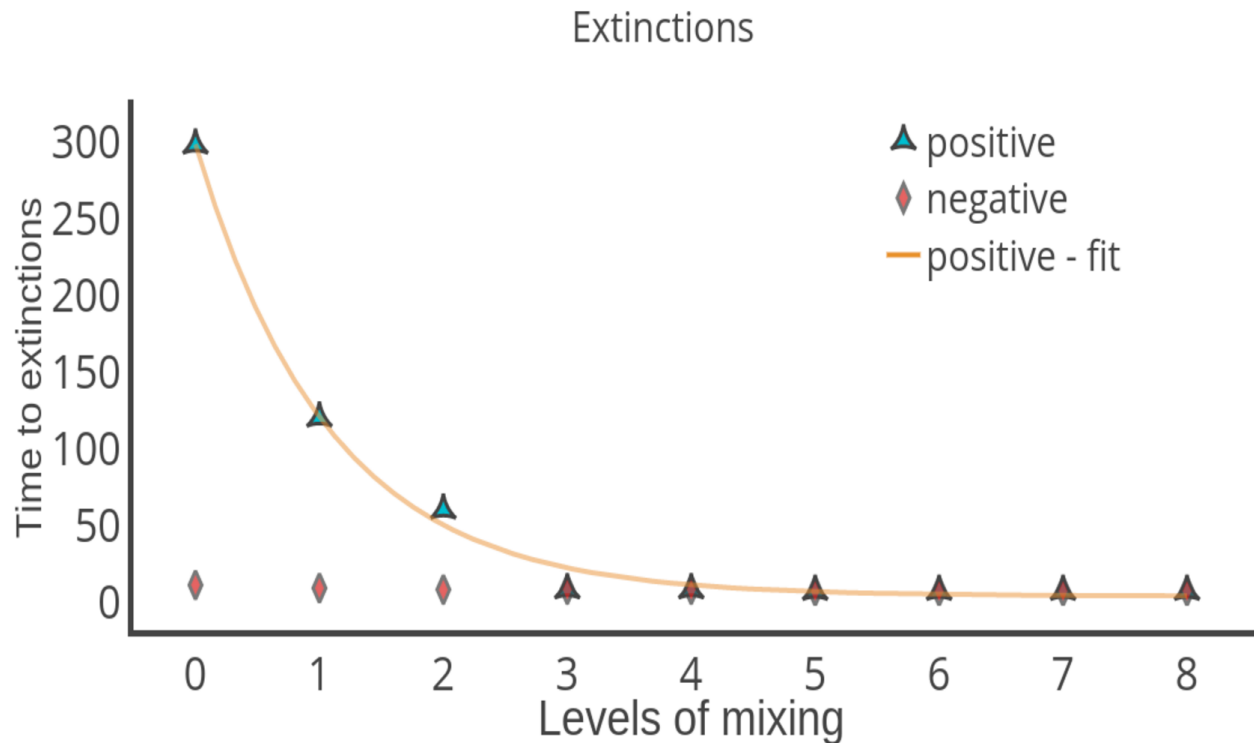
Fig 1.2 Time to extinction with increasing levels of mixing. The y-axis represents the generation time for the first species extinction to occur and x-axis represent mixing ranging from 1-8 neighboring cells. Positive covariance gradually declines in species richness as mixing increases. Zero-mixing has no extinction because of mosaic spatial structure, but as mixing intensity increases extinction increase. Extinctions occur uniformly across all mixing levels for the negative covariance
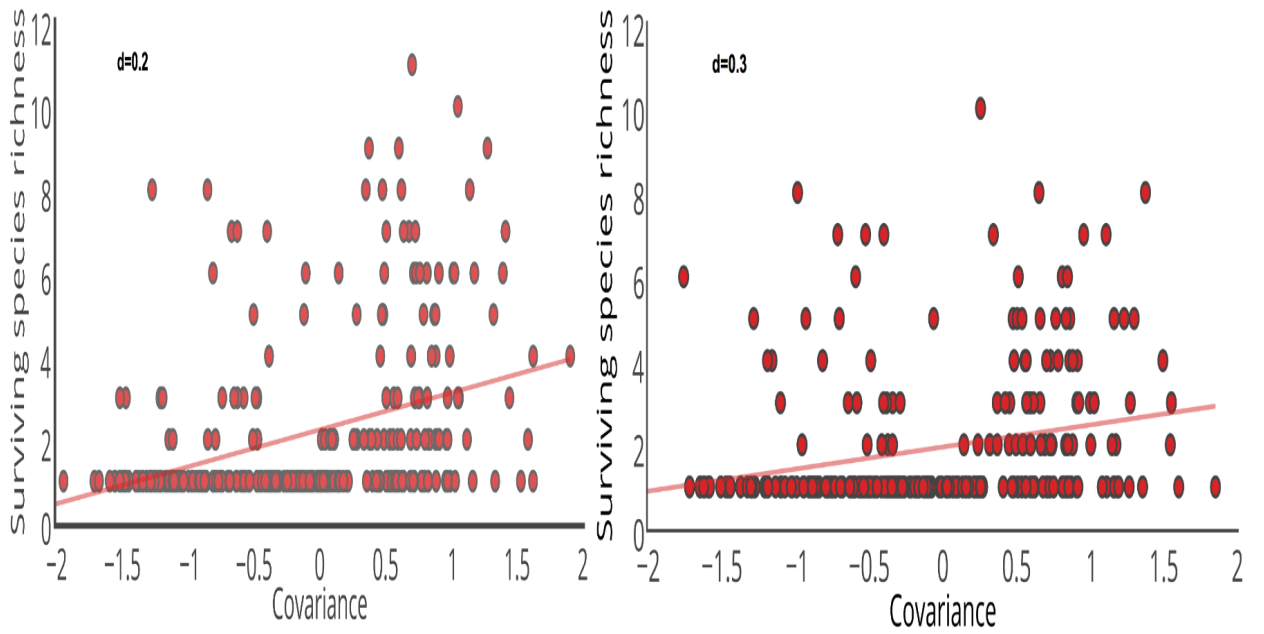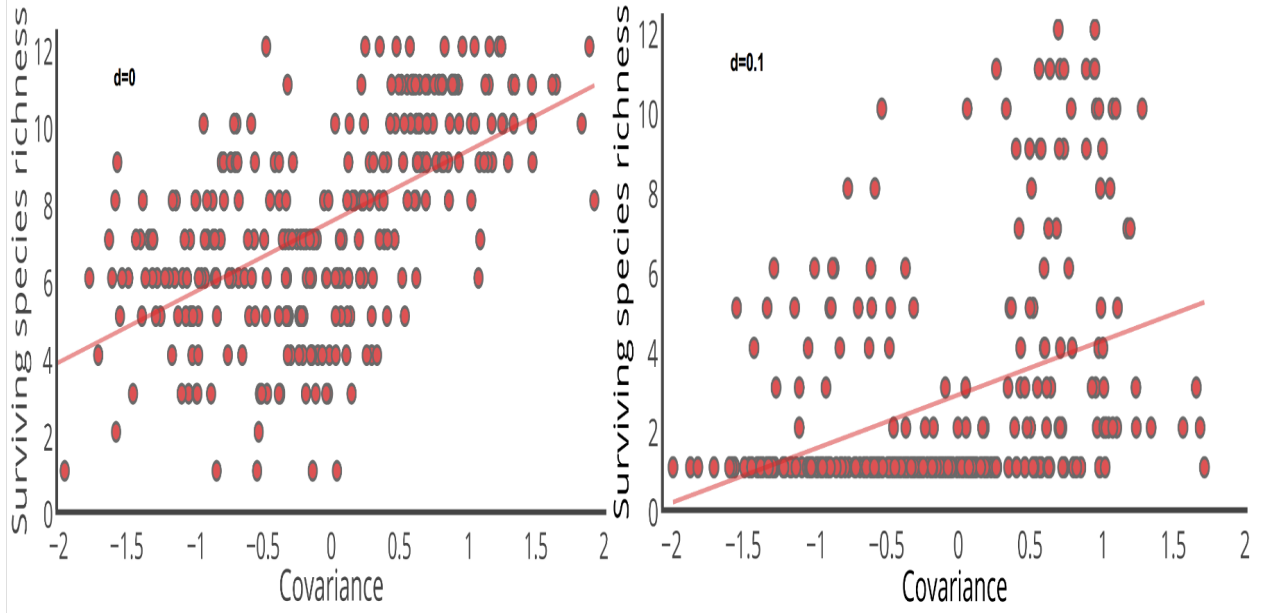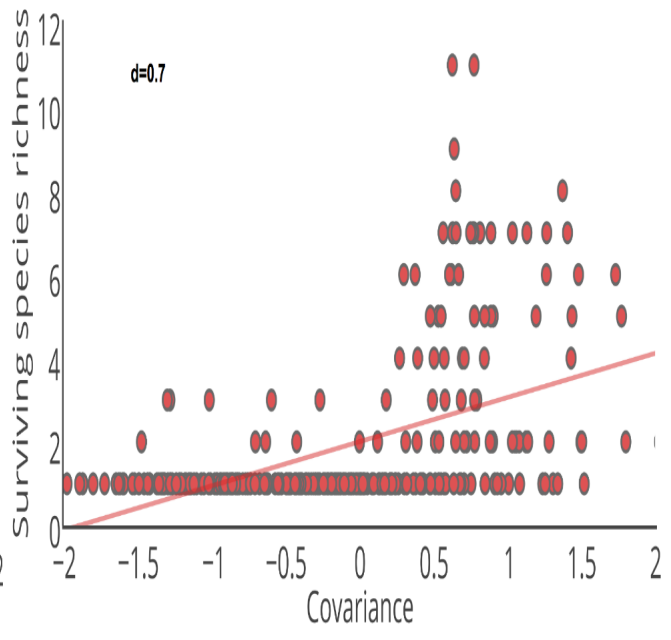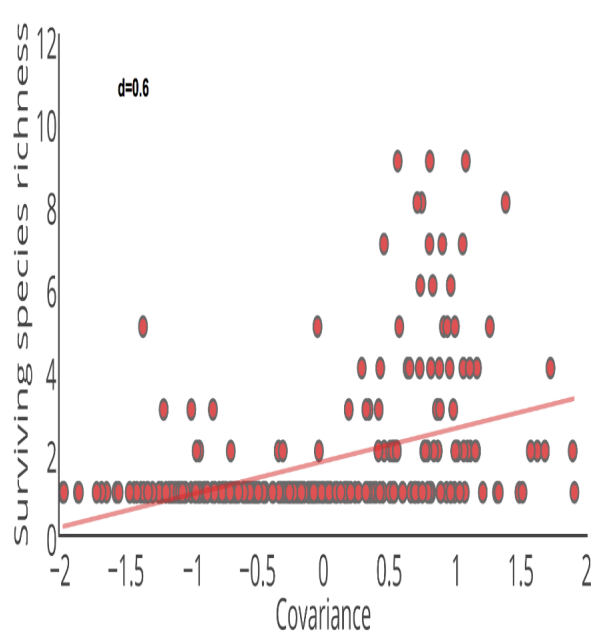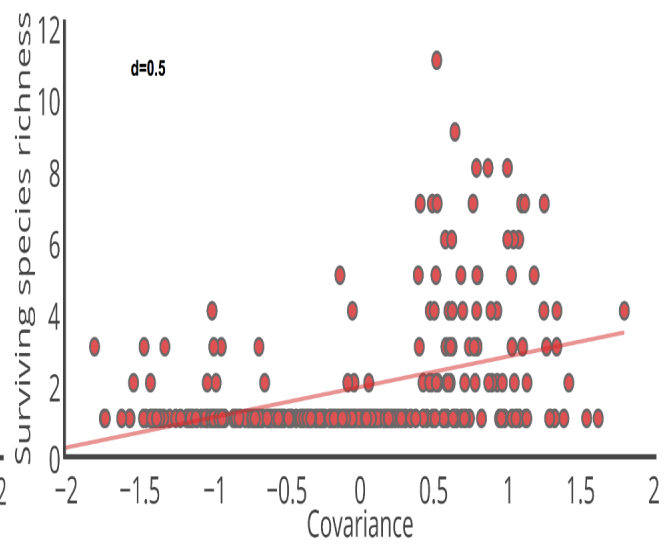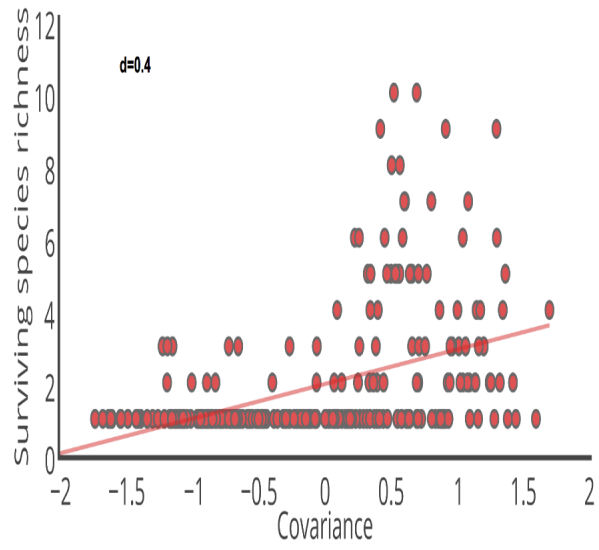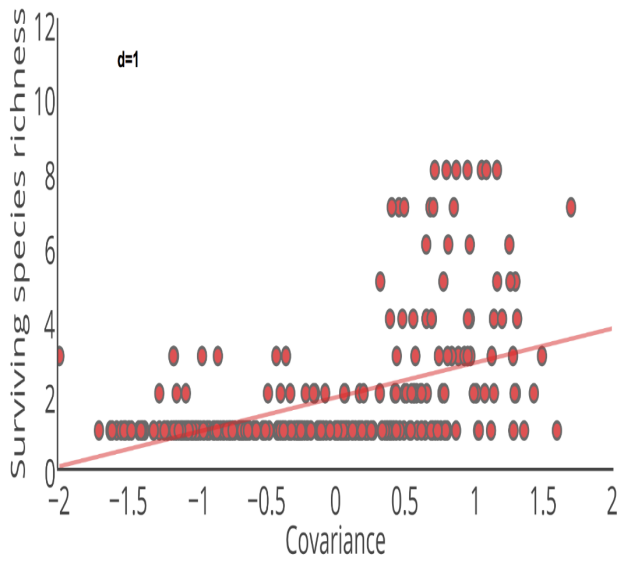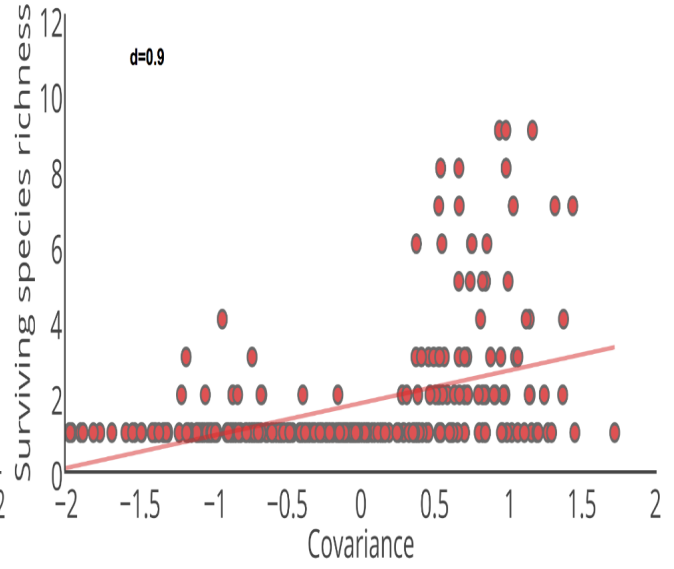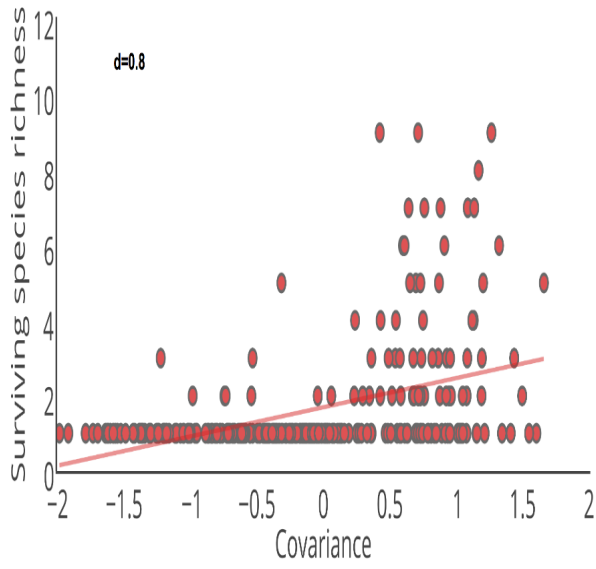
Fig 1.3 Relationship between the number of surviving species after 100 iterations and the covariance of the competition matrix under different mixing scenarios (the first graph is with no mixing, thus corresponding to the equivalent graph in Vandermeer and Yitbarek, 2012). Graphs show increasing dispersal (mixing) rates (ranging from 10% to 100%) when community undergoes incomplete mixing, such that 1 species is replaced in the local Moore Neighborhood by a randomly choosing long-distance migrant in the lattice. Lines are best fit linear regressions, significant at p < 0.001.
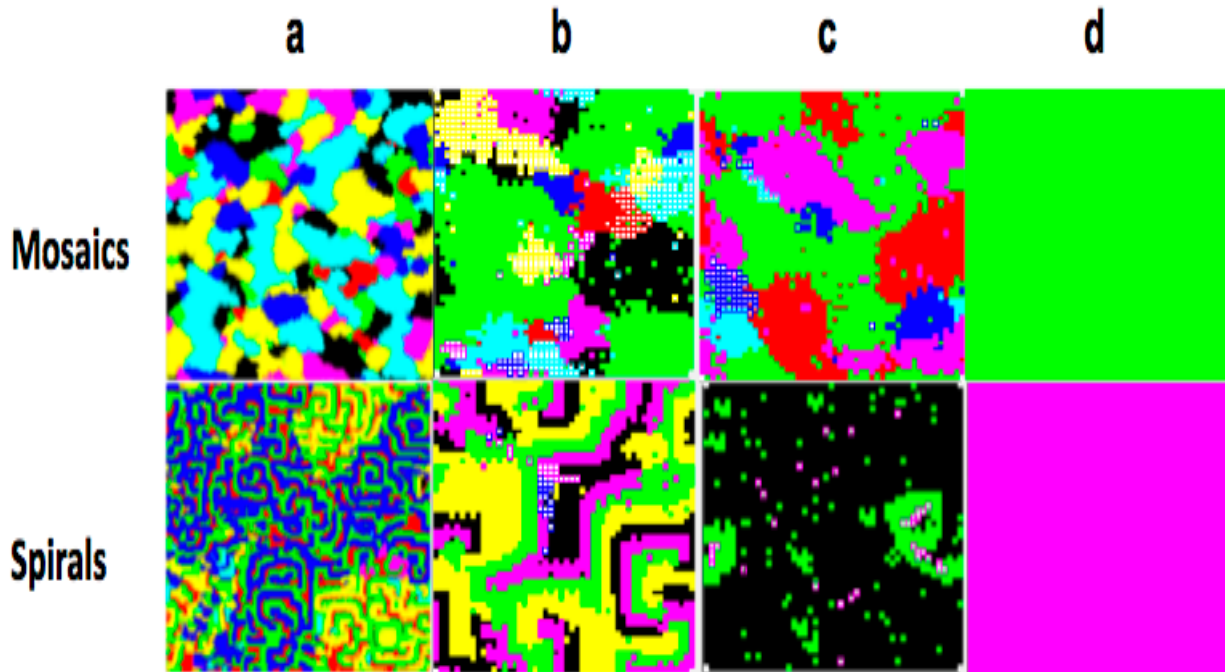
Fig 1.4 Spatial pattern disaggregation with increased dispersal rates. Representing a total of 12 species in the community each color/pattern indicating a different species. Top row shows four common mosaic patterns generated under positive covariance. Bottom row shows four common spirals under negative covariance. Spatial patterns range from a) no-mixing, b) 1-mixing (10%), c)1-mixing (100%), and d) 3-mixing (100%). Only takes small amount of mixing for the patterns to break down resulting in 1 dominant species (which of the species survives is random).
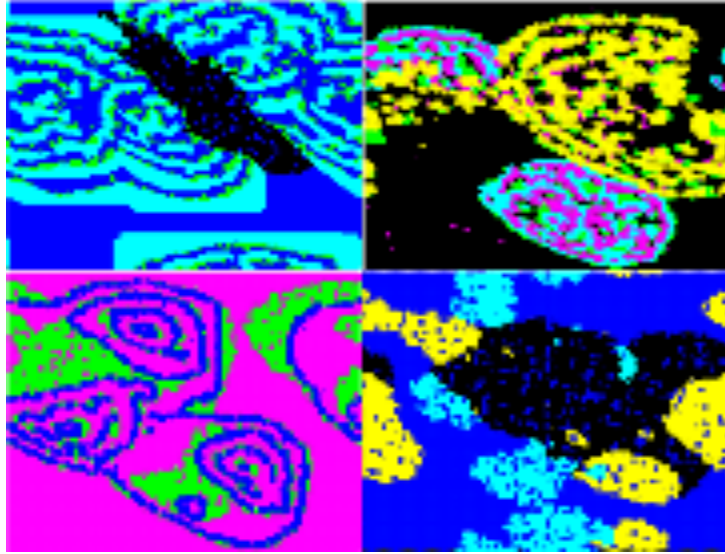
Fig 1.5 Two special cases of spatial patterns when community covariance is near zero. Spatial patterns occur when probability of dispersing 1 individual is extremely low, representing weakly mixed communities. Top row shows combined formation of mosaics and spiral patterns when probability of dispersal is 0.01. Bottom row spatial patterns show similar pattern when probability of dispersal is 0.03.
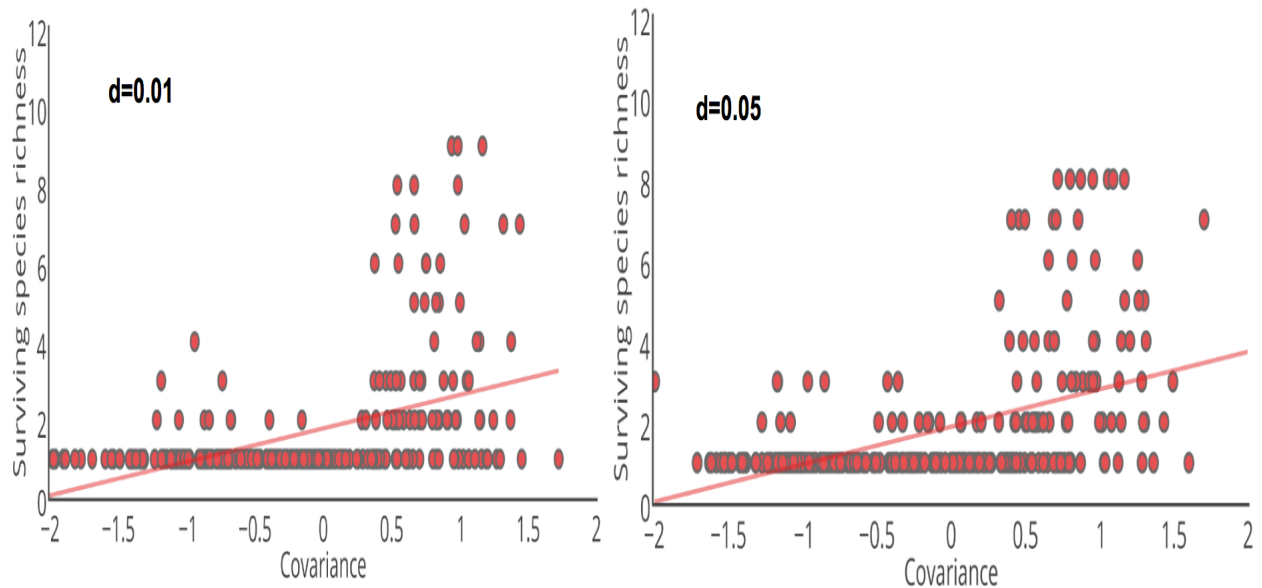
Fig 1.6 The number of surviving species after 100 iterations and the covariance of the competition matrix. In this particular case, when dispersal rates are extremely small, species can quickly go extinct under intermediate levels of competition (near zero covariance). Lines are best fit linear regressions, significant at $p < 0.001$.

