

The role of higher order interactions in structuring competitive communities: an empirical study
in ant communities

Iris Saraeny Rivera Salinas¹, John Vandermeer², Ivette Perfecto¹

1 School for Environment and Sustainability, University of Michigan, Ann Arbor MI, USA.

2 Ecology and Evolution Biology, University of Michigan, Ann Arbor MI, USA.

Table of Contents

	Pag.
Abstract	1
Introduction	2
Methods	7
Results	9
Discussion	13
References	17

Table of figures

- Fig. 1** Rarefaction curves for the number of arboreal ant species at sites with young age nests (high TMII's), intermediate age nests (intermediate TMII's) and old age nests (low TMII's).
- Fig. 2** Average number of arboreal ant species at specific distances from nest with high TMII's (young age nests), intermediate TMII's (middle age nests) and low TMII's (old age nests). Each nest is at TMII's pressure spectrum indicated going from higher pressure (young nests) to low pressure (old nests).
- Fig. 3** Proportion of baits occupied by *Azteca sericeasur* and by other ants, at specific distances from nest. Each plot represents sites located at gradient of TMII's strength from high TMII's (A), intermediate TMII's (B) and low TMII's (C).
- Fig. 4** Rarefaction curves for the number of leaf litter and ground ant species at sites with young age nests (high TMII's), intermediate age nests (intermediate TMII's) and old age nests (low TMII's).
- Fig. 5** Figure 5. Average leaf litter ant richness for old, intermediate and young *A. sericeasur* nests.

Acknowledgments

I would to thank my advisors Ivette Perfecto and John Vandermeer, for inspiring me with their ideas, helping me create my own, and for their ongoing dedication to opening pathways for underrepresented students in ecology and other sciences. I would also like to thank Zachary Hajian-Forooshani for all the support throughout the years and for always believing in me. I would not be here without the support of my parents Sara and Manuel, my brother Paco and Ivan, my niece and nephew Crystal and Victor, and the rest of my family.

A special thanks to all of my friends, Esteli Jimenez, Stacy Philpott, Eloise Reid, Beatriz Otero, Chatura Vaidya, Sarah Barney, Hagan Capnerhust, Jonathan Morris, Kristel Sanchez, Lauren Schmidt, Fern MacDougal, Nicholas Medina, Gordon Fitch, Senay and Diana Yitbarek, Liz Wason Kaleigh Fisher, Aldo de la Mora, Gustavo Bautista, Braulio Chilel, Brett Zeuner, Monserrat Piza, Jessica Pedroza, Israel Castrejon, Kenia Roque, Yessica Ching, for all the cheering up, amazing conversations and for all the advise.

Abstract

Understanding the mechanisms which allow for the maintenance of diverse communities is one of the central foci of ecology. Recent work suggests that complex interactions such as trait-mediated indirect interactions (TMIIIs), and more generally higher-order interactions, may play an important role in structuring ecological communities. Here we use a well-studied system of arboreal ants in coffee agroecosystems to empirically explore the role of TMII's in structuring this community. We use, *Azteca sericeasur*, a dominant arboreal ant which excludes other ants from occupying coffee bushes near the trees where its nest is located. Prior work in the system has established a TMIIIs between *A. sericeasur* and its specialist *Pseudacteon* spp parasitoids. Furthermore, this TMIIIs is far greater on younger nests than older nests. Here we ask how varying strengths of TMIIIs /parasitoid pressure influence the community of ants associated with *A. sericeasur*. For this, we surveyed *A. sericeasur* nests of varying ages to understand the influence of the parasitoids on the structure of the arboreal and leaf litter ant community in space and through time. At each nest we surveyed the arboreal ants on all the coffee plants that fall within a radius of 8-10 m around the nest. For leaf litter ants, at each nest we traced two linear transects from which we collected six samples of .5 m² of leaf litter, in total 12 samples per nest. Then, the ants from each sample were extracted using winklers and identified to species and morpho species.

Our results show that next to *A. sericeasur* younger nests the richness of other ants closer to the nest (0-4 m) is higher in comparison to the same distance to older nests where the richness of other ants was lower. Interestingly near old nests the richness of the other ants starts increasing rapidly at 4 m up to 9 m contrary to the richness of the other ants next to young nests where the richness from 2 m to 6 m remains constant. The results from this study show the potential role of the Trait-Mediated Indirect Interactions in structuring competitive communities, since next to younger nests, the richness of ants is higher in comparison to low density of phorids nests. This particular system allows us to determine if the communities of ants is different when we have high TMIIIs (high density of phorids) and low TMIIIs (low density of phorids).

Introduction

Understanding the mechanisms that allow for the maintenance of diverse ecological communities is one of the central foci of ecology (May 1972; May 1973; Levine et al. 2017). One of the major challenges for ecologists has been to develop theory that is complex enough to explain observed patterns but simple enough to be tractable. Classic experiments by Gause in the mid-1930s demonstrated, for the first time, that ecological systems can behave similarly to the mathematical equations developed to describe them and solidified the potential importance of competition in structuring community dynamics (Gause 1934).

Following in a similar vein of Gause, Vandermeer (1969) was able to use the same laboratory system of ciliates to successfully make predictions about the role of competition in structuring more complicated communities with higher number of species interacting, suggesting that the relatively simple mathematics of the pair-wise competition equations (Lodka-Volterra) could be extrapolated to understand community dynamics. Vandermeer noted his surprise at the ability of these equations to make successful predictions about the experimental community, and predicted that higher-order (non-linear) interactions were important features structuring the ecological communities. Although Vandermeer did not support this intuition with his experiment, Neil's (1974) experiments in freshwater microcosms did indeed support the notion that higher-order interactions are important for structuring the community. These relatively simple laboratory/microcosm experiments have suggested to ecologists that as we begin to approach the complexity of interacting species observed in nature, higher-order interactions likely play a large role in structuring community dynamics.