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CHAPTER II

FROM INSINUATOR TO DOMINATOR: A UNIQUE MECHANISM FOR AN EXOTIC ANT

Abstract

Understanding the ecological conditions that determine invasive success requires information on the ecological dynamics in both the native and introduced range of exotic species. While numerous studies of the little fire ant, *Wasmannia auropunctata*, have focused on the evolutionary aspects of invasiveness, we know little about possible ecological dynamics that might contribute to the remarkable invasiveness of this species. We investigate the ecological differences in resource discovery and recruitment by *W. auropunctata* within its native range (Mexico) and introduced range (Puerto Rico). We conducted experimental trials on coffee plants by comparing 1) the rate of resource discovery by *W. auropunctata* at various distances from main foraging trails and 2) the recruitment rate between *W. auropunctata* in the introduced range of Puerto Rico. Our experiments revealed that *W. auropunctata* took nearly twice as long to discover baits in Puerto Rico, as compared to Mexico. *W. auropunctata* was relatively slower at recruiting workers than other dominant ants. We conclude that competitive traits such as resource discovery and recruitment are not necessarily indicative of invasive success, but contradict traditional expectations. We propose that *W. auropunctata* behaves as an insinuator species in Mexico (i.e., workers maintain a low profile), while in Puerto Rico it acts as an aggressive dominator. The switch in foraging strategy might explain the astounding success of this exotic species.

Introduction

Much has been learned about the spread and impact of exotic species on ecological communities ever since the pioneering work by Elton (1958). Nevertheless, the development of a general theoretical framework that codifies the underlying causes for invasion has been elusive. Some studies comparing native and introduced ranges of exotic species have highlighted important evolutionary differences including reproductive variation in plants (Blair & Wolfe, 2004), dispersal abilities in toads (Phillips et al., 2010), and physiological tolerance levels to fresh water in fish populations (Lee et al., 2011), among others. Yet, detailed comparisons that highlight ecological determinants of invasion (Van Kleunen et al., 2010; Vilà et al., 2011), while common for plants , are relatively rare for insects (Lawton et al., 1986)

Ecological studies comparing native and exotic biodiversity in plant communities have postulated that exotic species can successfully establish themselves into a new environment when escaping predators, parasites, or pathogens from their native range, commonly referred to as the natural enemy release hypothesis (Power & Mitchell, 2004). The lack of biological control agents in the introduced range enables exotic species to gain an advantage over other species. Less attention has been paid to competitive interactions when it comes to invasions, especially in the case of ant invasions (Lebrun & Feener, 2007). Elton (1958) suggested that areas with high species richness are more difficult to invade as compared to areas with low species richness, because exotic species are less likely to find open niches in large communities. This is, commonly referred to as the biotic resistance hypothesis (Elton, 1958). An open question in invasion biology is whether exotic species that thrive in new environments are limited by competitors in their native habitat. The competitive pressure exotic species face in their native range can limit their foraging range and consequently reduce their ability to acquire food resources (Krushelnycky et al., 2010).

It is common to assume that interspecific competition plays an important role in structuring ant communities (Fellers, 1987; Savolainen & Vepsäläinen, 1988; Andersen & Patel, 1994; Parr, 2008; Perfecto & Vandermeer, 2011). In particular, the discovery-dominance trade-off has been proposed as a mechanism explaining species coexistence (Fellers, 1987; Davidson et al., 2007), with, effectively, species arranged on a gradient from pure discoverer to pure dominator, much as species are arranged along a more traditional environmental gradient. Adjudicating whether the arrangement of any two species on that gradient overlaps sufficiently

to suggest strong competition is parallel to the same adjudication on any resource gradient. Minimal overlap implies separate niches.

The biotic resistance hypothesis suggests that when a large array of species coexists, it is less likely that an exotic species can penetrate the community structure. In the case of ants, it is evident how this hypothesis can refer to competition – species are arranged along the gradient from discoverer to dominator and can thus partition this implied niche space, corresponding to more classic population notions of competition on an environmental gradient. The ability of an exotic species thus is determined by the availability of a place on that gradient, thought to be more likely when fewer species are occupying it.

It should be noted that the discovery-dominance trade-off refers to behavioral characteristics, not population characteristics. Nevertheless, there is an obvious connection between the behavioral characteristics and the population characteristics. A species that is a good discoverer may be so because it has established many and/or large nests, such that it is always close to any potential resource and thus gets to that resource rapidly, or, it could be a good discoverer because it is characterized by workers that search broadly and locate potential resources efficiently. It is a good dominator either because it lives in a habitat that is favorable for establishing many and/or large nests, such that it is always close to any potential resource and thus recruits to that resource rapidly once discovered, or because workers communicate with one another efficiently and mobilize rapidly once a resource is discovered. These categories translate into the following ecological scenario's: 1) living in a habitat that is favorable for establishing many and or large nests suggests a *large carrying capacity* and 2) being characterized by workers that search broadly and locate potential resources efficiently and/or communicating with one another efficiently and mobilizing rapidly once a resource is discovered suggests a *high competitive effectiveness*.

If it is the case that an exotic species faces fewer and/or less effective competitors in its introduced range two concrete patterns might be expected. First, where nests of the exotic species occur, they will dominate an area more completely in a non-native site, having won many local competitive battles. Second, because they dominate more area within their general nesting site, they will appear to be better discoverers and dominators in their introduced range, compared to their native range.

It is frequently assumed that strong competition characterizes ant communities, with differences in discovery and dominance leading to the formation of mosaic patterns thus serving as a possible mechanism for species coexistence (Majer, 1972; Leston, 1978; Parr & Gibb, 2009). Such observations would be in line with the notion of biotic resistance of native communities, in which exotic ants are deterred from expanding due to strong competition. In the case of the exotic ants *Linepithema humile* (Mayr, 1870) and *Anoplolepis gracilipes* (Smith 1857), for example, it has been suggested that they break down the discovery-dominance trade-off by being efficient at both, discovering and dominating resources in their introduced range (Holway et al., 2002). However, studies investigating the relative differences in discovery and dominance rates between the native and introduced range of exotic ant species are non-existent. Although recent laboratory experiments have found correlations between dominance hierarchies and relative differences in discovery-dominance traits (Bertelsmeier et al., 2015), it is not clear whether these same patterns hold true in natural settings. Here we seek to compare the relative differences in territories occupied and resource discovery by *Wasmannia auropunctata* (Roger, 1853) between sites in its native range (Mexico) and sites in its introduced range (Puerto Rico).

W. auropunctata is considered to be one of the most devastating exotic ant species on the globe (Lowe et al., 2004). It is omnivorous and nests both terrestrially and arboreally (Wetterer, 2013). It is native to Central and South American and has in recent decades been introduced on islands across the Caribbean and Pacific Oceans, Australia, Florida and most recently in Israel (Wetterer & Porter, 2003; Vonshak et al., 2009). Within its native range, *W. auropunctata* may occur at high densities and become relatively ecologically dominant in agricultural areas, while in forested areas it's non-dominant and occurs at low densities (Armbrecht & Ulloa-Chacón, 2003; Orivel et al., 2009; Tindo et al., 2011). All of the introduced populations that have been studied, share clonally reproductive population with the native range of *W. auropunctata* (Foucaud et al., 2010). Dispersal into introduced ranges occurs primarily through human-mediated dispersal (Mikheyev et al., 2009; Tindo et al., 2011).

Here, we present abundance and distribution data of *W. auropunctata* and seek to compare differences in foraging strategies of *W. auropunctata* in coffee agroecosystems in its native range of Mexico versus its introduced range of Puerto Rico. We specifically address the role of competition and invasion within the context of founder-controlled local competition. In this context, the founding effect is referred to as the ability of *W. auropunctata* to arrive at a

resource before the arrival of a more dominant ant species resulting in the ultimate winner. The expectation is that in its introduced range, *W. auropunctata*, having established greater control over areas it occupies will more often be a better discoverer and recruiter (relative to other species) than native species, giving it a competitive advantage. Thus we expect that the rate of discovery of a resource will be greater in Puerto Rico, its introduced range, as compared to Mexico, its native range. We compare differences in this rate based on the time necessary to locate resources and distances at which the resources are located from either the nest or already established foraging trails in coffee bushes.

Materials & Methods

Study sites

The study was conducted on organic shaded coffee plantations in Mexico and Puerto Rico. Like many tropical regions, they experience an annual wet and dry season. The data was collected during the wet season between the months of June and July from 2012 to 2013. The Mexico site consisted of a 45 hectares plot on a medium-shade organic coffee farm (15.1735835,-92.3382748) a 30-hectare plot on a low-shade conventional coffee farm (15.172465,-92.3301377) and a 6-hectare plot, in a portion of the organic farm that had a much higher shade level (referred to at the time as rustic coffee). All three plots were located in the Soconusco region of the state of Chiapas, Mexico. In Puerto Rico the study was conducted in 10 small (most of them less than 5-hectares) coffee farms in the central mountainous region within the municipalities of Orocovis, Lares, Adjuntas and Utuado (18.175850, -66.4155700). Shade levels varied depending on coffee management practices, with 5 of the farms classified as high shade plantations and the other 5 farms as low-shade plantations. However, habitat types (i.e. levels of shading) did not seem to impact *W. auropunctata* populations as both high and low level shaded farms had similar density levels. The differences in the size of the farms surveyed were due to the fact that the typical farms in the Soconusco region of Mexico are large (approximately 300 hectares) while small-scale farms (<5 hectares) are typical of the central mountain region of Puerto Rico.

Wasmannia auropunctata surveys

      To determine the abundance and spatial distribution of *W. auropunctata* in Mexico we surveyed the three plots in Mexico by walking the dense trail system within the plots and placing tuna fish baits on coffee plants every 4 meters. Baits were left for 30 minutes before checking. We placed 27 baits per ha in the 45-hectare plot (a total of 1181 baits within the medium-shaded organic coffee farm), 33 baits per ha in the 30-hectare plot (a total of 992 baits within the low-shade conventional coffee farm), and 38 baits per ha in the 6-hectare plot (a total of 229 baits within the high-shade organic farm). The two large plots were surveyed between June and July 2012 and the 6-hectare plot was surveyed in June for two consecutive years, 2012 and 2013. In addition 200 ground baits were placed along the trails in the 6-hectare plot in 2012 to determine species boundaries. Finally, in the 6-hectare plot, we set up an additional three transects extending the area were the *W. auropunctata* was found in the trail surveys in order to determine the extent of the patch. In Puerto Rico the method was similar but since the farms were much smaller, we set an average of 32 baits per ha on 10 coffee farms (approximately 20 ha total farm sizes). Baits were left for 30 minutes before checking them.

Discovery/dominance field trials

      To quantify the time to resource discovery and recruitment for *W. auropunctata* we measured 1) the time it took ants to discover baits placed at different distances from the ant's foraging trails and 2) the time it took ants to recruit at least 10 ants to the baits. Coffee plants that had *W. auropunctata* nests had its workers foraging on the main stem. *W. auropunctata* that nested in the soil arrived from the ground and foraged up the main stem. Three cleaned bamboo poles of approximately 1.5 m in length were placed leaning at approximately a 45^0 angle touching the main stem, and small tuna baits were placed at 5, 15 and 25 cm from the top of the pole (Fig. 2.1). *W. auropunctata* workers arrived to the baits from the ground and coffee trunk with nests found in both habitats. When the space around the plant would not allow to set up all three poles at the same time we place one or two poles and tested for only one or two distances respectively. Once the baits were placed on the poles, we recorded the number of ants at the bait every minute for a maximum of 200 minutes or until all baits were occupied by 10 ants or more. In Mexico we conducted the experiment at two sites within the 45-hectare plot and one site within the 30-hectare plot, with a total of 5, 6, and 5 replicates for 5cm, 15cm and 25cm

distances respectively. In Puerto Rico, these experiments were conducted in three of the 10 farms, for a total of 16, 15, 13, replicated for 5cm, 15cm, 25cm, and a total of 13 and 14 replicates for 35cm and 45cm distances respectively (the data for 35cm and 45cm was not used for the comparisons with Mexico since we only had data for the first three distances). In addition, in Puerto Rico we conducted trials with two other species for comparative purposes. With *Linepithema iniquum* (Mayr, 1870) we conducted 7, 6, 5, 6 and 5 replicates for 5cm, 15cm, 25cm, 35cm and 45cm distances respectively, and for *Monomorium floricola* (Jerdon, 1851) we conducted 4 replicates for 5cm distance and 3 replicates for all remaining distances.

Statistical analysis

To detect temporal differences in resource discovery rates between Puerto Rico and Mexico, we tested the effects of distance (continuous variable) and geographical locations (categorical variable) by means of an ANCOVA, on the recruitment time to resources by *W. auropunctata*. We used a two-way ANOVA to detect differences in recruitment by *W. auropunctata, L. iniquum, and M. floricola* in Puerto Rico. We examined the effects of distance and species on the recruitment time to resources by all three species.

<div align="center">

Results
</div>

Ant surveys in Mexico and Puerto Rico

The ant surveys revealed a very low abundance of *W. auropunctata* in the three plots surveyed in Mexico and a high abundance in the ten farms surveyed in Puerto Rico. In Mexico, in the 45-hectare plot (medium shade organic farm) we recorded a total of 84 morphospecies of ants including *W. auropunctata,* which was present in only 3.2% of the baits. In the 30-hectare plot (low-shade conventional farm) we recorded a total of 58 morphospecies of ants with only 0.40% of the baits containing *W. auropunctata*. In the 6-hectare plot within the high-shade area of *Finca* Irlanda we recorded *W. auropunctata* at 7.9% and 3.9% of the arboreal baits in 2012 and 2013 respectively, and in 0.5% of the ground baits in 2012. Notably, the presence of *W. auropunctata* was highly clustered (Fig. 2.2), as would be expected if the species forms "supercolonies" as is widely assumed (Foucaud et al., 2010).

In the surveys of 10 small-scale farms in Puerto Rico we found a total of 16 morphospecies of ants and *W. auropunctata* was recorded in 41.17% of the baits on average (Fig.

2.3). We detected patches of *W. auropunctata* in all 10 farms surveyed. In most cases, these *W. auropunctata* patches were dense with no other ant species recorded within a given patch. Indeed, in the largest farm surveyed (A 1.1), a 20x20m subsample within the large patch of *W. auropunctata* encountered 100% of the baits occupied with this species, and no other species at all.

 W. auropunctata was found to have a highly patchy distribution in both the Mexico and Puerto Rico sites. In Mexico we identified five patches in a sampling area of more than 80 has, each of which occupied an area of about one hectare or less (Fig. 2.2). However, even within these "*Wasmannia* patches", the dominance of *W. auropunctata* was not absolute with many other species scattered among coffee plants dominated by *W. auropunctata.* For example, in the irregular 6-hectare plot within *Finca* Irlanda, we were able to determine the presence of a "*Wasmannia* patch" of close to a hectare in size (Fig. 2.2). But within this area only 40% of the baits placed were occupied by *W. auropunctata*, with multiple other species occupying the rest of the baits. In Puerto Rico, we found that *W. auropunctata* occupied nearly 100% of the largest patch with only a few trees occupied by *L. iniquum* (Fig. 2.2). However, in the smaller patches *W. auropunctata* was less dominant ranging anywhere from 10-30% occupancy levels.

Discovery/dominance field trials

The number of trials for which complete recruitment to the bait (10 or more ants) was effected within two hours was dramatically different for Mexico versus Puerto Rico. Contrary to expectation, Puerto Rican *W. auropunctata* ants were far slower in discovering and recruiting to the baits than the counterparts in Mexico. Time to discovery, was distinct for the two sites with *W. auropunctata* ants from Puerto Rico taking almost twice as long to get to the saturation point than the *W. auropunctata* ants from Mexico (df= 77, P< 0.001, Fig. 2.4). Each coffee bush within the *W. auropunctata* patch in Puerto Rico was characteristically filled with *W. auropunctata* individuals such that they could be seen from afar foraging on the trunk of the bush. Indeed, placing a small bait directly on the trunk resulted in occupancy within a few seconds. Contrarily, in Mexico, while foragers could always be found on the trunk of an occupied bush, it took some effort in examining the trunk to encounter the sparsely foraging individuals. The difference, simply from an observational standpoint, between Mexico and Puerto Rico, is substantial.

When comparing recruitment time among the three species, *W. auropunctata*, *L. iniquum* and *M. floricola,* in Puerto Rico, it is evident that *W. auropunctata* took longer to recruit for all 5 distances as compared with *L. iniquum* (df=2, P<0.001, Fig. 2.5), but the differences with *M. floricola* were not significant (P=0.34).

Discussion

Differences in local densities and foraging activities of the exotic ant *W. auropunctata* were detected on coffee farms, between its native range of Mexico and introduced range of Puerto Rico. Arboreal foraging experiments on coffee plants revealed that *W. auropunctata* populations took nearly twice as long to discover resources in Puerto Rico as compared to Mexico, completely opposite with what was expected. Within the introduced range of Puerto Rico, we observed that *W. auropunctata* populations were slower at recruiting workers to baits located at new sites as compared to the native Puerto Rican competitor *L. iniquum*. Despite its local and regional dominance in Puerto Rico (A1.1), competitive traits were not indicative of invasive success. As measured strictly by discovery-dominance, we find no evidence that invasiveness is determined by competitive ability. Clearly other modes of competition (i.e. nesting sites, diet), could be responsible, but as measured strictly by discovery-dominance, we find no evidence that invasiveness is determined by relative competitive ability.

Interspecific interactions are generally considered to be important in the establishment and spread of exotic species (Dickman C, 2011). In the case of ant species, the discovery-dominance trade-off has been proposed as a possible mechanism for ant coexistence (Adler et al., 2007; Perfecto & Vandermeer, 2011). Some species are good at rapidly discovering food sources and recruiting workers (i.e. superior exploitative ability), while other species are slow at discovering but excel at displacing other species and dominating areas. Evidence for this trade-off operating in ant communities has been found in temperate (Fellers, 1987; Holway et al., 2002; Stuble et al., 2012) and tropical ecosystems (Feener et al., 2008; Perfecto & Vandermeer, 2013). Exotic ant species have been hypothesized to be more successful, than local ant species, at foraging (Holway et al., 2002). In particular, exotic ants are believed to excel at both discovering and dominating resources. However, studies investigating exotic ant invasions have primarily focused on *L. humile* populations in their introduced range (Human & Gordon, 1996; Holway &

Suarez, 1999). These studies suggest that *L. humile* populations are able to dominate communities by excelling at discovering and dominating resources. These behavioral traits enable *L. humile* populations to control available resources and expand the edges of their territories while displacing native ant communities.

While these studies shed considerable light on invasion processes, we lack similar detailed studies of other exotic ant species, in particular *W. auropunctata*, between their native and introduced home range (McGlynn, 1999). Recent work by Vonshak et al. (2012) investigated the competitive interactions between *W. auropunctata* and native ant species in a laboratory setting. They found that over a short time span (2 h), *W. auropunctata* had the poorest foraging abilities (i.e. time to discovering, retrieving, and defending resources) when worker densities were low. However, over 21 days *W. auropunctata* rebounded and displaced the other ant species by raiding their nests (Vonshak et al., 2012). One explanation is that *W. auropunctata* behaves as an "insinuator" species, in which workers do not display aggression at low worker densities enabling them to forage undetected alongside dominant ant species. Only when gaining a numerical advantage will *W. auropunctata* display aggressive behavior towards other ants.

This switching of foraging strategies has been observed in other ant species (Morrison, 1996) and has been hypothesized to characterize *W. auropunctata* explaining in part why it is such a successful invader. While the success of exotic ant species in their introduced range has been attributed to their foraging abilities, in particular the discovery-dominance trade-off (Clark et al., 1982; Holway et al., 2002), our results do not support this generalization for *W. auropunctata*. To understand the foraging dynamics of *W. auropunctata* in the native range of Mexico, we propose to extend the classical discovery-dominance framework into a three dimensional trade-off strategy between discoverer-dominator-and insinuator ant species, dependent on the average effective size of key resources (Fig 2.6). In the case of an environment offering resources that are generally very large (e.g., dead vertebrate carcasses, large fruits fallen to the ground, dead fish on beaches), dominators will be largely able to control large areas, excluding discoverers from establishing nest sites at all, as noted in at least one other case (Perfecto & Vandermeer, 2011). But the few smaller sized resources that inevitably fall to the ground (or become offered arboreally) can be utilized by insinuators (i.e. *W. auropunctata*), ants that cannot withstand the aggressive behavior of the dominators, but have a nest structure that enables them to effectively scavenge smaller resources. Effectively, the insinuators are

discoverers with highly mobile nests. In the case of an environment offering resources that are general very small (e.g., small dead insects, small arthropod prey items) efficient discoverer species will remove them quickly as they fall to the ground, effectively excluding them from the foraging abilities of the dominators. Insinuators, like *W. auropunctata*, are likely to be partially successful in this scenario likewise. The time to discovery was faster in their native habitat of Mexico, presumably due to lower workers density and increased competitive pressure exerted by the native species pool. In the introduced range of Puerto Rico, we propose that *W. auropunctata* switches its foraging strategy from insinuator to dominator. In this scenario, *W. auropunctata* attains a numerical advantage allowing it to displace other species and dominate resources for longer periods of time. This is indicated by the apparent difference in spatial distribution of *W. auropunctata* patches. In Mexico, the patches were diffused, with many other species found in nearby coffee bushes and, sometimes even within the same coffee plant where *W. auropunctata* was found foraging. However, in most of our sites in Puerto Rico the *Wasmannia* patches were very dense and in almost all cases other species were not encountered within the patches (A 1.1). As a result of these high abundance levels, we speculate that *W. auropunctata* was able to completely dominate each coffee plant where it is found establishing foraging trials to secure resources, such as tending hemipterans, for longer periods of time. In Mexico there are many other species that compete for these resources with *W. auropunctata*. Indeed, in Mexico we rarely observe *W. auropunctata* tending hemipterans while in Puerto Rico it is a common occurrence. A fairly secure resource can decrease the need for exploration and search for new foraging areas, as in Puerto Rico, reducing the probability that a new resource can be discovered. Meanwhile, in Mexico strong competition with native ants forces *W. auropunctata* to quickly search for new resources. Thus, we propose that the switch from insinuator to dominator may explain the astounding success of this species as an invasive
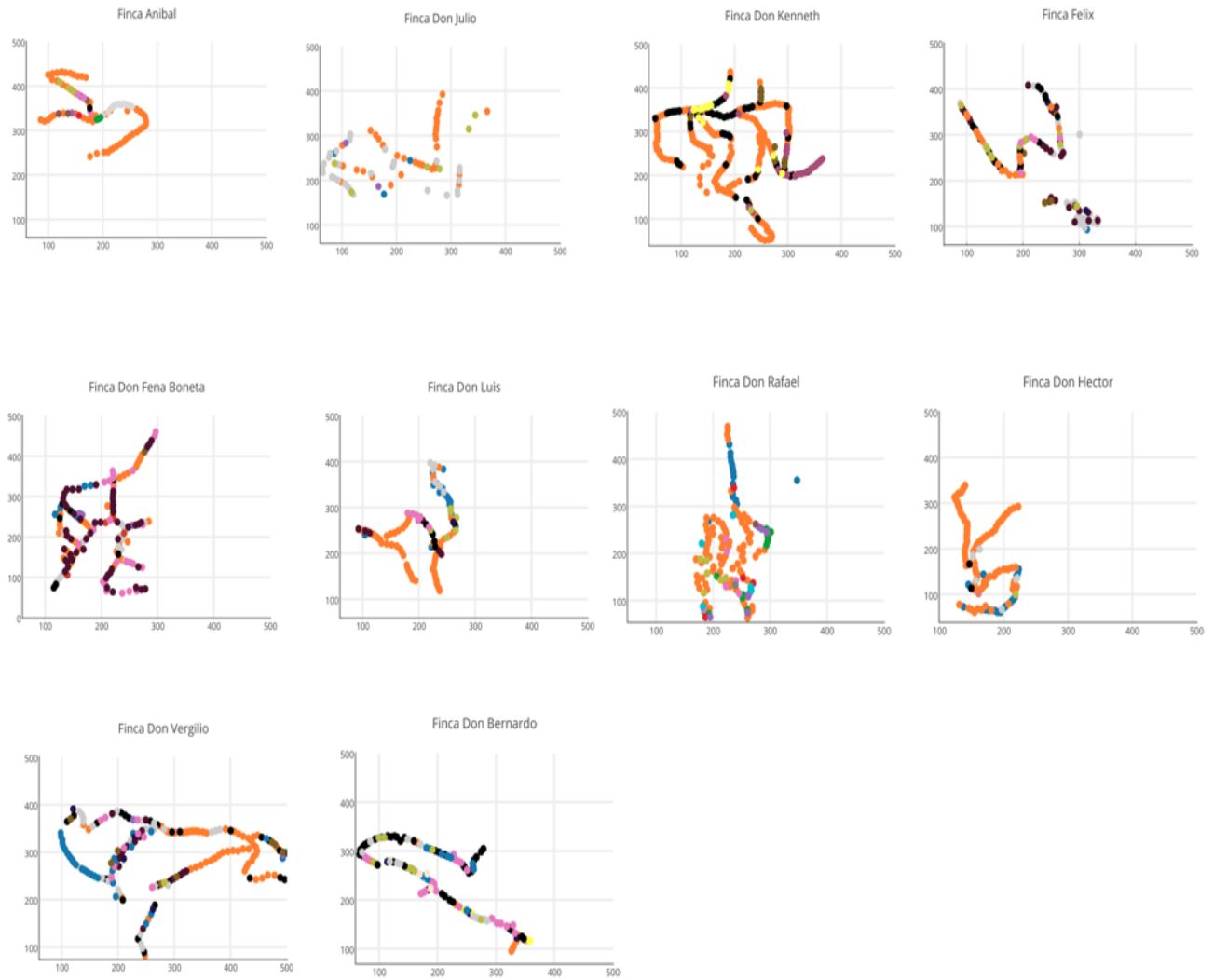
Apendix 1.1 The distribution of *W. auropunctata* on all 10 farms in Puerto Rico. The orange circles indicates baits on coffee bushes where *W. auropunctata* was found foraging along major paths. In nearly all farms, *W. auropunctata* was the most abundant species and occurred in dense patches. The other color circles indicates other baits where other ant species were found.

Figure 2.1. Bamboo treatment on coffee plants with tuna baits placed at 3 different distances from the nest: 5, 15, 25 cm.
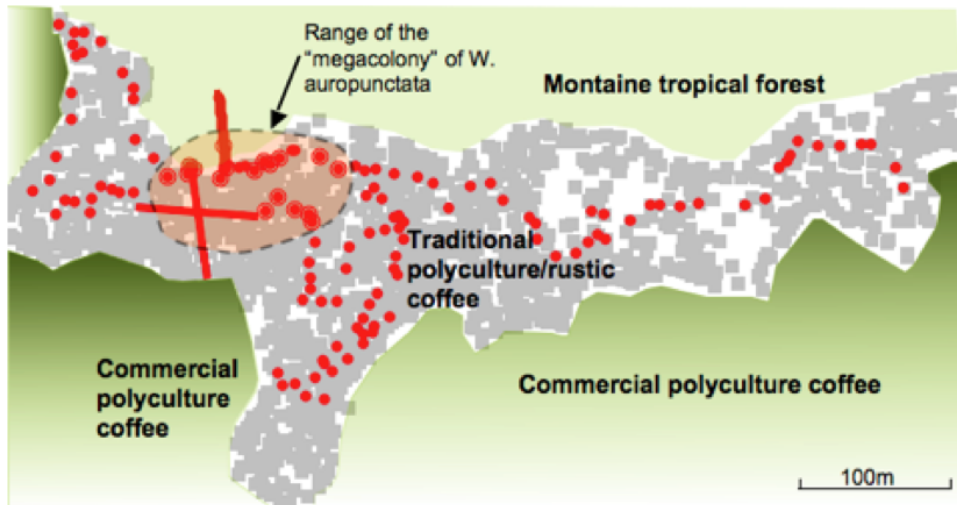
Figure 2.2. Intensively sampled area illustrating the distribution of a single mega-colony of *W. auropunctata* in the Mexican system. Grey squares are shade trees in the coffee system. Closed red circles are sampling stations (four baits at each station, two arboreal two terrestrial) where no *W. auropunctata* were encountered. Closed circles outlined by open circles are sampling stations where at least one of the four baits was occupied by *W. auropunctata*. Thick red lines were intensive transects with baits placed every 2 meters, indicating precise location of borders of the mega-colony.

Figures 2.3 Spatial survey *W. auropunctata* distribution on a 6-ha Puerto Rican coffee farm. Red region (~1ha) indicates a single mega-colony of *W. auropunctata*. White and grey circles indicate smaller patches of *L. iniquum* interspersed with *W. auropunctata* nests (red). Thick gray lines were intensive sampled transects with baits placed every 2 meters.
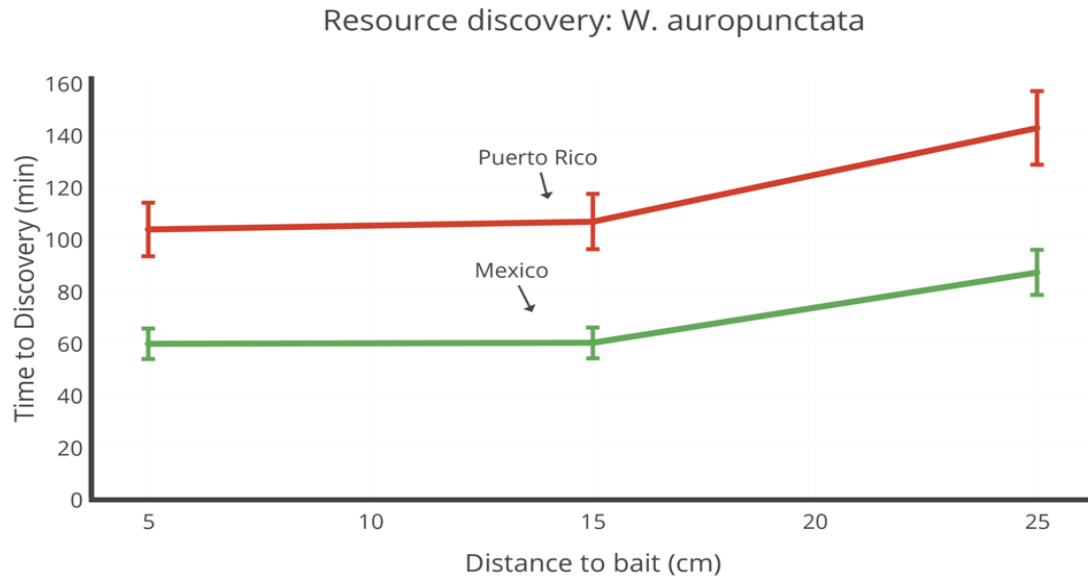
Figure 2.4. Average discovery time to resources with 95% confidence intervals on both sides. Baits were placed at different distances from the nest, respectively 5, 15, and 25 cm. Shows that average discovery rate was slower in the introduced range (i.e. Puerto Rico) of *W. auropunctata* than the native range (i.e. Mexico).
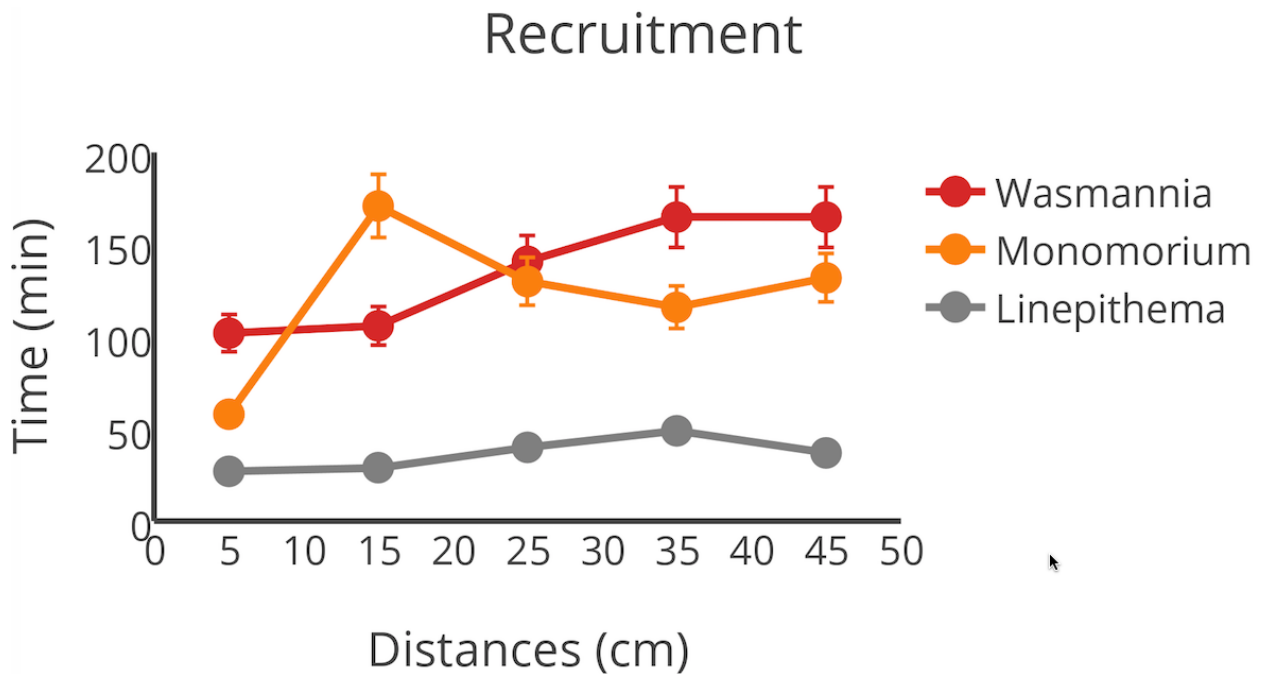
Figure 2.5 Average time to recruitment in Puerto Rico between *W. auropunctata*, *L. iniquum*, and *M. florica* with 95% confidence intervals on both sides. Shows that *W. auropunctata* has a faster discovery rate as compared to competitors.
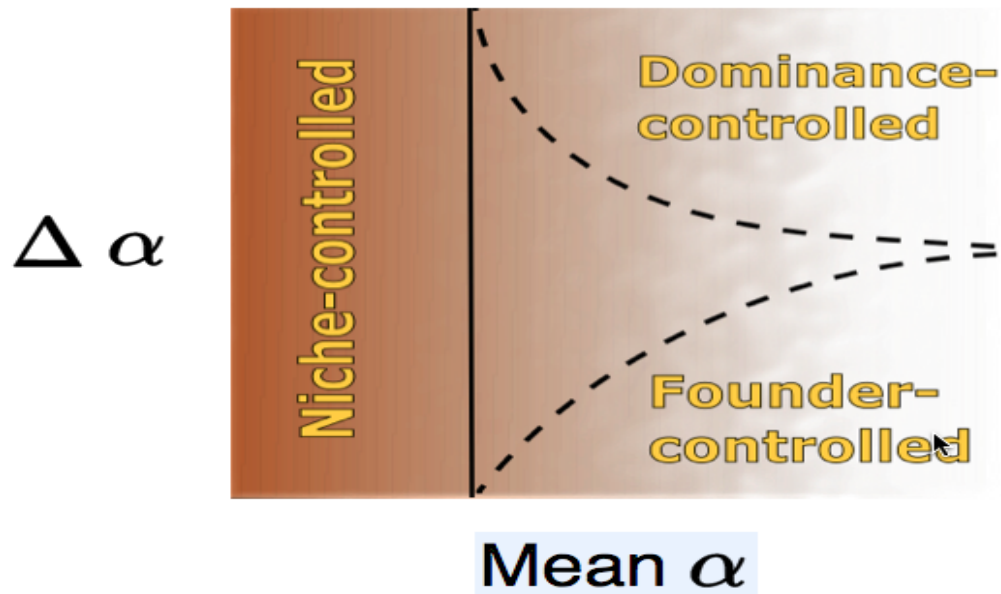
Figure 2.6. Conceptual framework for Yodzis' classification of communities. Mean alpha refers to the mean value of alpha in the case of a community assemblage. Delta alpha refers to absolute value in the case of a given pair of species, or to the covariance of A (the community matrix, Levins, 1968; Vandermeer 1972) in the case of a community assemblage. Dashed lines indicate approximate division of the space into the three Yodzis types.

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CHAPTER III

BIOTIC RESISTANCE AND THE INVASION DYNAMICS
OF *W. AUROPUNCTATA*

Abstract

A major goal of invasion ecology is to understand under what conditions exotic species can invade ecological communities. The biotic resistance hypothesis posits that diverse local communities may be able to resist exotic species due to limited available niche space. An inverse relationship is expected between the diversity of local communities and invasiness by exotic species. While the plant community literature has found a mixed relationship between native and exotic richness, far less is known about ant communities. In particular, we lack compare studies investigating the invasion dynamics between the native and introduced range of exotic ant species. Here, we investigated the invasion dynamics of the little fire ant *Wasmannia auropunctata* between its native range of Mexico and introduced range of Puerto Rico. We studied competitive interactions between *W. auropunctata* and native ants in Mexico and Puerto Rico. We conducted experiments over short-term and long-term time intervals in both the field and laboratory to determine relative differences in number of workers found at baits, time to resource discovery, and recruitment time to resources. Our results provide support for the biotic-resistance hypothesis in which native ant species in Mexico are able to resist *W. auropunctata* as compared to the introduced range of Puerto Rico. However, this pattern depends strongly on the temporal aspect of invasion. We found that the ground foraging ants *S. geminata* and *P. protensa* were stronger competitors against *W. auropunctata*, while the arboreal ants *P. synantropica* and *S. picea* were more dominant in coffee trees. However, long-term competitive dynamics revealed that *W. auropunctata* displaced *S. picea*. Meanwhile, *W. auropunctata* faced fewer competitors in Puerto Rico with only *S. invicta* showing resistance in isolated areas, while the arboreal ant *L. iniquum* was unable to resist *W. auropunctata*. We propose that temporal considerations are necessary when determining the competitive abilities of native and exotic ants.

Introduction

Biological invasions are drivers of global change and pose a major challenge for biological diversity and human welfare (Vitousek 1990; Simberloff 2013). Studies on ecological invasions have sought to explain biodiversity patterns describing the relationship between native and exotic species richness across spatial and temporal scales (Fridley et al. 2007). Early work on invasions suggested that regions with high species diversity are more resistant to exotic species than depauperate regions (Elton 1958), since later arriving species are less likely to fill up available niche space due to strong competitive effects exerted by resident species (May and MacArthur 1972). The "biotic-resistance" hypothesis formulates a negative relationship between native and exotic species richness. The biotic resistance hypothesis has been well studied in the plant invasion literature with some mixed results (Fridley et al. 2007). At smaller spatial scales, studies have shown a negative correlation between the number of native residents in a community and the number of exotic species as a result of biotic interactions (Levine 2000; Kennedy et al. 2002). At larger spatial scales, there exists a positive relationship between native and exotic species richness ("biotic acceptance") largely due to abiotic conditions and spatial heterogeneity (Stohlgren et al. 1999; Davies et al. 2005). These opposite findings between native biodiversity and exotic species present us with an "invasion paradox" in attempts to make any broad generalizations across ecological communities(Fridley et al. 2007). While studies testing the biotic resistance or acceptance have primarily focused on plant communities, we lack such experimental tests in ant communities between native and introduced ranges. Exotic ants have successfully spread across the globe as is evident from their expansion across distinct bio-geographical regions (McGlynn 1999). Exotic ants impact native biodiversity, economic systems, and human health (Holway et al. 2002; Lowe et al. 2004). Exotic ants negatively reduce the abundance and species richness in areas with high densities of exotic ant species. In invaded habitats, fewer native ants tend to co-occur with invaders with some estimates showing 70 % reduction in native ant species richness(Porter and Savignano 1990). Interspecific competition is a major driving factor structuring ecological communities (Hölldobler and Wilson 1990). Studies on exotic ants and competitive dynamics have primarily focused on interference and exploitative competition (Holway et al. 2002). Interference competition (i.e. contest competition) involves direct aggressive encounters among individuals by hindering foraging activities or reproductive

efforts. Exploitative competition (i.e. scramble competition) typically involves indirect encounters through competition for limited resources such as food and nesting sites. Rapid recruitment of workers and movement of nests to resources are examples of exploitative competition that enables colonies to outperform competitors (Parr and Gibb 2009). Within native communities, interference and exploitative traits are known mechanisms for interspecific competitions as they can promote species coexistence in ant communities (Adler et al. 2007). Interspecific interactions by resident ant species may prevent exotic ants from invading. Evidence for biotic resistance by resident ants in curbing the spread of the Argentine ant *Linepithema humile* in the introduced range of California has been mixed. For example, the expansive spread of *L. humile* in this region was found to occur, irrespective of the native ant species richness (Holway 1998; Sanders and Gordon 2003). However, studies in species rich communities in Australia suggest that resistance can limit the spread of exotic ant species, including *L. humile*, due to competitively dominant ant species (Majer 1994; Andersen 1997). Studies on exotic ants have primarily focused on their invasion dynamics in the introduced range. However, comparative studies between the native and introduced ranges of exotic ants are currently lacking (Calcaterra et al. 2016). In particular, it's important that we understand how exotic ants are organized within local species assemblages in the native range in order to determine their success in the introduced range. Only a few studies on exotic ants, mainly focusing on *L. humile* and *S. invicta*, have studied biotic interactions within the native range (Lebrun and Feener 2007; Feener et al. 2008). Yet more observational and experimental studies are needed to study the ecological dynamics of other globally important exotic ants. To this end, our study focuses on the ecological dynamics of the exotic ant species *W. auropunctata* between its native and introduced range. In its introduced range, *W. auropunctata* is considered to be one of the worst exotic pest ant species by competing and displacing native ant communities (Lubin 1984; Le Breton et al. 2003; Walker 2006; Orivel et al. 2009). *W. auropunctata* is native to Central and South America and has in recent decades invaded tropical and subtropical regions of the world including Caribbean and Pacific islands, the United States (Florida), and Western parts of Africa (Gabon and Cameroon) (Wetterer 2013). Most recently it has spread to parts outside of the tropics such as in the Mediterranean region of Israel, suggesting that a tropical species can successfully adapt to colder climates (Vonshak et al. 2009).

Studies on the evolutionary history of *W. auropunctata* suggests that two genetically distinct clades within *W. auropunctata* populations coincided in central Brazil, with clade A distributed to Central America and the northern parts of South America while clade B was distributed to the southern parts of South America (Mikheyev and Mueller 2007; Chifflet et al. 2016). Recent evidence suggests that Caribbean populations are introduced and non-native and likely underwent multiple introductions presumably from the northern regions of South America (Foucaud et al. 2010). Within the native range of *W. auropunctata*, demographic and reproductive differences distinguish between dominant clonal populations occupying human-disturbed habitats and non-dominant sexual populations that occur in natural forested habitats (Fournier et al. 2005; Foucaud et al. 2009; Orivel et al. 2009). Introduced populations have all been found to be clonal and originate from native dominant populations (Foucaud et al. 2010). While the success of *W. auropunctata* has been partially attributed to its clonal reproductive system (Foucaud et al. 2009), we lack a comparative ecological analysis of how *W. auropunctata* ranks relative to its competitors in invaded regions and areas of origin. Our study compares the invasion dynamics of *W. auropunctata* populations between the native range of Mexico and introduced range of Puerto Rico. Recent laboratory competition experiments (Vonshak et al. 2012), highlight temporal differences in competitive outcomes between *W. auropunctata* and two other ant species. In the short-term, *W. auropunctata* had the poorest foraging and discovery abilities for finding resources, but long-term dynamics revealed that *W. auropunctata* was able to overtake food resources quickly through aggressive interactions. It's successful competitive strategy was attributed to its insinuating behavior in which workers did not initiate aggression by maintaining a low profile enabling them to forage alongside more dominant ants (Vonshak et al. 2012). The relative importance of competitive mechanisms by exotic ants under field conditions in relation to native competitors remains unexplored. This study investigated temporal and biotic resistance mechanisms by native ant communities in response to the invasion by *W. auropunctata* populations. To do so, we compared the competitive interactions between *W. auropunctata* and native ant competitors in Mexico (native range) that were absent in the introduced range of Puerto Rico. We assessed dynamics under field conditions during short-time intervals between *W. auropunctata* and native ant species in regards to discovery time to resources and recruitment abilities by species. Additionally, we studied displacement mechanisms by *W. auropunctata* during long-term competition experiments.

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Materials and Methods

Study Site and sampling

In the summer of 2012, a 45-ha plot was surveyed to map the spatial distribution of *W. auropunctata* colonies in a medium shade organic coffee farm in the state of Chiapas in southern Mexico (15.1735835, -92.3382748). In addition, a 30-ha plot was surveyed in a low-shade conventional coffee farm (15.172465, -92.3301377). We observed a total of 4 colonies in the 45-ha plot and 1 colony in the 30-ha plot ranging from 0.25-1 ha in size (fig 3.1). Surveys were conducted to map the spatial distribution and abundance of dominant ant species. We walked dense trail systems by placing tuna baits on coffee plants approximately every 4 meters. Baits were checked every 30 minutes for the presence of ant species. A total of 1181 baits were placed within the 45-ha plot and another 229 baits within the 30-ha plot (fig 3.1). Within the largest *W. auropunctata* patch (1 ha) we established a 50 by 50 m plot during the summer of 2013 (fig 3.1). Descriptions of the farm in Mexico and the 45-ha plot have been reported elsewhere (Vandermeer et al. 2010). In the summer of 2014, we surveyed 10 small coffee farms in the mountainous regions of Puerto Rico within the municipalities of Orocovis, Lares, Adjuntas, and Utuado (18.175850, -66.4155700). Within the largest shaded coffee farm in Orocovis (5 ha), we surveyed the trails by placing tuna baits every 4 meters and mapped the distribution of dominant ant species on the farm (fig 3.2). We subsequently established a 20 x 20 m plot within the largest *W. auropunctata* clusters. Site locations in both Mexico and Puerto Rico were selected so that native ant species, both arboreal and ground foraging, overlapped in their ranges with *W. auropunctata* populations. Differences in farm size reflected the fact that coffee farms in the Soconoscu regions of Mexico are relatively large in size (300 ha) as compared to the central region of Puerto Rico, where the average farm size is considerable small (5 ha).

Competition experiments

In Mexico, a 4- by 4 m grid was established within the 50 x 50 m plot during the summer of 2013. Ants were sampled once with tuna baits in the summer of 2013, 2014, and 2015. Tuna

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baits were placed on the ground and the nearest coffee plants, yielding a total of 154 grid points. Species were checked at each grid point after 30 minutes and their presence or absence was recorded. Identification of ant species was primarily done in the field except for unknown species that we identified in the lab to genus level and assigned a morphological species list. While cross-yearly morphological species list was approximate, the five most commonly occurring species forming spatial patterns were readily identifiable in the field. In Puerto Rico, the same sampling protocol was implemented using a 2-by-2m grid within a 20 x 20 m during the summer of 2014 yielding 196 grid points. The main difference is that in Puerto Rico the species richness was considerably lower (< 20 species) as compared with our Mexican field site (> 100 species). Both the large-scale spatial surveys and more detailed surveys helped us select potential dominant competitors of *W. auropunctata*. In Mexico, we conducted competition experiments in the field between *W. auropunctata* and dominant ant species. In particular, we conducted short-term competition experiments between *W. auropunctata* and ground-foraging ants *Solenopsis geminata* and *Pheidole protensa* as well as with arboreal ants as *Solenopsis picea* and *Pheidole synanthropica*. We estimated the timing of discovery and recruitment to baits by placing small tuna baits in a 1-m line right at the border between ant colonies and subsequently checked the baits at 30-s intervals for up to 80 minutes (Perfecto 1994). For the ground-foraging experiment ten replicates were carried out per species. For our arboreal competition experiments, we placed tuna baits on bamboo branches between coffee trees. We conducted 5 replicates for each of the arboreal species. We recorded the discovery time, recruitment time, and the total number of workers at baits. For the long-term laboratory competition experiments between *W. auropunctata* and *S. picea*, we assessed the total number of live ant workers after 14 days of running the experiment. In Puerto Rico, we followed the same protocol for assessing the competitive dynamics between *W. auropunctata* and dominant ants. We performed *W. auropunctata* competition experiments with the ground-foraging ant *Solenopsis invicta* and arboreal ant *Linipethema iniquum* for 90-minutes. Furthermore, we conducted a long-term competition experiment between *W. auropunctata* and *L. iniquum* for 14 days.

Statistical analyses

We analyzed the differences among species with respect to total number of workers at baits, time to discovery, and the time to recruitment to baits. Prior to conducting statistical analyses, we

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plotted the data to test for normality using the Shapiro-Wilk test. Because of the non-normality, we used the non-parametric Kruskal-Wallis rank sum test with the library stats(R Core Team 2013). Nemenyi's post-hoc tests were applied for pairwise multiple comparisons using the PMCMR package in R, v. 2.15. ANOVA analysis was performed to detect differences in the number of live ant workers found between treatments in the long-term competition experiments.

Results

Wasmannia surveys in Mexico and Puerto Rico Within the native range of Mexico, we found a low overall abundance of *W. auropunctata* surveyed as compared to Puerto Rico, where *W. auropunctata* was found to occur in much higher abundances. In the 45-hectare plot in Mexico (medium-shade organic coffee), we documented a total of 84 morphospecies, 3.4 % of which consisted of *W. auropunctata* found at baits. In the 30-hectare plot (low-shade conventional farm), we documented a total of 58 morphospecies of which only 0.4% occupied baits by *W. auropunctata*. In the 6-hectare plot (rustic coffee, within high shaded coffee), we detected *W. auropunctata* at 7.9 and 3.9% respectively at arboreal baits, whereas ground-baits occupancy by *W. auropunctata* was only 0.5%. While *W. auropunctata* distribution on the farm was limited in the native range, we detected a large cluster of *W. auropunctata* colonies that presumably make up part of a larger super-colony, as reported elsewhere (fig 3.1). In Puerto Rico, we detected a total of 16 morphospecies throughout our surveys on ten smaller-sized coffee farms (ranging from 1-6 ha). On average, we found 41.7 % of arboreal trees occupied by *W. auropunctata*. In most cases, *W. auropunctata* was widely distributed across all farms reaching high densities in patches it dominated thereby excluding other ant species from occupying nearby trees. On the largest coffee farm (fig 3.2), we surveyed a 20 x 20 m sub-patch that was nearly 100% occupied by *W. auropunctata* populations. Overall, we found that *W. auropunctata* was patchily distributed between Mexico and Puerto Rico. The main difference, however, is that patches dominated by *W. auropunctata* included a greater diversity of native ant species in Mexico. For example, native species diversity in the largest patch (1 ha) ranged anywhere from 30-50 native ant species, with only 40 % of baits occupied by *W. auropunctata* (fig 3.1). In Puerto Rico, farms had less than 20 native ant species present, with the largest patch occupying containing only 3 dominant ant species with more than 90% occupation by W. auropunctata (fig 3.2).

Short-term competition: Mexico and Puerto Rico

Competition between *W. auropunctata* and native ant species revealed important differences during contest. Interactions with *S. geminata* showed that *W. auropunctata* was able to rapidly recruit workers to baits during the first 20 minutes of the experiment (fig 3.3a), after which *S. geminata* took over and dominated the majority of baits by the end of the experiment (X^2=55.976, P < 0.0001). Competitive interactions between *W. auropunctata* and *P. protensa* revealed oscillatory dynamics (fig 3.3 b). *W. auropunctata* rapidly increased at baits within the first 25-minutes after which P. protensa dominated for some time until getting surpassed by *W. auropunctata* (X^2=15.641, P < 0.0001). Arboreal competitive interactions between *W. auropunctata* and *S. picea* were equally intense (fig 3.3 c). *S. picea* initially dominated the baits but was overtaken by *W. auropunctata* after 30-minutes (fig 3.3 c). Despite *S. picea* maintaining a constant recruitment rate throughout the experiment, *W. auropunctata* steadily increased recruitment of workers enabling it to dominate most baits (X^2= 9.8396, P = 0.0017). However, the arboreal ant *P. synanthropica* was competitively superior against *W. auropunctata* (fig 3.3 d) during the experiment resulting in the complete dominance of baits (X^2= P < 0.0001). In Puerto Rico, we compared competitive dynamics with *W. auropunctata* and the dominant ant competitors S. *invicta* and *L. iniquum*. Against *S. invicta*, *W. auropunctata* initially increased its recruitment rate but was quickly overtaken by *S. invicta* as more of its workers moved between baits and occupied them. Although we didn't detect a significant interaction in the experiment (X^2= 3.485, P= 0.062), *S. invicta* held on to more baits and its rapid recruitment of workers to baits enabled them to push out *W. auropunctata* workers (fig 3.4). Following this, we conducted laboratory experiments with the arboreal ant *L. inquum*. In the experiment, we observed oscillatory dynamics, as one commonly encounters in predator-prey systems (fig 3.5), with *L. iniquum* rapidly discovering resources and recruiting its workers during the first hour, after which *W. auropunctata* dominates the baits and is eventually overtaken by *L. iniquum* (X^2= 47.982, P <0.0001).

Long-term competition: Mexico and Puerto Rico

W. auropunctata workers were superior against *S. picea* during the long-term experiment in Mexico (fig 3.6). We observed greater survival of *W. auropunctata* workers throughout the 14-day experiment (F=5.4371, P= 0.01356). During the first couple of days, *S. picea* recruited

higher number of workers to the foraging arena and displaced *W. auropunctata* workers at baits in the majority of replicates. As aggression intensified, *S. picea* preempted *W. auropunctata* workers from accessing resources. In response, small groups of *W. auropunctata* workers attacked *S. picea* invidivuals from the arena. In most of the replicates, we observed that *W. aurpunctata* had a clear numerical advantage over *S. picea*. In five of our replicates, *W. auropunctata* invaded the nest boxes of *S. picea*. In three of our replicates (#3, #4, #5) we found high densities of *W. auropunctata* workers in *S. picea* nests, including many brood and queens. In one replicate (#3), we observed a nest invasion by *W. auropunctata* workers into a *S. picea* nest, with queens and brood moved into the invaded nest. Further inspection into nests through a tiny camera revealed that *W. auropunctata* workers frequently dispersed their brood and queens within nests. In Puerto Rico, the number of live *W. auropunctata* workers was not significantly higher than *L. iniquum* (F=1.87, P=0.17). In the first two days, *L. iniquum* was much faster at recruiting workers to baits compared to *W. auropunctata*. In about one quarter of the replicates, no live *L. iniquum* workers were found in the nest boxes as they were killed by *W. auropunctata* workers. We did observe occassional fighting between both species, but *L. iniquum* was quick enough to avoid *W. auropunctata* workers in the foraging arena (fig 3.7).

Discussion

One of our main findings is that locally diverse ant assemblages resisted *W. auropunctata* in the native habitat of Mexico, while the depauperate native ant fauna on the island of Puerto Rico was not able to withstand *W. auropunctata*. We identified several dominant species from the local ant assemblage in the native and introduced habitats and compared their competitive interactions with *W. auropunctata*. In particular, we examined resource and interference competition across short and long-term time scales. We found that in Mexico the ground-foraging ants *S.geminata* and *P.protensa* displayed superiority against *W. auropunctata*, while the arboreal ants *S.picea* and *P. synantropica* also dominated *W. auropunctata* at baits. However, long-term competitive interactions in the laboratory showed a reversal trend with *W.auropunctata* displacing *S. picea* through interference competition. In Puerto Rico, another exotic ant *S. invicta* outcompeted *W. auropunctata* in areas where they overlapped. Laboratory experiments with the native ant *L. iniquum* showed that *W. auropunctata* was superior at baits across the short and long-term

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competition experiments. Interspecific competition is considered to be an important determinant in the structuring of local ant communities (Hölldobler and Wilson 1990). Exotic ants can displace native ant species through interference competition (e.g. biting, aggressiveness, charging) and resource competition (e.g. foraging strategies)(Sakai et al. 2001). While these traits have been implicated in the success of exotic ants, they don't always explain why exotic ants excel at displacing native ant species(Holway et al. 2002). Within native communities, trade-offs have been identified between the ability of a species to discover resources versus their ability to dominate resources, which are thought to maintain coexistence(Fellers 1987; Adler et al. 2007; Bertelsmeier et al. 2015). Exotic ants can violate the discovery-dominance trade-off, in the case of Argentine ants in California, which provides exotic ants with a competitive advantage over native ants species(Holway 1998). While the breaking of the discovery-dominance tradeoff has been linked with the invasive success of Argentine ants, we lack such information on other major invasive ant species. Laboratory experiments involving *W. auropunctata* and native ant species, showed that *W. auropunctata* had the poorest foraging abilities in terms of discovering resources and recruiting workers(Vonshak et al. 2012). In previous work, we compared competitive trade-offs and found that *W. auropunctata* was less efficient in discovering and recruiting worker to baits in their introduced habitat of Puerto Rico relative to their native habitat, suggesting that competitive trade-off are not indicative of invasive success (Yitbarek et al. 2016). In this study, we seek to understand how *W. auropunctata* compares to other ants with which it is potentially competing for resources in its local assemblage. During short-term competition in the field, we found several native ant species from the local assemblage that withstood *W. auropunctata*. In Mexico, the tropical ant *S. geminata* showed high levels of aggressivenss towards *W. auropunctata* at baits. Although *W. auropunctata* was initially able to dominate resources, *S. geminata* high recruitment of workers and interference abillities led to the displacement of *W. auropunctata*. *S. geminata* is frequent victim to attacks by phorid flies which can interfere with its abillity to rapidly discover resources(Feener and Brown 1992; Morrison et al. 2000). However, *S. geminata* agressiveness gives it a competitive advantage at baits. In comparison, *P. protensa* is a slow moving ground forager ant with many small nests that are widely distributed. Although *W. auropunctata* was initially dominant at baits, *P. protensa* was able to overtake the baits for some time after which *W. auropunctata* regained its dominance again. These cyclical patterns are illustrative of the transient nature of competitive interactions

over time. The arboreal ant *S. picea* is a minute ant that primarily forages on coffee where its nests can be found under the bark on the trunks of the coffee tree. *S. picea* was initially more dominant but as *W. auropunctata* recruited its workers from the leaf litter and arboreal nests to the baits it started to regain its dominance. The ability to forage and nest on the ground and the trees enables *W. auropunctata* to hold a competitive advantage over native species. We confirmed this pattern in the long-term experiment were *W. auropunctata* interference ability enabled it to invade *S. picea* nests. The ground-foraging ant *P. synanthropica* nests in the ground but forages both in the leaf litter and in the coffee trees. *P. synanthropica* was competitively dominant over *W. auropunctata* as it quickly discovered baits and vociferously defended against *W. auropunctata* intruders. *P. synanthropica* dominance has also been observed in competition experiments against *S. geminata* and *P. protensa* (Perfecto and Vandermeer 2013). In Puerto Rico, the exotic ant *S. invicta* was superior to *W. auropunctata* at baits. *S. invicta* reached high population densities at baits which forced W. auropuncatata to being pushed out at baits. While *S. invicta* attained a numerical advantage over *W. auropunctata*, the extent of their colonies was limited to areas of the farm that received more sun, which allowed *W. auropunctata* to retain its dominance in other areas where *S. invicta* did not occur. Laboratory experiments showed an oscillitory trend between *W. auropunctata* and *L. iniquum* competition. We found that *L. iniquum* workers were faster at discovering resources but were less efficient at guarding baits against *W. auropuncta* workers. As *W. auropuncta* recruited more workers it slowly attained dominance. These patterns are reflected across the long-term experiment were we found higher numbers of live *W. auropunpuncta* workers. *W. auropunctata* displaced *L. iniquum* by raiding their nest and killing its workers and brood, in some cases moving its entire nest into the invaded species. Our long-term experiments show that nest invasions is a mechanism by which *W. auropunctata* displaces native ant species. Previous lababotory experiments showed that *W. auropunctata* displaced the native ant species *Monomorium subupacum* by invading its nest and consuming workers and brood (Vonshak et al. 2012). Similar evidence for nest raiding of ant colonies has been found for the invasive ants *L. humile* and *P. megacephela* in the introduced ranges (Holway et al. 2002; Dejean et al. 2008; Zee and Holway n.d.).

Recent evolutionary studies suggest that the invasive success of *W. auropunctata* invasion is associated with its clonal reproductive system in human disturbed habitats (Foucaud et al. 2009; Rey et al. 2013). High levels of heterozygosity are hypothesized to confer advantages

to *W. auropunctata* populations when facing highly variable abiotic conditions in human disturbed habitats (Orivel et al. 2009). It remains unclear, however, to what extent clonality perse contributes to ecological dominance in *W. auropunctata* populations. In shaded coffee ecosystems, biotic and abiotic factors can simultaneously determine which ant species thrive. For instance, variation in shade quality and leaf litter has been shown to impact competitive interactions among ant species in a shaded Costa Rican coffee system (Perfecto and Vandermeer 2013). Also, environmental filtering has been associated with arboreal nesting opportunities (Armbrecht et al. 2004). Nontheless, it has been well-established that competition is a major driving force structuring ant communities(Parr and Gibb 2009).

In this study, we have sought to compare the ecological aspects of invasiveness between the native and introduced ranges of *W. auropunctata*. While our study has shown that native ant diversity in Mexico can exert biotic resistance against *W. auropunctata* as compared to Puerto Rico, our approach was limited to one trophic level. In general, interactions between invaders and native species have been studied in the context of competition or predator-prey interactions (Levine et al. 2004; Alofs and Jackson 2014). However, food web connectance (i.e. high versus low connectance) that account for complex interactions, including density and trait-mediated indirect interactions, maybe a more appropriate indicator of resistance to invaders by communities than a small subset of interactions within a foodweb (Smith-Ramesh et al. 2016). Therefore, future studies should seeks to compare food web connectance and invasion resistance across ecosystems. To this end, coffee ecosystems provide us with an experimental model system between the native and introduced range of W. auropunctata in which we can test the relationship between food web connectance and invasive resistance by ant communities.

In sum, we found that both ground-foraging and arboreal ant species in Mexico provided resistance against *W. auropunctata* populations in short-term competition experiments. However, laboratory experiments revealed that W. auropunctata regained its dominance over the long-term. In Puerto Rico, we found that the ground forager *S. invicta* displaced *W. auropunctata*, but that *W. auropunctata* was superior to the aboreal ant *L. iniquum*. Overall, temporal aspect of competition played an important role in the dominance of *W. auropunctata*. Numerical dominance enhanced *W. auropunctata* abillity to displace competitors at baits. Nest invasion including the transfer of workers, brood, and queens to invaded nests was a commonly employed

strategy by *W. auropunctata* during long-term experiments. We suggest that future studies should consider temporal aspects of invasion dynamics.
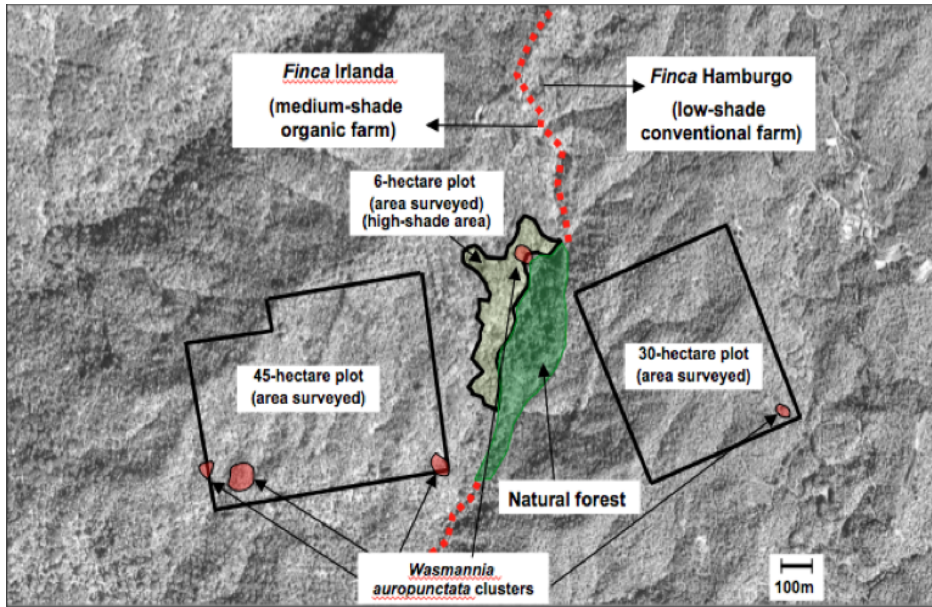
Fig 3.1 Intensively sampled areas on a shaded coffee farm in Mexico. Showing the distribution of the five clusters of *W. auropunctata* already located in the Mexican system. Bold lines indicate area already intensively sampled. Note that extensive sampling reveals the complete absence of *W. auropunctata* in all the area within the perimeter of the dotted lines, except for the five clumps indicated.

Fig 3.2. Spatial surveys of *W. auropunctata* distribution on a 6-ha Puerto Rican coffee farm. Red region (~1ha) indicates a single mega-colony of *W. auropunctata*. White and grey circles indicate smaller patches of *L. iniquum* interspersed with *W. auropunctata* nests (red). Thick gray lines were intensive sampled transects with baits placed every 2 meters.
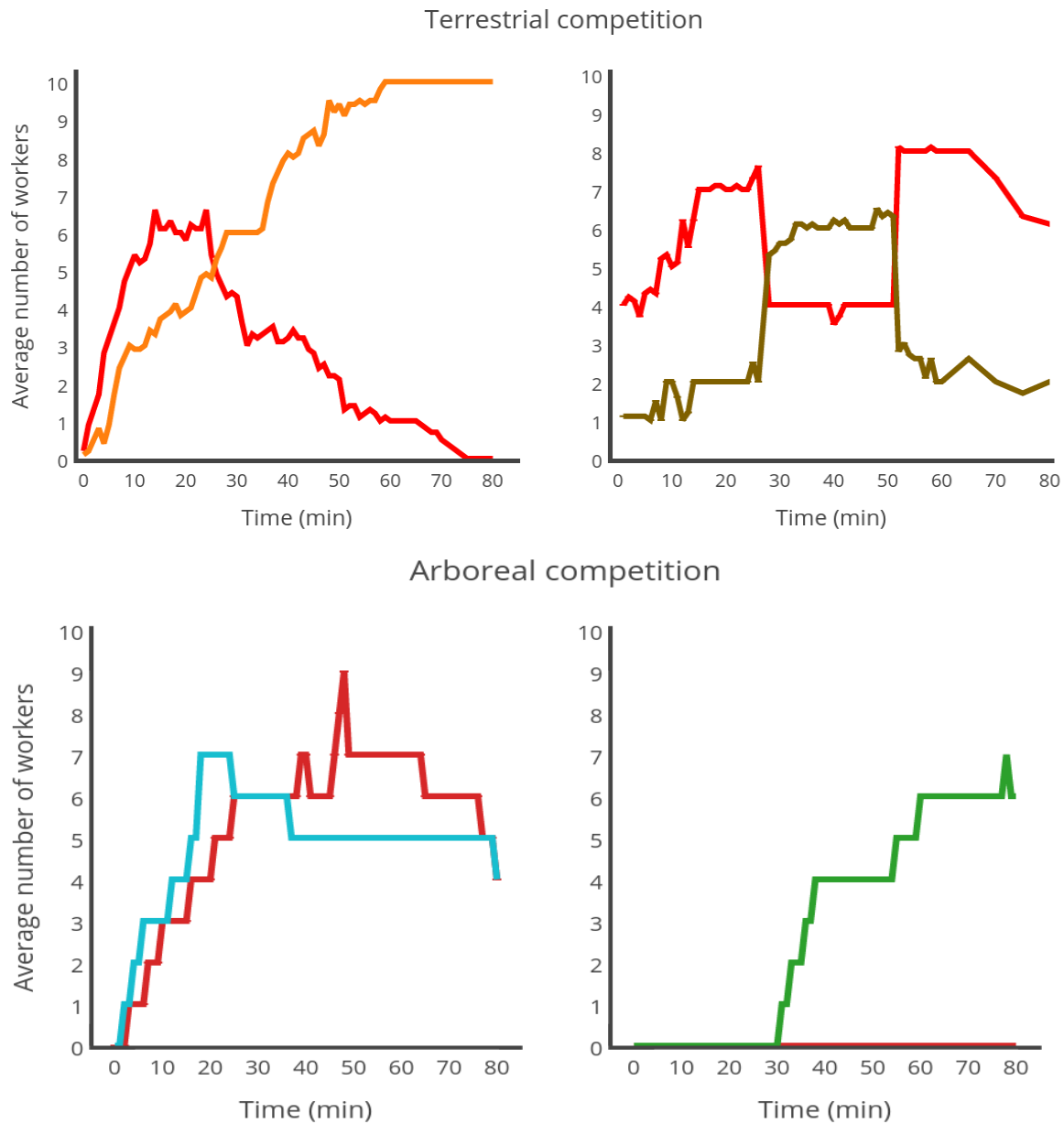
Fig 3.3 a-d. Resource competition dynamics between *W. auropunctata* (red) and native ant species in Mexico. Foraging dynamics of species at tuna baits over time (i.e. expressed as the average number of workers). Top graphs interactions between *W. auropunctata* (red) and ground foraging ants *S. geminata* (yellow) and *P. protensa* (dark green). Bottom graphs show interactions with the arboreal ants *S. picea* (cyan) and *P. synanthropica* (light green).
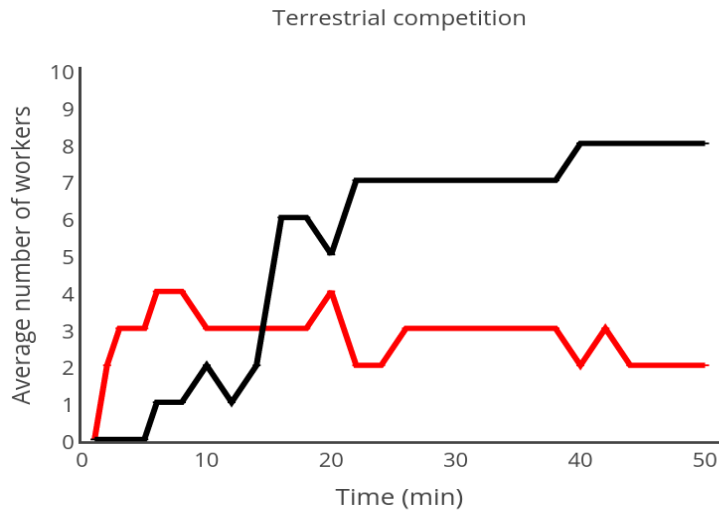
Fig 3.4. Short-term competitive interactions in Puerto Rico between ground-foraging ants *W. auropunctata* (red) and *S. invicta* (black). Foraging dynamics of species at baits over time (i.e. expressed as the average number of workers).
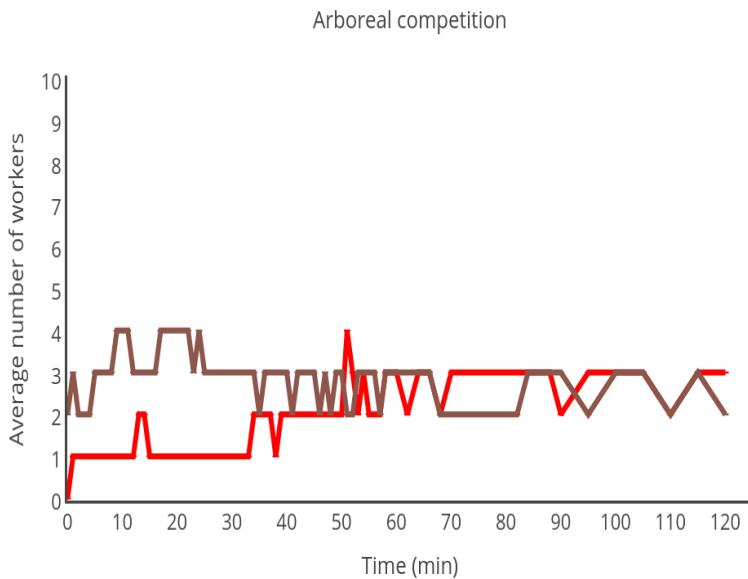
Fig 3.5. Short-term competitive between arboreal ants *W. auropunctata* (red) and *L. iniquum* (brown) in a laboratory experiment. Foraging dynamics of species at baits over time (i.e. expressed as the average number of workers).
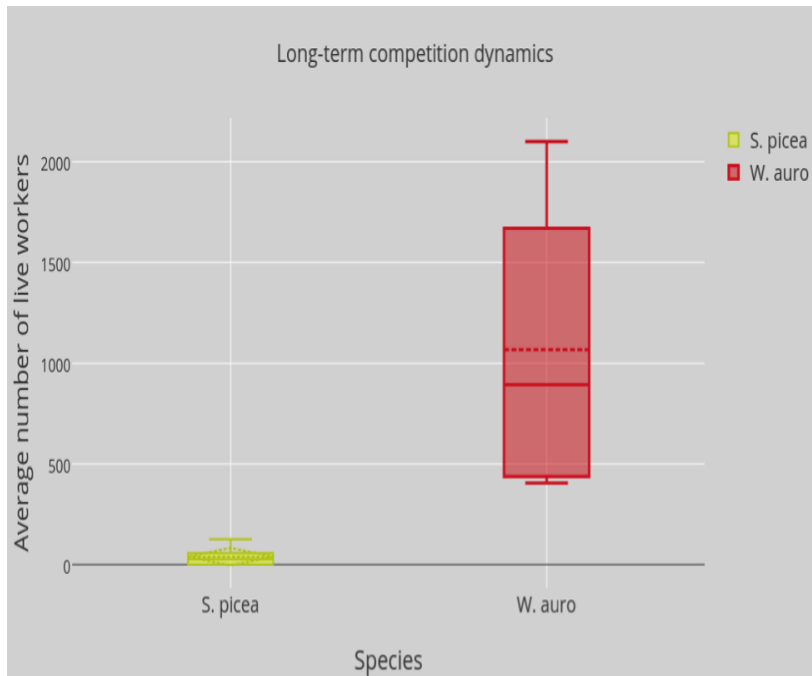
Fig 3.6. Long-term competitive interactions in Mexico between ground-foraging ants *W. auropunctata* and *S. picea*. Shows differences in the average number of live ant workers recorded at the end of experiment (14-days). Error bars are standard errors of mean.
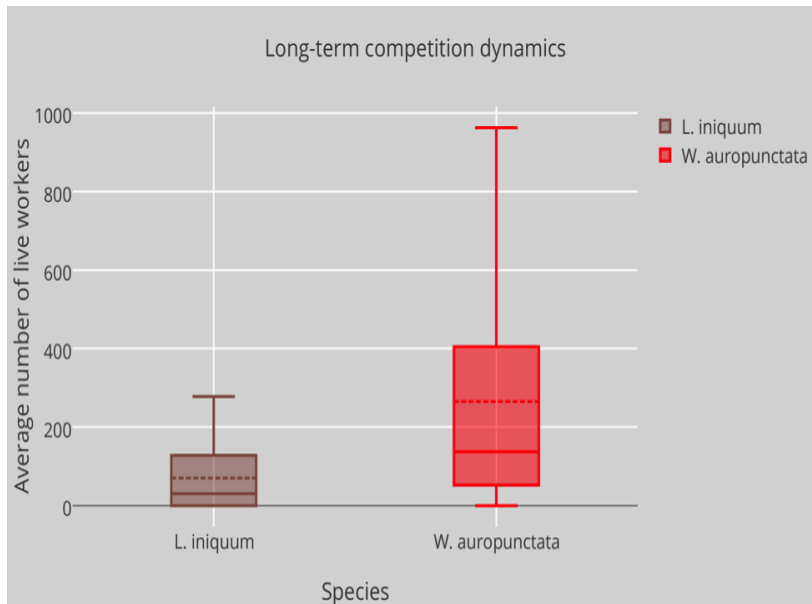
Fig 3.7. Long-term laboratory competition experiment between arboreal ants W. auropunctata (red) and L. iniquum (brown). Shows differences in the average number of live ant workers recorded at the end of experiment (14-days).

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CHAPTER IV

**PHORID FLY PARASITOID EFFECTS ON THE NATIVE ANT *L. INIQUUM*
INDIRECTLY FACILITATES THE COMPETITIVE ABILLITY AND SPREAD OF
THE INVASIVE LITTLE FIRE ANT *W. AUROPUNCTATA* IN PUERTO RICO.**

Abstract

Parasites play an important role in invasion success with important consequences for biodiversity and community structure. While much research has focused on direct effects of parasites on biological invasions, parasites can also indirectly influence interactions within the invaded community across trophic levels. For instance, parasites can mediate competitive interactions between native and exotic species through trait-mediated indirect effects. We consider the interactions between the parasitoid fly Pseudacteon sp. (Diptera: Phoridae), and its native host ant *Linipethema iniquum*, and the exotic ant *Wasmannia auropunctata* in the introduced range of Puerto Rico. We examined the effects of phorid flies on the competitive outcome between the arboreal ants *W. auropunctata* and native ant *L. iniquum*. Furthermore, we investigate the searching efficiency of phorid flies in detecting *L. iniquum* nests. To study the indirect effects on ant competition, we monitored ant recruitment to baits over a 60-min time interval in the presence and absence of phorid fly parasitoids. We then performed field experiments and measured phorid arrival time to arboreal nests of *L. iniquum* located in both a) *W. auropunctata*

patches and in b) isolated patches dominated by *L. iniquum* nests. We found that the presence of phorid fly significantly reduced recruitment of *L. iniquum* workers to baits through induced behavioral changes thereby increasing the ability of *W. auropunctata* to acquire resources. In addition, we found that phorid arrival time in isolated patches of *L. iniquum* patches was faster as compared to *L. iniquum* nests located within *W. auropunctata* patches. Our results show that phorid fly parasitoids indirectly may influence competitive interactions by attacking the host-ant *L. iniquum* and consequently providing an advantage to local spread of *W. auropuntata* populations in Puerto Rico. However, the spatial dynamics of arboreal ants shows that *L. iniquum* seeks protection from phorid fly parasotoids by moving their nests to *W. auropunctata* dominated patches.

Introduction

Biological invasions pose a major challenge to ecosystems with consequences for community structure and biodiversity (Dunn et al. 2012). The global spread of introduced species is altering native communities and is rapidly accelerating due to human activities (Mooney and Cleland 2001). In recent years, there has been growing interest in the role of parasites in invasion success (Tompkins et al. 2010). Much of the research involving the role of parasites in invasions has focused on direct interactions, including competition and predation studies, and on their subsequent effects on community dynamics (Wilson et al. 1998, Corbin and D' Antonio 2004). However, indirect effects are believed to play a key role in the structuring of ecological communities (Holt 1977, Miller 1994, Bonsall and Hassell 1998, Peacor and Werner 2001). The extent to which indirect effects influence the invasion process and their consequences on native communities remains unexplored (White et al. 2006). Parasites can indirectly structure ecological communities within the same trophic level through parasite mediated competition (Bowers and Turner 1997). During biological invasions, the absence of parasites can indirectly enhance the competitive ability of an exotic species (Torchin et al. 2003) by reallocating resources against defense to competitive traits (Blossey and Notzold 1995).Parasites can affect the outcome of competitive interactions between exotic and native species through both density-

mediated indirect effects (DMII) and trait-mediated indirect effects (TMII). For instance, competitive interactions between the native ant *Solenopsis geminata* and invasive ants *Solenopsis. invicta* were altered by the phorid parasitoid *Pseudacteon browni* (Morrison 1999). In the presence of phorid flies, *S. geminata* had to defend themselves against *P. browni* resulting in 50 % decline in resource retrieval thereby giving the invasive ant *S. invicta* a competitive advantage. As such, Pseudacteon phorid fly parasitoids (Diptera: Phoridae) have been used as a biological control agent against *S. invicta* populations (Mehdiabadi et al. 2004). Interspecific competitive trade-offs are believed to play an important role in the structuring of ant communities (Lebrun and Feener 2007). The discovery-dominance trade-off describes the ability of a species to discover a food resource versus the ability of a species to dominate a food resource (Fellers 1987, Savolainen et al. 1988). The discovery-dominance trade-off allows for species coexistence and has been documented in studies involving only a few ant species (Lynch et al. 1980, Perfecto 1994, Morrison 1996, Feener et al. 2008). However, exotic ants are believed to break down this trade-off in their introduced range by excelling at both traits (Holway 1999). Another trade-off involves the ability of species to defend itself against natural enemies in contrast to maximizing their competitive abilities (Lebrun and Feener 2007). For instance, specialized phorid fly parasitoids have been found to attack host ants and limit their foraging activities resulting in the frequent loss of resources to their competitors (Feener and Brown 1992) (Orr et al. 1995, Morrison et al. 2000, Philpott 2005). Together these trade-offs interact with one another to influence community structure in such a way that a species ability to maximize it's competitive potential is balanced by its vulnerability to parasitism (Adler 1999). An optimal fitness strategy is to minimize competitive ability to the level of the entire ant assemblage in order to avoid parasitism (Adler et al. 2007). While the presence of phorids has been found to reduces foraging rates to baits, phorids may not always determine the outcome of competitive interactions between native and exotic ant species (Morrison 1999). In addition, phorids were not influential in competitive outcomes between *Solenopsis invicta* and *Solenopsis geminata* in a laboratory setting (Morrison 2000). Furthermore, the spatial distribution of hosts can affect the searching efficiency and attack rates by phorids (Philpott et al. 2009). Empirical studies are needed to address the relative importance of phorid parasitoids in influencing invasion dynamics and community structure.

Our study focuses on the invasion dynamics of *W. auropunctata* and competitive interactions with the arboreal ant *Linipethema iniquum* in Puerto Rico. *W. auropunctata* is native to Central and South America and has in recent decades expanded to island groups in the Carribean and Pacific Oceans (Foucaud et al. 2010). It has also spread to parts of Western Africa, including Gabon and Cameroon, and most recently to the Middle East (Walker 2006) (Ndoutoume-Ndong and Mikissa 2007, Vonshak et al. 2009, Mikkisa et al. 2013, Wetterer 2013). Within its native range, *W. auropunctata* is regarded as a common, but sub-dominant species as it faces intense competition by dominant ant species (unpublished data). *W. auropunctata* is widely distributed in Puerto Rico and can reach high populations densities on coffee farms (Wetterer 2013). At our site, phorid parasitoids were found to be attacking *L. iniquum* workers (*Pseudacteon* sp.). This study addresses whether trait-mediated indirect effects by phorids mediate competition and facilitate the invasion of *W. auropunctata* in Puerto Rico (fig 4.1). We examined the effects of phorid parasitoids on resource competition between host *L. iniquum* and non-host *W. auropunctata* and the effects of the spatial distribution of ants on phorid searching efficiency.

Materials and Methods

Study sites and species

The study was conducted in the months of February, June, and July, in 2015 and 2016, on a coffee farm in Puerto Rico. The field site consisted of a 5-hectare plot within a high-shade organic coffee farm located in the central mountainous region in the municipality of Orocovos (18.175850, -66.4155700). The plot consisted primarily of coffee and banana trees where *W. auropunctata* and *L. iniquum* were found to be nesting. *W. auropunctata* invasion into the Carribean region is the result of multiple introductions due to human-induced dispersal and likely originates from it's native habitat along the northern coast of South America (Foucaud et al. 2010). The Caribbean region represents an important zone from where secondary dispersal that led to the global expansion of *W. auropunctata*. The native range of *L. inipethema* extends from South to Central America into the eastern parts of the Caribbean (Wild 2008). *L. iniquum* is

an arboreal ant species and has been found nesting in hollow twigs and leaf petioles of plantain in Puerto Rico (Wheeler 1908).

We surveyed the 5-ha plot to determine the abundance and spatial distribution of *W. auropunctata* and *L. iniquum* populations (fig 4.2). Tuna baits were placed along transects of coffee and banana trees spaced out every 2 meters. Baits were subsequently checked every 30 minutes to determine the presence or absence of *W. auropunctata* and *L. iniquum*. In order to examine competitive interactions a small plot (30 m x 14 m) was established along the edges of *W. auropunctata* and *L. iniquum* territorial boundaries. A total of 324 baits were placed on trees in the large plot (within the high-shade organic farm). Surveys were completed in June and July of 2015.

Indirect effect of parasitoids on ant competition

To test the trait-mediated indirect interactions by phorid flies on ant interactions we experimentally 1). Quantified the number of ant workers competing over time in the presence and absence of phorid flies. 2) Transplanted nests in trees dominated by *W. auropunctata* and *L. iniquum*. To assess competitive ant interactions, colonies of *W. auropunctata* and *L. iniquum* were randomly selected from coffee trees in the plot. To attract and collect phorid flies in the field, workers of *L. iniquum* were squashed by hand at each tree stand. Phorid flies were aspirated and placed in plastic containers in tents. Due to their fragility, phorid flies were kept in containers for less than 2 hours. Controls consisted of collected *W. auropunctata* and *L. iniquum* nests placed in containers connected by an artificial platform with droplets of honey resources placed at the center. Treatments consisted of *W. auropunctata* and *L. iniquum* colonies, in addition to phorid flies that were introduced at the beginning the experiment. Once the ants began foraging and replenished with honey, we recorded the number of ants at the bait ever minute for a maximum of 60 minutes or until all baits were occupied by 10 or more ants. Experiments were replicated 4 times for each interaction.

Parasitoid searching efficiency

We measured arrival times of phorid flies to trees occupied by *L. iniquum*. We identified four major ant clusters within the 5-ha plot. The overwhelming majority of trees were occupied by *W. auropunctata*, while the remaining trees were dominated by *L. iniquum* and Brachymyrmex

species (fig 4.2). Within the largest *W. auropunctata* cluster, several trees were occupied by *L. iniquum*. Within the three smaller clusters, *W. auropunctata* was detected on several trees. We randomly selected four trees occupied by *L. iniquum* in the largest cluster and four trees occupied in the smaller clusters. At each tree, we disturbed *L. iniquum* nests by squashing their workers by hand and recorded the arrival time of phorid flies.

Data analysis

To compare recruitment of *W. auropunctata* and *L. iniquum* to baits with and without phorids, we used fisher's exact test to compare the number of ant workers recruited over time to baits, testing the null hypothesis that the number of foragers is the same between treatments. Each treatment consisted of *W. auropunctata* and *L. iniquum* colonies competing for tuna baits resources in the presence of phorids, while in the controls phorids were excluded. To investigate the effects of the spatial distribution of arboreal ants on phorids, we examined the arrival time of phorids to trees dominated by *L. iniquum*. We used a simple t-test to determine differences in phorid arrival time between sites that included *L. iniquum* trees within clusters dominated by *W. auropunctata* and sites with trees dominated by *L. iniquum* with *W. auropunctata* trees interspersed (fig 4.2).

Results

Phorids flies influenced the competitive interactions between *W. auropunctata* and *L. iniquum*. We observed that *L. iniquum* in the presence of phorids underwent a 3-fold reduction in less than 15 minutes, which caused significant declines of *L. iniquum* abundance (p = 0.01). *W. auropunctata* abundances significantly increased abundance levels by 2-4 times in the presence of phorids (p < 0.0001). Phorid flies limited the recruitment rate of *L. iniquum* (fig 4.3), likely restricting resource uptake, which in effect increased the abundance of *W. auropunctata* in the presence of phorids. The spatial distribution of *L. iniquum* nests in trees significantly affected the searching efficiency of phorids. The majority of trees where occupied by *W. auropunctata* nests (N=166), followed by *L. iniquum* nests (N=129), and unidentified ant species (N=29). We found a significant effect of phorid arrival in *L. iniquum* dominated patches as compared to *W. auropunctata* dominant patches. Phorids in nearby *L. iniquum* patches took anywhere between 3-

5 minutes to arrive at trees, while phorids took much longer to detect *L. iniquum* trees within *W. auropunctata* patches (fig 4.4). Thus, the spatial distribution of *L. iniquum* limited the effectiveness of phorid control in areas where *W. auropunctata* dominates.

Discussion

Phorid fly presence significantly affected competitive interactions between *W. auropunctata* and *L. iniquum*. Phorid flies significantly affected the recruitment of *L. iniquum* workers to tuna baits, which significantly increased the overall abundance levels of *W. auropunctata* workers. In the absence of phorid flies, *L. iniquum* workers had a higher recruitment rate to baits and gained a competitive advantage over *W. auropuntata*. In the presence of phorids, *W. auropunctata* workers were able to overtake baits through a combination of direct interactions (i.e. competition) and indirect attacks by phorids on *L. iniquum*. This double-whammy led to the rapid decline of *L. iniquum* workers over time.

The effect of phorids on ant community structure depends on the spatial scales of interaction. Our results indicate that phorid searching efficiency depends on the spatial scale of both the phorid fly and distribution of *L. iniquum* nests. It took much longer for phorids to locate *L. iniquum* nests within the patch of *W. auropunctata* as compared to areas where *L. iniquum* was more prevalent. As distance increased from densely populated areas of *L. iniquum*, phorid attack rates diminished because of the time it took to locate nests. Although we don't claim to have information on the population density of phorids at local spatial scales, it appears that phorid flies increase their local population densities nearby areas dominated *L. iniquum*. Phorid flies are known to use chemical cues to locate their hosts (Brown and Feener 1991, Morrison 1999, LeBrun and Feener 2002, Hsieh and Perfecto 2012). During competitive encounters, ants release alarm pheromones resulting in the rapid response by phorid flies. One study found that phorid attack rates increased when *Linipethema* was in the presence of dominant ant competitors (Orr et al. 2003). Thus, a behavioral response by *Linipethema* during competitive encounters elicits a positive feedback by increasing phorid attack rates which increases the number of foragers of its opponents (Hsieh and Perfecto 2012, Philpott 2005). At larger spatial scales, we found that phorid attack rates diminished at greater distances from *L. iniquum* clusters. Interestingly, *L. iniquum* nests found within *W. auropunctata* clusters were temporarily relieved

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from phorid attacks. There was a five-fold reduction in phorid attack rates in isolated *L. iniquum* trees within *W. auropunctata* clusters which suggests that *L. iniquum* species disperse to patches dominated *W. auropunctata* in order to receive protection against phorid parasitoids.

The effects of phorids in mediating ant competition may vary temporally. Our results demonstrate that *L. iniquum* abundances were reduced in the presence of phorids during the experiment. However, ants can adapt the timing of their foraging activities as a way of avoiding phorid attacks (Philpott et al. 2004). For example, the ground forager ant *Atta cephalotes* primarily forages during the night time in order to avoid phorids during the day time that tend to build up their populations outside of *A. cephalotes* nest colony entrances (Orr 1992). Several *Linipethema* species construct mobile nests that are often disguished from phorids making it more difficult to find (Markin 1970). In our system, *L. iniquum* species have many different shallow nest entrances throughout coffee trees making it even more difficult for phorids to figure out where to attack. Therefore, species differences in nesting ecology and habitat complexity may play an important role in phorid attacking abilities (Orr et al. 2003) (Philpott 2005).

Another important factor in assessing TMII on competition is resource size (Mehdiabadi et al. 2004, Philpott et al. 2004). In our study, both *L. iniquum* and *W. auropunctata* were provided with large resources. However, this may not have given *L. iniquum* enough time to defend itself from phorids as they recruit large number of workers to uptake resources. In our experiment, *L. iniquum* was rapid at resource discovery, as compared to *W. auropunctata*, but spent longer time recruiting workers to carry baits. Although not enough is known about species response to variation in resources, small resources distributed over larger spatial scales may enable *L. iniquum* to avoid persistent phorid attacks. (LeBrun 2004) showed that phorids take a much longer time locating ants consuming smaller resources. As fewer ants are recruited to smaller resources, less pheromones are being released that phorids can exploit to detect ant foraging activities (Folgarait and Gilbert 1999) (Feener and Brown 1992).

These findings have important implications for the invasion dynamics of *W. auropunctata* in a coffee agricultural ecosystem. In the absence of phorids, *L. iniquum* reaches higher abundance levels resulting in increased access to resources. This pattern changes however when phorids come into the scene and *L. iniquum* abundance diminish rapidly enabling *W. auropunctata* to increase its abundance levels. At the population level, *L. iniquum* builds up

locally dense clusters but undergoes increased attacks by phorids, which provides an opportunity for *W. auropunctata* to invade. To counter this two-fold attack, *L. iniquum* disperses into patches dominated by *W. auropunctata*, providing temporary protection from phorid attacks. These factors taking together show clear effects of phorids on ant competition.

Studies of ant competition have shown the existence of competitive trade-offs among species can structure ecological communities and promote coexistence (Fellers 1987, Savolainen et al. 1988, Perfecto and Vandermeer 2013). The trade-off implies that some species have strong resource discovery abilities as opposed to other species that have strong resource domination abilities. TMII mediated competitive interactions by phorids can break the discovery-dominance trade-off and enable invasive species to spread (Hsieh and Perfecto 2012). In the absence of phorids, *L. iniquum* is a faster resource discoverer and gains a competitive advantage over *W. auropunctata* species, which are known to be poor resource discoverers (Bertelsmeier et al. 2015). However, phorids can tip the balance and limit the rapid acquisition of resources by *L. inquum* thereby providing *W. auropunctata* species with ample time to dominate resources and spread. A similar pattern was found in a pine-oak woodland ecosystem involving *Pheidole* host species that in the absence of phorids increased their discovery abilities, thereby breaking the discovery-dominance trade-off. The presence of phorids reduced the competitive ability of the host species to the level of the ant assemblage reinforcing the discovery-dominance trade-off (Lebrun and Feener 2007). Phorid incuced TMII attacks on *L. iniquum* enable to *W. auropunctata* to spread in Puerto Rico.

A key question that remains is what potential factors limit the expansion of *W. auropunctata* in its native range. To our knowledge no phorid parasitoids have been recorded in the native range of *W. auropunctata*. However, previous research in the native range of Mexico suggests that dominant ant species can limit the expansion of *W. auropunctata* in a Mexican agricultural ecosystem, providing further support for the biotic resistance hypothesis (Yitbarek et al. in press). In the case of another invasive ant species *S. invicta*, phorid induced TMII and interspecific competition influenced the ecological success of the invasive ant *S. invicta* (Feener et al. 2008). However, this pattern was found to vary geographically depending on the presence of phorid parasitoids in the region. In the case of Puerto Rico, we find that a combination of release from competitors in the native range and TMII contributes to the expansion of *W. auropunctata*.

Our study on the role of phorid parasitoids mediating competitive ant interactions has important consequences for biodiversity maintenance. Competitive dynamics between *W. auropunctata* and *L. iniquum* for resources suggest that two different trade-offs operate. The ability of *L. iniquum* to arrive at resources quickly and the ability for *W. auropunctata* to hold on to acquired resources shows that a discovery-dominance maintains species coexistence in the absence of phorids. The discovery-dominance vanishes in the presence of phorids and in place a new trade-off emerges between the ability to compete for resource versus the ability to defend against parasitoids (Lebrun and Feener 2007). This so-called competition-defense trade-off reduced *L. iniquum* workers at resources while *W. auropunctata* was able to increase its workers to baits. The interplay between these trade-offs can amplify within complex ecological networks whereby the addition of a parasitoid reduces the dominance of a species to the level of the entire assemblage resulting in coexistence. From a practical standpoint, *W. auropunctata* has been found to be an effective biological control against the coffee berry borer pest in Mexico (Gonthier et al. 2013). Indirect effects by phorids enables *W. auropunctata* to expand in shaded areas with relatively high densities of the coffee berry borer. One potential mechanism for limiting the expansion of *W. auropunctata* on coffee farms is through the management of shade trees. Pruning of trees provides enough sunlight to attract ant competitors that can potentially limit the expansion of *W. auropunctata* while also providing ecosystem services.

These findings open up a new set of inquiry on the effects of TMII on ant community structure across temporal and spatial scales. While phorids reduced the abundance level of *L. iniquum* resulting in a competitive advantage for *W. auropunctata*, we know very little about the long-term population level consequences of TMII on ant communities. In particular, it's important to explore whether parasitoid phorids attacks on *L. iniquum* have implications for colony growth (Mehdiabadi et al. 2004). Although phorids reduce the number of workers of host species this may not necessarily affect the colony as a whole and therefore future investigations should evaluate the long-term dynamics between ants and phorids (Philpott 2005). Spatial considerations between ants and phorids need to take into account the foraging range of phorids. While phorids appear to build up their populations nearby *L. iniquum* clusters it's not clear how far the range of phorids extends. Within *W. auropunctata* clusters several colonies of *L. iniquum* have been established in order to limit phorid attacks. This feedback between phorid range and ant competition leads to the formation of spatial clusters. In this regard, spatially explicit models

can serve us useful guides to disentangle complex direct and indirect interactions between ants and phorids that give rise to spatial pattern formation and have important consequences for biodiversity (Li et al. 2016).
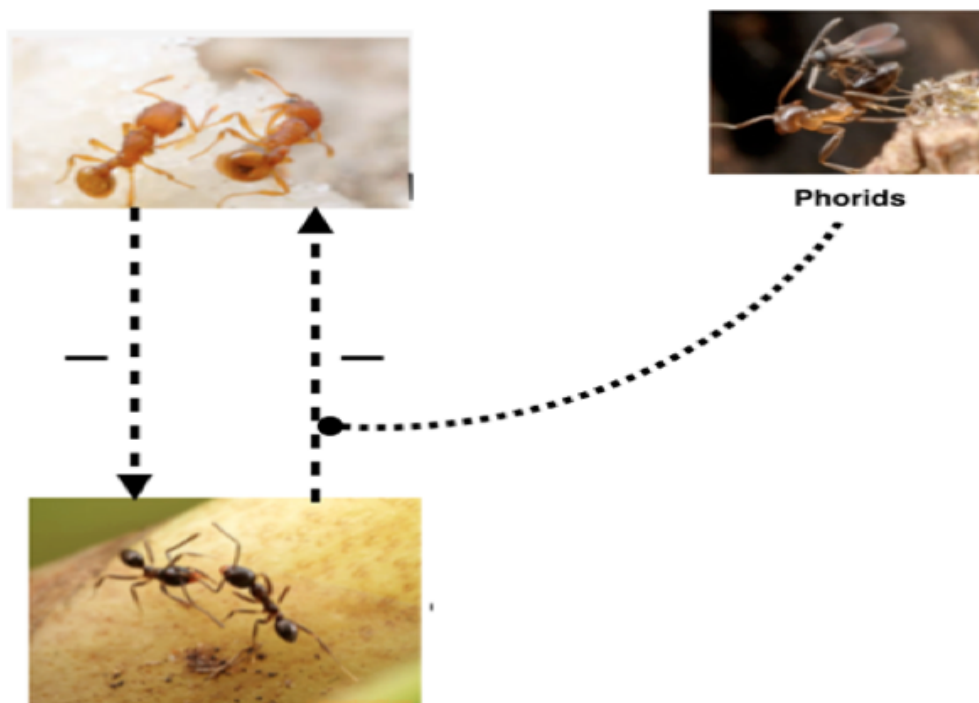
Figure 4.1 Trait-mediated indirect effects on competition. Direct competitive interactions for resources between *W. auropunctata* (top picture) and *L. iniquum* (bottom picture). The parasite decreases the per-capita impact on host ant *L. iniquum* on the resource and enhances the competitive ability of non-host ant *W. auropunctata*.

Figure 4.2 The spatial dynamics of *W. auropunctata* (red) and *L. iniquum* (white) arboreal nests. There is one 1-large patch dominated by *W. auropunctata* and several smaller satellites clusters of *W. auropunctata* are found within the patches dominated by *L. iniquum*. Within the large patch of *W. auropunctata* several trees were occupied by *L. iniquum* nests. Phorid attack rates occurred faster in patches dominated solely by *L. iniquum* as compared to the large *W. auropunctata* patch. This potentially suggests that *L. iniquum* may be nesting in *W. auropunctata* patches in order to avoid phorid parasitoids.
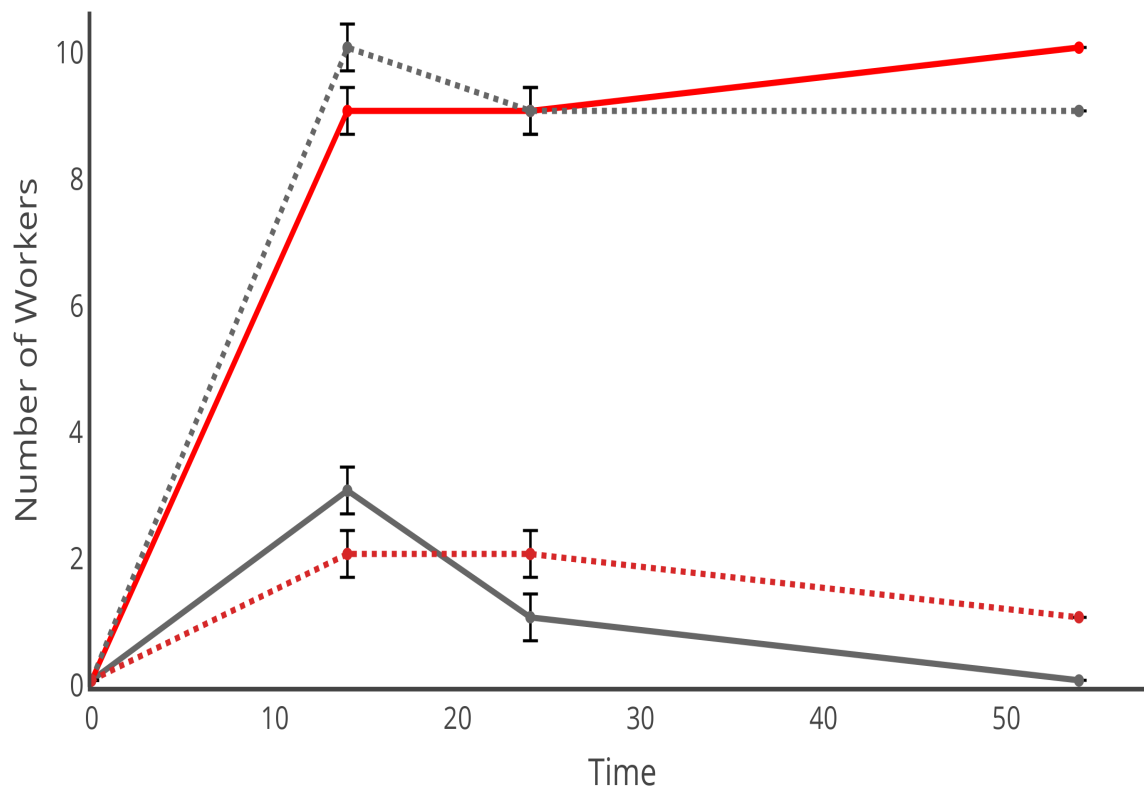
Figure 4.3 Competitive dynamics between *W. auropunctata* and *L. iniquum* in the presence and absence of phorid parasitoids. In the absence of phorids, *L. iniquum* (control) outperforms *W. auropunctata* (control) in terms of the number of workers at baits (P= 0.01). In the presence of phorids, *L. iniquum* (solid grey) workers rapidly decline while the number of *W. auropunctata* (solid red) remains relatively constant (P< 0.0001). The phorids appear to induce a behavioral response in *L. iniquum* that effectively reduces their workers at baits giving *W. auropunctata* a competitive advantage.
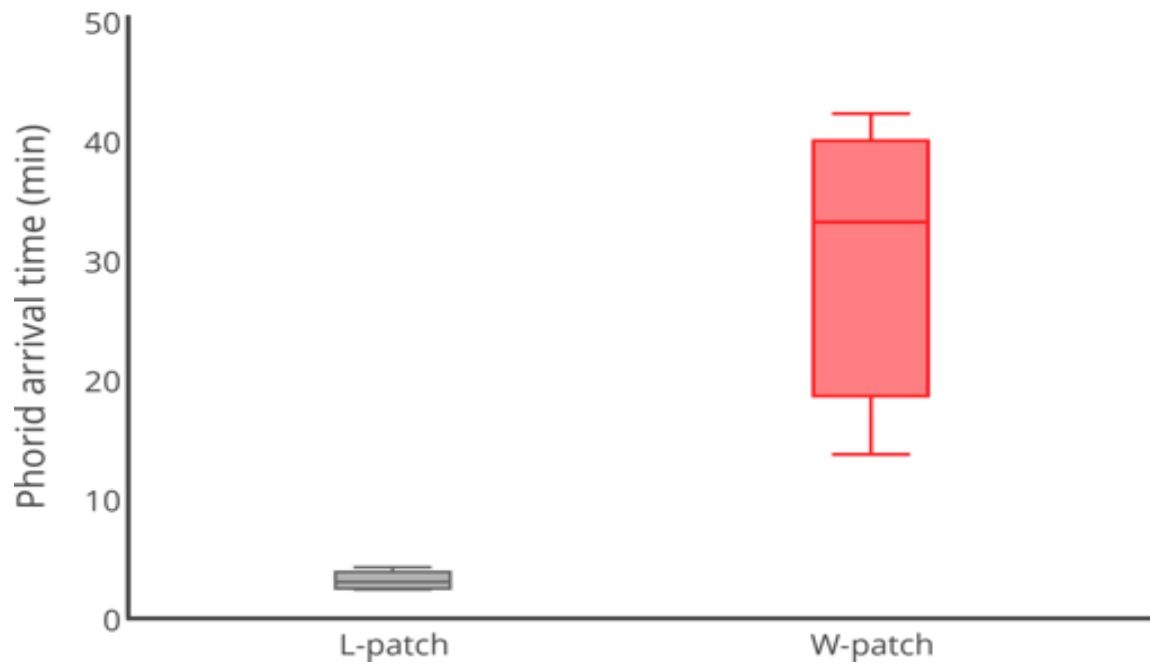
Figure 4.4 Phorid arrival time to *L. iniquum* occupied trees. The time of arrival by phorids to *L. iniquum* trees occurred faster in patches dominated by *L. iniquum* (grey) as compared to patches dominated by *W. auropunctata* (red), (t=-3.14, df=4, p=0.03).

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CHAPTER V

THE EFFECT OF COMPETITIVE NETWORK STRUCTURES ON TWIG-NESTING ANT ABUNDANCE PATTERNS IN A TROPICAL AGRICULTURAL ECOSYSTEM.

Abstract

Spatial processes influence the structure and assembly of ecological communities. Several proposed mechanisms of species coexistence operate across spatial scales. However, very little is known about the relative importance of multiple factors driving community assembly. This study seeks to examine spatial dynamics of community assembly in tropical twig-nesting ant assemblages in coffee ecosystems. We examined for the presence of competitive network structures and relative abundance patterns at two distinct spatial scales for arboreal twig-nesting ants in a coffee agro-ecosystem. We specifically addressed whether competitive structures (i.e. transitive versus intransitive structures) correlate with field abundance patterns. We conducted lab experiments to assess competitive structures of twig-nesting ants, and correlated this with abundance data from field surveys in small, 1 ha plots (local scale) and across a large 45 ha area agricultural ecosystem (regional scale). Dominance rank of ant species was not correlated with relative abundance across the entire coffee farm; however, transitive structures correlated with increases in relative abundance at the local scale compared with relative abundance at the regional scale. However, we did find a significant number of intransitive structures than expected by chance. This study thus demonstrates that simple network structures may predict local abundance patterns in competing ants, but that at larger spatial scales, other factors impact community assembly.

Introduction

Differences in competitive abilities of species have been attributed to differences in the relative abundances of species assemblages (Meserve et al. 1996; Ulrich et al. 2014). Competitive trade-offs are thought to be an important mechanism in explaining species coexistence and in determining relative abundance patterns in ecological communities (Chesson 2000; Levine and Rees 2002; Tilman 2011). In plant communities, competitively inferior species are negatively correlated with low species abundances, raising the question of how multiple species can coexist (Stanley Harpole and Tilman 2006; Fox 2013). In ant communities competitive hierarchies have been found to be positively correlated with relative species abundances by indirectly neutralizing the effects by lower ranked species (Andersen 1992; Arnan et al. 2011). Despite these observations, it remains unclear whether these patterns true across spatial scales.

A long-standing assumption in community ecology is that species form transitive dominance hierarchies (A→B → C→ Z) on the basis of competitive differences among species (Goldberg and Landa 1991) However, numerous empirical and theoretical investigations, in which species are arranged in intransitive dominance hierarchies, (A→B→C→A), have concluded that communities composed of three or more species can coexist and thus provide us with a mechanism for biodiversity maintenance (Sinervo and Lively 1996; Kerr et al. 2002; Lankau and Strauss 2007; Vandermeer and Yitbarek 2012). Although it has proven to be challenging to infer intransitive competition networks from empirically derived abundance data in natural populations (Allesina and Levine 2011; Ulrich et al. 2014), recent meta-analysis in plant communities show that intransitivity is promoted by temporal heterogeneity(Soliveres et al. 2015). Despite these observations we lack studies quantifying network structures across landscapes with spatial heterogeneity. To this extent, we are interested in the effects of competition network structures on relative abundance patterns in ants across two different spatial scales.

Ants are useful organisms for testing hypotheses about community assembly and species co-existence (Palmer et al. 2000; Stanton et al. 2002a; Sanders et al. 2003; Palmer 2003; McGlynn 2006; Dunn et al. 2007). Ants are abundant and diverse and represent a large fraction of tropical animal biomass (Hölldobler and Wilson 1990). Several local factors may contribute to

ant community assembly including, 1) preferences or requirements for certain microhabitats (Nestel and Dickschen 1990; Morrison 1998; Kaspari and Weiser 2000; Albrecht and Gotelli 2001; Ribas et al. 2003), 2) the number, size, or diversity of available nesting sites (Leston 1978; Herbers 1989; Torres and Snelling 1997; Armbrecht et al. 2004; Powell et al. 2011), 3) food availability and distribution (Kaspari and Weiser 2000; Blüthgen et al. 2004), 4) competition (Leston 1978; Savolainen and Vepsäläinen 1988; Holway et al. 2002), 5) changes in dominance hierarchy due to environmental conditions (Cerda et al. 1997), and 6) impacts from predators, fungal diseases, or parasites (Feener 2000; LeBrun 2004). In addition, landscape or regional factors such as dispersal limitation (Yu et al. 2004; Bruna et al. 2005), habitat connectivity, size, and arrangement (Perfecto and Vandermeer 2002; Brühl et al. 2003) may also affect ant assembly. Among all of the local and regional factors known to affect ant communities and assembly, competition has frequently been examined in ant communities, and may play an important role in determining species composition and distribution (Leston 1978, Savolainen and Vepsäläinen 1988, Holway et al. 2002). For twig-nesting ants, nest takeovers are common and nest sites are often limiting, thus competition for nest sites is commonly inferred (Brian 1952; Yamaguchi 1992), and in at least one case has been experimentally demonstrated (Palmer et al. 2000). Competition between queens or individuals of budding colonies may limit founding of new colonies (Stanton et al. 2002b). Ants in coffee agroecosystems are nest-site limited (Philpott and Foster 2005), dominant canopy ants limit abilities of twig-nesting ants to colonize new nests (Ribas et al. 2003; Philpott 2010), and changing habitat conditions can lead to changes in dominance hierarchies (Ribas et al. 2003). Yet the specific role of other twig-nesting ants in limiting recruitment of new colonies, and which species have the ability to take over nests from others or hinder recruitment is relatively unknown. Although competition for non-nest resources is likely important, we focus here on competition for nesting resources as a possible driver of community assembly.

The arboreal twig-nesting ant community in coffee agroecosystems in Mexico is diverse. There are ~40 species of arboreal twig-nesting ants at the study site including *Brachymyrmex* (3 species), *Camponotus* (8), *Cephalotes* (2), *Crematogaster* (5), *Dolichoderus* (2), *Myrmelachista* (3), *Nesomyrmex* (2), *Procryptocerus* (1), *Pseudomyrmex* (11), and *Technomyrmex* (1) (Philpott and Foster 2005; Livingston and Philpott 2010). Both arboreal and ground-dwelling twig-nesting ants in coffee agroecosystems are nest-site limited in terms of number (Philpott and Foster

2005), diversity (Armbrecht et al. 2004) and sizes (Jiménez Soto and Philpott 2015) of nesting resources. Arboreal twig-nesting ants nest in dry coffee twigs, as well as dry twigs and branches in the shade tree canopy, and also readily occupy artificial nests. Loss of ant diversity with coffee management intensification has been associated with decreases in canopy cover and tree richness (Philpott 2010). Furthermore, distances to forest fragments resulting from a lack of needed resources or dispersal limitation, reduces ant diversity (Perfecto and Vandermeer 2002). Lastly, changing environmental conditions, such as variation in microclimates, result in changing dominance hierarchies with consequences for ant diversity (Perfecto and Vandermeer 1996). Despite these observations, the influence of competition for nest sites and dominance hierarchies across large-scale spatial distribution patterns for twig-nesting ants is less clear.

While several studies have shown a positive relationship between transitive hierarchies and relative abundance levels (Fellers 1987; Savolainen and Vepsäläinen 1988; Andersen 1992; Arnan et al. 2011), it remains unclear whether strict dominance hierarchies persist across spatial scales. Therefore, we aimed to develop a competitive network structure for twig-nesting ants that live in hollow coffee twigs in coffee agroecosystems to examine whether any distinct network structure among coffee-dwelling twig-nesting ants in controlled environments correlates with the relative abundance patterns for these ants in the field.

Methods

Study Site and System

We conducted fieldwork at Finca Irlanda (15°20' N, 90°20' W), a 300 ha, shaded coffee farm in the Soconusco region of Chiapas, Mexico with ~250 shade trees ha^{-1}. The farm is located between 900-1100 m a.s.l. Between 2006-2011 the field site received an average rainfall of 5726 mm per year with most rain falling during the rainy season between May and October. There are ~50 species of shade trees that provide between 30-75% shade to the coffee bushes below. In 2004, a 45-ha plot was established and has been surveyed annually since 2007 for tree species and tree occupation by the dominant, canopy ant *Azteca sericeasur* (Vandermeer et al. 2008). This plot has been periodically pruned between 2007-2013. In 2009 a 7-ha plot was established in an additional area of the 300-ha farm that remains under 75% shade cover. This 7-ha area thus acts as a control and an area in which the distribution of trees and *Azteca* ants is not significantly different that in the affected area of the farm (Jackson et al. 2014). The 7-ha area is a traditional polyculture and the 45-ha area is a mixture of commercial polyculture coffee and shade monoculture coffee according to the classification system of Moguel and Toledo (1999).

Field surveys

Between 2008-2013, we surveyed twig-nesting ants in 6-8 hectares of the 45-ha plot and in 0-2 hectares of the 7-ha plot (fig 5.1). In each hectare, we surveyed ants at two distinct spatial scales: the full hectare scale, and in 20 x 20 m plots randomly located within each larger plot. For full hectare surveys, we sampled ants on the coffee plant nearest to each tagged tree within the hectare (alternating by survey year to N, S, E, then W of the tree). We removed all dry twigs, counted hollow and occupied twigs, and identified all occupant ants. For 20 x 20 m plot surveys, we randomly placed the plot in a different location within the 1-hectare plot each year, and then sampled every coffee plant within the plot (~100-250 plants) by removing all dry twigs, counting hollow and occupied twigs, and identifying all occupant ants. The numbers of full-hectare and 20 x 20 m plots surveyed each year varied due to logistical and management constraints. We included each plot surveyed during a different year as a replicate and thus we surveyed ants in a total of 100 plots (56 full hectare plots, and 44 20 x 20 m plots). Twigs are an ephemeral resource, with relatively high turnover. As such, removing twigs on plants once per year is unlikely to affect census data during later sample periods. After destructive sampling of twigs, all

ants and nest pieces (minus twig nests collected for 'real estate' experiments - see below) were left at the sample location to facilitate recolonization of nest sites.

Local and global abundance patterns

We examined differences in the local and global relative abundance patterns found during surveys. We combined data for all plots into one database and then calculated the total number of twigs and the total number of coffee plants occupied by each species in each sample plot. Then for each plot, we calculated the percent of twigs and coffee plants occupied by each species. For each of the ten species used in 'real estate' trials (see below), we calculated local and global relative abundance. We defined local abundance as the mean percent of twigs or coffee plants occupied by a species in a plot where that species occurred. We defined global abundance as the mean percent of twigs or coffee plants occupied by a species across all plots (including plots where the ant species did not occur, and thus had a percent occupied of zero).

'Real estate' experiments

We examined the relative competitive ability of twig-nesting ants by constructing competitive hierarchies based on 'real estate' experiments conducted in the lab. We collected twig nests during field surveys in 2007, 2009, 2011, and 2012. We first removed ants from individual twigs, and then placed ants (workers, alates, brood) from two different species (one twig per species) into sealed plastic tubs with one empty artificial nest. The artificial nest, or 'real estate', consisted of a bamboo twig, 120 cm long with a 3-4 mm opening. After 24 hours, we opened the bamboo twigs to note which species had colonized the twig. All ants collected were used in 'real estate' trials within two days of collection, or were discarded. We conducted trials between pairs of the ten most common ant species: *Camponotus abditus*, *Camponotus* sp. 1, *Myrmelachista mexicana*, *Nesomyrmex echinatinodis*, *Procryptocerus hylaeus*, *Pseudomyrmex ejectus*, *Pseudomyrmex elongatus*, *Pseudomyrmex filiformis, Pseudomyrmex* PSW-53, and *Pseudomyrmex simplex*. We intended to replicate trials for each pair (out of a total of 45 two-species pairs) at least ten times. However, low encounter rates for some species, and for pairs of species within two days of one another precluded obtaining ideal sample sizes. We replicated trials for each species pair on average 5.73 times; four species pairs were replicated once, nine species pairs were replicated twice, and 31 species pairs were replicated three or more

times. Only one species pair (*M. mexicana* and *P. filiformis*) was not tested. We conducted 42 trials in 2007, 105 trials in 2009, 82 trials in 2011, and 30 trials in 2012 for a total of 259 trials.

To create a competitive ranking for each species, we created a matrix of wins to losses and computed the proportion of trials won for each species. We tested for linearity and intransitivity in the matrix with competitive network analysis (see below).

Statistical analysis of field data and 'real estate' experiments

Once a competitive rank for each species was established, we used that competitive rank to examine whether competitive rank correlates with relative abundance of common ant species. We first conducted simple linear regressions correlating the percent of plants or twigs occupied by a species across all survey plots, and the competitive rank of that species. Because ant communities may also be constrained by environmental filters or dispersal limitation, we also wanted to examine whether competitive rank was a better indicator of local abundance (e.g. where an ant occurs) than global abundance (e.g. at the scale of the entire farm). To do this, we conducted simple linear regressions with local abundance (percent of twigs or plants occupied in plots where occurs) as the response variables and global abundance (percent of twigs or plants occupied across all plots) as the explanatory variable. We then extracted the residuals from those regressions, and regressed the residuals against the proportion of trials won by each species during 'real estate' experiments to see if an increase or decrease in abundance locally, compared with global abundance of a species, could be explained by the competitive rank of the ant species. We used a logit transformation for the proportion of trials won (Warton & Hui 2011).

Motif Analysis

We sought to investigate how linear dominance hierarchies developed in twig-nesting ant communities. In addition to examining the role of individual ant attributes in determining linear dominance hierarchies, we were interested in assessing how the organization of linear dominance hierarchies emerged at higher levels. While individual attributes of species serve as a good predictor of dominance hierarchies among dyadic pairs, the pattern becomes less clear when seeking to explain linear dominance hierarchies at higher levels of species interactions (Chase 2011). Therefore, we examined the formation of dominance hierarchies using motif analysis that identifies network structures composed of transitive and cyclical triads (Faust 2007, 2010).

To test whether competition for nesting sites resulted in the emergence of transitive or cyclical dominance hierarchies, we analyzed an interaction matrix of replicated 'real estate' trials among twig-nesting ant species using motif analysis (Shizuka & McDonald 2012). Motif analysis is commonly used in social network analysis to detect emergent properties of the network structure as an explanation for dominance hierarchies by comparing the relative frequencies of motifs in the observed network to the expected value for the null hypothesis of a random network (Holland & Leinhardt 1976, Faust 2007). We carried out motif analysis with customized randomization procedures (McDonald & Shizuki 2013) to compare the structure of our network model against random network graphs. Species interaction data were represented as a directional outcome matrix. The nodes in the network represent individual ant species and the one-way directional arrows of the edges represent dominant-subordinate relationships. In the random networks, we maintained the same number of nodes and edges as in the observed network, but the directionality and placement of edges were generated randomly. Using the adjacency matrix, we calculated the triad census (McDonald & Shizuka 2013). The triad census allows us to examine directed species interactions (Pinter-Wollman et al. 2012). We used the seven possible triad configurations fully composed of three nodes that either have asymmetric or mutual edges (Holland & Leinardt 1976). We used the network analysis packages 'statnet' (Handock et al. 2013) and 'Igraph'' (Csardi & Nepsutz 2006) in R (R Development Core Team 2013) to calculate the frequencies of triad configurations (total triads = 220) and to compare the observed (N=10) to the random network graphs (N=10).

To test for statistical significance between the observed and randomly generated networks, we computed the triangle transitivity (Shizuka & Mcdonald 2012). The triangle transitivity represents the number of transitive triangles relative to the total number of transitive and cyclical triangles. A transitive triangle is one in which the ant species A beats both species B and species C. A cyclical triangle is one in which the ant species A beats species B, species B beats species C, and species C beats species A. A pass-along triad is one in which species A beats species B, and species B beats C, but A and C are neither dominant nor subordinate to one another. In random networks the expected frequency of transitive triangles is 0.75. A scaling factor for the triangle transitivity is applied such that the transitivity value ranges from 0 (random expectation) to 1 (high transitivity) (Shizuka & McDonald 2012). On the other hand, the triangle transitivity can be negative if cyclical triangles occur at higher frequencies than the random

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expectation of 0.25. We compared the emergence of dominance hierarchies by calculating the expected percentage difference in each random network replicate (N=10,000) to the expected percentage in the empirical network. Visualization of network graphs and descriptive statistics of the triad types were generated using the 'Igraph' package in R (R Development Core Team 2013). We plotted the mean observed and expected difference with a 95% confidence interval.

Results

Field surveys

During the six survey years, we sampled a total of 17,294 coffee plants searching for hollow twigs and twig-nesting ants. We found 5160 hollow twigs on 4395 coffee plants. Of those, 7280 hollow twigs (78.45%) and 3650 coffee plants (83.04%) were occupied by one of the 36 ant species encountered. The ten species included in real estate experiments occupied 94.81 ± 0.01 (SE) % of nests and 94.92 ± 0.01% of plants and the other 26 species occupied the remaining twigs and plants.

Competition experiments

In all 259 trials except one, there was a clear winner to the 'real estate' battle after 24 hours, indicating that one of the two species in the arena had occupied of the artificial nest. From examining the wins and losses, a clear competitive hierarchy emerged, with some species winning the vast majority (>70%) of trials in which they were involved, and other species winning few trials (<30%). The one trial that did not result in a winner was a trial involving *P. elongatus* and *P. ejectus*.

Local and global abundance patterns

The percent of competitive trials won by a species (e.g. the competitive rank) was not a good indicator of the percent of nests or of plants occupied by a species at the global scale. Competitive rank was not significantly correlated with the percent of nests occupied (y = -0.0026x + 0.2286, R^2=0.269, P=0.124) or of the percent of plants occupied (y = -0.0028x + 0.240, R^2=0.282, P=0.115) across the entire survey area. However, competitive rank was a good indicator of the relative increases in local relative abundance in plots where certain ant species occurred. The local and global relative abundance of ants in twigs and on coffee plants were

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highly correlated (Fig. 5.2 a, b). For occupied twigs, local relative abundance was positively correlated with global relative abundance ($F_{1,9}$=518.868, P<0.001). Likewise, for coffee plants, local relative abundance was positively correlated with global relative abundance ($F_{1,9}$=1925.261, P<0.001). The proportion of real estate trials won by ant species was significantly positively correlated with the residuals of the local and global abundance regressions (Fig. 5.2 c, d). Specifically, for hollow twigs, the proportion of real estate trials won was positively correlated with the regression residuals ($F_{1,9}$=5.618, P=0.045). For coffee plants, the proportion of real estate trials won was positively correlated with the regression residuals ($F_{1,9}$=8.025, P=0.022). This result in both cases indicates that the more competitively dominant ants were more abundant locally than globally.

Motif analysis: Triad patterns

The motif analysis of the triad distribution showed that the observed network has a significant excess of transitive triads (N=76) followed by a significant deficit of cyclical triads (N=8). Triad types that are positive (i.e. non-overlapping at 0) occurred in excess in the observed network, while triad types that are negative showed a deficit in the observed network as compared to the random null network.

The remaining five triads in the network did not show any significant differences in the mean triad percentage rates between the observed and expected network (Fig. 5.3). While the data showed a clear excess of transitive triangles (34.55 %) and deficit for cyclical triangles (3.6%), the distribution for pass-along triads shows a less typical pattern with the 95% confidence intervals crossing the zero line but the mean percentage still showing a deficit.

A closer look at the cyclical triads reveals that certain individual ant species participated more frequently in cyclical interactions than others. Out a total of eight cyclical triads in our data set, *Camponotus abditus* participated in six, *Pseudomyrmex elongatus* participated in five, and *Pseudomyrmex filiformis* in four. We found that these three ant species tended to have high in betweenness, with *Camponotus abditus* showing the highest in-between-ness.

Discussion

Both deterministic and stochastic factors that act at local and regional spatial scales likely influence the community assembly and structure of arboreal twig-nesting ants. In this study, we tested first for the presence of a dominance hierarchy and determined that a transitive hierarchy exists among twig-nesting ants. Second, we tested whether the existence of such a hierarchy explained a significant portion of relative abundance at the global (e.g. farm) and local (e.g. plot) scales. We demonstrated that competitive rank alone did not significantly explain relative abundance patterns for the ten most common twig-nesting ant species. For example, one of the weakest ants in the hierarchy, *P. ejectus*, occupied a relatively high proportion of twigs (18.7%) and plants (18.7%) despite the low competitive ability of this species. Likewise, relative abundances for the highly ranked competitors were much lower; *M. mexicana* won >90% of its trials, but only occupied 2.4% of twigs and 1.5% of plants and *N. echinatinodis* that won nearly 70% of its real estate trials but only occupied 7.1% of twigs and 7.4% of plants. Thus the general abundance patterns were not positively correlated with the competitive abilities of ants. However, deviations in the patterns of relative abundance of ant species in plots where they did occur, compared with their abundance at the global scale, did correlate with competitive rank. In other words, those ants that were more abundant locally than they were globally were those ants that were superior competitors, and ants that were less abundant locally than globally were the poorer competitors. These results indicate that competition is a factor in structuring the arboreal, twig-nesting ant community in coffee systems, but this appears to act only at a very local scale in plots into which competitively dominant ants are able to recruit. Other factors such as environmental filters, dispersal abilities, and nest abundance, not tested in this study, may also likely be important factors in determining composition of ants within patches of coffee farms.

Our extensive study on the competitive interactions of twig-nesting ants shows the formation of a stable dominance hierarchy. Based on the triad census analysis, we found a significant excess of transitive triads and a significant deficit of cyclical triads. We found no significant difference for all the other triad types. Based on the triangle transitivity index, the total proportion transitive and cyclical triads, we found an overwhelming dominance of transitive triads. While pass-along triads can either tip to become transitive or cyclical triads, it's clearly the case that the vast majority of pass-along triads switched to transitive triangles given that the mean observed minus expected difference showed a positive trend. The deficit of pass-along

triads in our study goes along with other studies showing a negative mean percentage difference (McDonald & Shizuka 2012). Only one study has been reported to show a positive mean percentage trend (Nakano 1994), despite overlapping 95 % confidence intervals. Thus, individual attributes cannot solely explain the formation of dominance hierarchies in our system but in addition competitive structural processes can play an important role in determining the outcome of dominance hierarchies (Chase 2011).

Numerous theoretical and empirical investigations in biological systems have found that cyclical competition can serve as a potential mechanism for maintaining biodiversity when spatial structure is included (Sinervo 1996, Durrett & Levin 1997, Laird & Schamp 2008, Lauka & Strauss 2007, Allesina & Levine 2011, Vandermeer & Yitbarek 2012). However, we are not aware of any study that has detected cyclical relationships in ant communities. In one study, Sanders & Gordon (2012) suggested that variations among sites and resource quality influence the competitive interactions among ants. Thus, dominance hierarchies at local sites may not necessarily be reflected at the community level and might possibly transition from stable linear hierarchies to cyclical cycles.

In this study we implemented a metacommunity approach to study the spatial dynamics of tropical arboreal twig-nesting ants. Our experimental approach consisted of a metacommunity landscape composed of local communities coupled by dispersal at the regional community level. Within the metacommunity framework, transitive dominance hierarchy can be explained by the abundance or competitive dominance of arboreal ants at local sites (Levin 1974, Amaraskare & Nisbet 2001). One important consideration is the interaction between spatial heterogeneity and dispersal rates. In a well-mixed system with high dispersal rates, the local competitive dominance of species can be overturned leading to high extinction events. However, in weakly mixed systems the dispersal threshold becomes an important determinant in the long-term persistence of communities. In such cases, species coexistence can still be maintained at the metacommunity level, even when local communities are prone to extinction (Schreiber & Killinback 2013).

While in our study, the emerging dominance hierarchy is mediated by resource competition and spatial interactions, other factors can play an important role. Transitive relationships can also be mediated by non-interactions between two individuals as the result of bystander-effects. For instance, in cichlid fish, social rank can be inferred by indirect information

when contestants avoid interaction against perceived stronger competitors (Grosenick et al. 2007). Due to the design of our experiments, ants were forced to compete for twigs. However, subdominant ants species might prefer to avoid interactions with dominant ants when competing for twig resources. Future studies might therefore be designed such that ants can perceive the dominance status of other ants before engaging in competitive bouts.
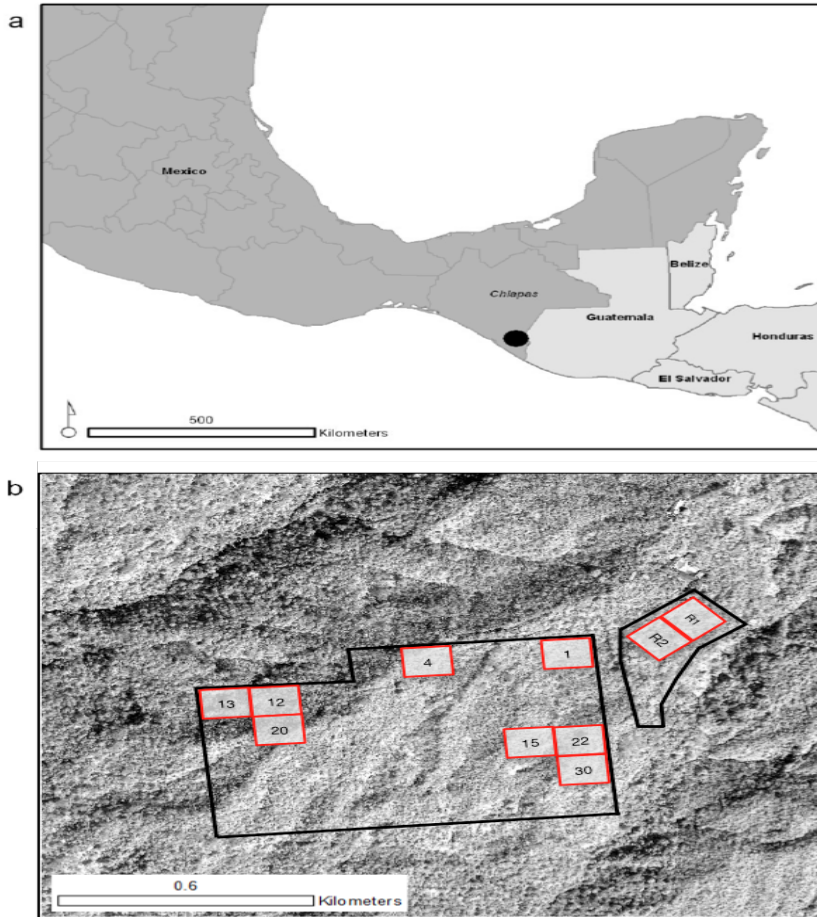
Figure 5.1 Maps showing (a) the region of Chiapas, Mexico where the field and lab experiments took place, and (b) the study plots in Finca Irlanda where twig-nesting ants were surveyed. In (b), the large box is the 45-hectare plot, and the small polygon is the 7-hectare plot. The red squares are the ten hectares that were surveyed annually; 20 x 20 m plots were randomly located within each 1-hectare plot each year.
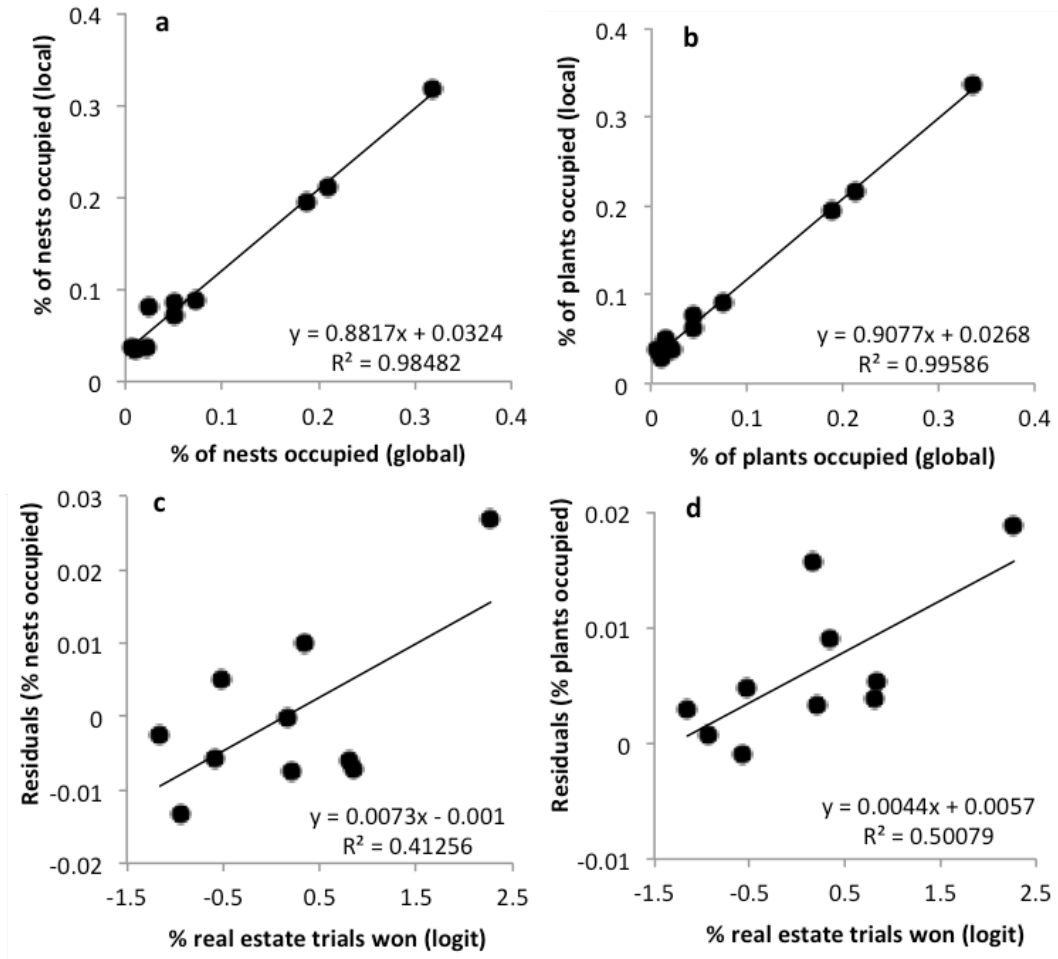
Figure 5.2 Local and regional relative abundance of twig-nesting ant species based on occupation of individual hollow twigs (a) and coffee plants containing at least one hollow twig (b). Each point in each figure represents one ant species. Regression residuals from occupied nests (a) and occupied coffee plants (b) are then plotted against the proportion of real estate trials won by individual ant species in panels (c) and (d). All regressions are significant.
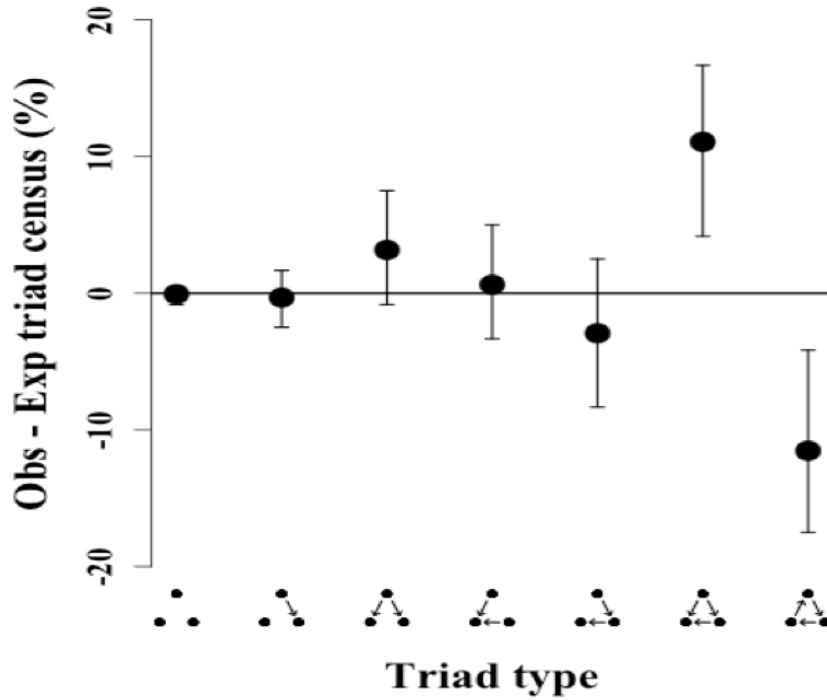
Figure 5.3 The triad census of twig-nesting ants. The y-axis represents the mean difference between the observed (ten ant species network) and expected (10,000 random networks) percentage of the triad subtypes (shown on the x-axis) and error bars show 95% confidence intervals. The twig-nesting ant data show a significant excess of transitive triads and a significant deficit of cyclical triads. All the other triad sub-types found were not significantly different from the expected random network. The following symbols define seven possible triad types: A= Null, B=Single-edge, C=Double-dominance, D=Double-subordinate, E=Pass-along, F=Transitive, G=Cycle.

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CHAPTER VI

DISCUSSION

The primary objective of my dissertation was to identify spatial mechanisms that generate and maintain biodiversity and to examine its implications for invasive species. To address my objectives, I developed network models that examined competitive processes across spatial scales. Previous work showed that the inclusion of spatial structure as a result of localized competitive processes resulted in the maintenance of multi-species coexistence (Vandermeer and Yitbarek 2012). One potential mechanism for species coexistence is balanced competition in which the effect of species A on species B is balanced by the effect of species B on species A. When modeling balanced competitive interactions in a spatial context mosaic patterns emerge resulting in species coexistence. At a qualitative level, spatial mosaics lead to highly stable patches with competitive stand-offs occurring along the boundaries of patches where neither species is capable of displacing the other. In contrast, unbalanced competitive interactions (i.e. intransitive competition) provide an alternative mechanism for species coexistence. In the case of unbalanced competitive interaction, there is no single winner at the community level despite intense competition among species (May and Leonard 1975, Vandermeer 2011). When we modeling unbalanced competitive interactions in space, we generated spiral wave patterns that result in species coexistence. Spiral patterns are highly dynamic in space and move around rapidly annihilating subdominant species. We find that the spatial self-organization of both mosaic and spiral patterns results in high species richness.

We used this general theory of biodiversity to develop a framework for species invasions. The critical connection between the spatial biodiversity of coexistence and invasion dynamics is the biotic resistance hypothesis. The biotic resistance states that areas with high species richness limit invasive species, while areas with low species richness are prone to invasion (Elton 1958). We focused our research on the exotic ant *Wasmannia auropunctata*, native ant species to Mexico and considered an invasive species on the island of Puerto Rico. Within a patch of *W.auropunctata* in Mexico, we observed that local ant species resisted the expansion of *W. auropunctata* with five colonies found across approximately 100 ha. The basic mechanism for

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resistance is the formation of territorial patch works composed of dominant species that buffer against *W. auropunctata* expansion. In contrast, in Puerto Rico where coffee farms are much smaller in size (~ 5 ha), we found that *W. auropunctata* was completely dominant with nearly 100 % occupancy. The difference in species richness between Mexico and Puerto Rico is in line with the biotic resistance hypothesis. We explored the ecological details of *W. auropunctata* interacting with native ants in light of our spatial biodiversity theory. In my dissertation, I specifically addressed the following: 1) The effects of spatial structure on species coexistence, ranging from small-world to random spatial networks 2) The ecological differences in the invasion dynamics by *W. auropunctata* between its native range of Mexico and introduced range of Puerto Rico, including direct and indirect competitive interactions.

In **chapter I**, I examined the effects of spatial network structure on species coexistence. Previously, we showed that the probability of survival was high in regular networks (i.e. no dispersal) due to the formation of spatial mosaic and spiral structures (Vandermeer and Yitbarek 2012). We extended this approach by modeling competitive interactions on small world networks on a spatial lattice, where connections surrounding a cell in the Moore neighborhood are randomly replaced at each iteration. We modeled competitive outcomes for balanced and unbalanced competitive network structures. In the case of balanced competition, we found that all 12 species were maintained in the community when interactions were strictly local. As we gradually replaced the number of neighbors surrounding each cell in the lattice (ranging 1-8 neighbors), species richness began to decline. It only took small amounts of mixing (2-small world links) for species richness to rapidly decline. This pattern was even more pronounced in the case of unbalanced competition. Without dispersal, half of the species remained in the community but this pattern quickly changes as we added 1 small-world connection resulting in rapid species declines. When examining the spatial patterns that emerged following small-world interactions we found that mosaic and spiral patterns gradually disaggregated into a monoculture. Following these results, we developed a probabilistic small-world network to examine species coexistence patterns with just 1 small-world network connection. As the probability of dispersal increased species richness declined rapidly under both negative and zero covariance values while for the positive covariance species richness declined at a slower rate. At lower dispersal rates, we detected a critical transition zone where species richness resulted in extinction with covariance values near zero. At the extreme positive end of the competitive balances species richness

remains high. When covariance is highly negative, species richness is still relatively high but the pattern drastically change as the covariance values increases resulting a monoculture system. This pattern seems to suggest that as we increase the dispersal rate, the probability of generating mosaic and spiral structures will be reduced which results in lower species richness. However, there is a zone near the zero covariance where species go rapidly extinct. This general pattern of spatial biodiversity has important implications for invasion dynamics and in particular biotic resistance by native communities. A highly positive covariance generates spatial mosaics, which essentially acts as a biotic deterrent against invaders from entering the community. In contrast, the probability of generating spiral patterns might be reduced when invaders are introduced in the community. As the covariance of the community matrix increases, invaders are more likely to enter the native community as a result of lower species richness.

We used these general outcomes on spatial competition and community structure to examine ecological details about invasion. We compared the invasion dynamics of the exotic ant *W. auropunctata* in its native range of Mexico and introduced range of Puerto Rico. In **Chapter II**, we examined ecological differences in resource discovery by *W. auropunctata* between Mexico and Puerto Rico. The discovery-dominance trade-off in ant communities is thought to provide a mechanism for species coexistence (Fellers 1987). In the case of invasive ants, such as the Argentine ant, it has been argued that they excel at both discovery and dominance of resources (Holway 1999). In this study, we focused on the resource discovery abilities of invasive ants and hypothesized that *W. auropunctata* is a faster discoverer in its introduced range of Puerto Rico as compared to Mexico where we expected it to be slower at discovering resources. Our results show the reversed pattern in that *W. auropunctata* was much slower in discovering resources in Puerto Rico as compared to its native range of Mexico. We speculate that these dramatic differences in resource discovery ability are due to its restricted chemical environment that *W. auropunctata* operates in. When resources were placed on the trunk of coffee plants *W. auropunctata* rapidly discovered resources, but were less efficient at finding resources further away. This seems to suggest that *W. auropunctata* is not detecting the chemical profile of other ant competitors in Puerto Rico which reduces the pressure of rapidly acquiring resources. On the other hand, in Mexico where species richness is relatively high *W. auropunctata* competes strongly with native ants for resources. In **chapter III**, we examined the competitive dynamics between dominant native ant species and *W. auropunctata* in both Mexico

and Puerto Rico. We conducted short and long-term competition experiments to test the biotic resistance hypothesis that predicts that areas with high species richness such as Mexico are less prone to invasions than areas with low species richness such as Puerto Rico. We showed that the ground ant forager *S. geminata* and the arboreal ant forager *P. synanthropica* were able to dominate *W. auroupunctata* in short-term competition experiment. However, we did not find significant differences between *S. picea* and *W. auropunctata* in the long-term competition experiments. In Puerto Rico, we performed long-term competition experiments between the native ant *L. iniquum* and *W. auropunctata*. Our results showed that while *W. auropunctata* was dominant we did not detect a significant difference between treatments. Thus, the biotic resistance hypothesis does not appear to be an important factor in our competition experiments. This led us to ask what other possible mechanisms could explain the invasion success of *W. auropunctata*?

In **chapter IV**, we examined the role of indirect effects in influencing the invasion dynamics of *W. auropunctata* in Puerto Rico. We performed experiments between *W. auropunctata* and *L. iniquum* in the presence of parasitoid phorids that are specialized natural enemies of *L. iniquum*. We found that in the control experiments (i.e. without phorids), *L. iniquum* workers dominated *W. auropunctata* workers at resources. In contrast, when phorids were introduced in treatments we found the reversed pattern with drastic reductions in the number of *L. iniquum* workers at resources whereas *W. auropunctata* increased their number of workers. Following up on this result, we measured phorid arrival time to *L. iniquum* nests in the field. The spatial distribution of arboreal nests showed clear clusters of *W. auropunctata* and *L. iniquum* patches. We found several nests of *W. auropunctata* occupying trees within *L. iniquum* patches. Similarly, we found several nests of *L. iniquum* nests occupying trees within *W. auropunctata* patches. Therefore, we hypothesized that phorids would be more efficient in finding nests dominated by *L. iniquum* within its own patch as compared to *L. iniquum* dominated trees within the *W. auropunctata* patch. Our results show that phorid arrival time was much faster in *L.iniquum* patches, while it took phorids longer to arrive to *L.iniquum* tree stands in *W. auropunctata* dominant patches.

Lastly, I examined community assembly process driving coexistence patterns across spatial scales in a twig-nesting ant assemblage in Mexico. In **chapter V**, I related competitive networks structures of twig-nesting ants to abundance data from field surveys at local and

regional spatial scales. We found that transitive network structures correlated with increases in relative abundance patterns at local scales. However, we did find a strong signal for intransitive network structures than would be expected by chance.

In summary, the combination of competitive structure plus the network structure interact to create spatial structure which, in turn, affects the survival of species. The biotic resistance hypotheisis of invasiness, when in the context of competition, may involve important pattern forming mechanisms. Competition details, including temporal aspects of comeptition, tradeoffs, and indirect effects, seems to operate differently in the native range versus the invasion range in the case of *W. auropunctata*.

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