Recently, excitement in the ecological literature about the role of higher-order interactions has renewed, particularly as it pertains to our understanding of their role in maintaining complex

communities (Bairey et al. 2016; Levine et al. 2017; Terry et al. 2017; Terry 2018). However, to date, we have only sparse empirical evidence of the impact of higher-order interactions in nature. While some of the most basic mathematical theory in ecology started with the Lotka-Volterra equations applied to competition and predator-prey interactions (Lotka 1925; Volterra 1928), explorations of mechanisms that contribute to diversity at the community scale began in the early to late sixties with work by MacArthur and Levins (MacArthur and Levins 1967), and arguably culminated in the early 1970s with work by Robert May (May 1973).

May's theoretical results from randomly constructed communities suggested that the more interactions and individuals a community has, the more unstable it will be (May 1973). Furthermore, May suggested that competitive and mutualistic interactions may be the primary culprits in the destabilization of communities. A huge literature has spawned from May's elegant analysis and suggested a number of complications to consider while noting, in particular, the importance of considering the distribution of interaction strengths in a community (McCann et al. 1998; Vandermeer et al. 2002).

Recently, Bairey and collaborators (2016) demonstrated a reversal of May's classic result when considering higher-order interactions in their model. They show that when considering these second order interactions, interaction strength and the number of species in the community have no impact on stabilization, and third-order interactions actually make the communities more stable as the strength and number of interactions increase. In short, much of the theoretical work shows that a continuum of sometime contradictory results can emerge from different conceptualizations of how to model ecological communities and measure stability. While simple experimental systems correspond quite well to simple models (Gause 1934; Vandermeer 1969), relatively little has been done to empirically explore these types of questions in real ecological communities.

We suggest that to be able to answer fundamental questions about complex interactions and the maintenance of communities, we have to add more complexity to empirical studies so as to approximate what is actually happening in real ecological systems. Here, we attempt to move forward with such an approach by explicitly considering the role of a well-studied higher-order interaction in the community structure of a tropical agroecosystem. In particular, we explore the impact of Trait-Mediated Indirect Interactions (TMIIIs) in structuring ant communities in a coffee agroecosystem.

TMIIIs are higher-order interactions that are indirect and non-trophic (Peacor and Werner 2004). In simple terms they can be described as the modifications of an interaction between two species effected by a third species (Peacor and Werner 1997, Vandermeer et al. 2010, Philpott 2005, Dattilo et al. 2016). As its name implies, a TMIIIs is an interaction that alters some trait (e.g., a behavior) of an organism, with the classic example of tadpoles not searching for food (reduction of its activity) in the presence of potential predators (Anholt et al. 2000), grasshoppers not feeding on grass in presence of their spiders predators (Beckerman et al. 1997) and ants reducing their activity in presence of flies parasitoids (Philpott 2005).

Generally, higher-order interactions and TMIIIs can be difficult to study in natural systems, but the successful examples that exist have suggested that their importance in structuring ecological dynamics has been underestimated (Vandermeer et al. 2010, Schmitz et al. 1997). Our work here attempts to bridge the gap between theory and empiricism by testing this new hypothesis from Bairey et al. (2016) about the role of higher-order interactions, in particular TMIIIs, in structuring ecological competitive communities.

***Azteca sericeasur* and its Trait Mediated Indirect Interactions (TMIIs) with *Pseudacteon* spp.**

Our model system is a tropical coffee agroecosystem that has been studied over the past two decades (Perfecto and Vandermeer 2015). Extensive work has focused on the ant communities within this coffee agroecosystem due to their prominent roles in providing ecosystem services to agroecosystems such as soil formation and biological pest control. The accumulation of knowledge surrounding the ant communities make them an ideal model system to explore outstanding questions in community ecology.

In particular, our study centers around the arboreal carton nesting ant, *Azteca sericeasur*, which has been described as a “keystone species” in the system (Vandermeer et al. 2010). *A. sericeasur* is dominant in the system and excludes other ant species and insects from areas near its nest and has negative impacts on the activity and abundance of other ants close its nest (Philpott 2005; Jimenez- Soto et al. 2013; Morris et al. 2015; Rivera-Salinas et al. 2018). *A. sericeasur* is associated with a wide range of higher-order interactions in this agroecosystem (Philpott 2005; Vandermeer et al. 2010), many of which are associated with *A. sericeasur*'s main parasitoids, phorid flies in the genus *Pseudacteon* spp. (Vandermeer et al. 2008 & 2010). Three species in the genus *Pseudacteon* are known to attack *A. sericesur* in this system, *P. lascinosus*, *P. planidorsalis* and *P. pseudocercus*, however, *P. lascinosus* is the most abundant species (Reese and Philpott 2012; Mathis and Tsutsui 2016).

The biology underlying the TMIIs is quite complex but, in short, the effect is mediated through chemical communication between *A. sericeasur* and the phorid parasitoids. When the *A. sericeasur* nests are disturbed or under stress they release an alarm-pheromone that causes the ants to flood from the nest and attack any intruder (Mathis et al. 2011). Interestingly, the parasitic phorid flies are able detect and use this alarm-pheromone and to locate *A. sericeasur* nests. Once

phorids arrive to an *A. sericeasur* nest and start attacking, the ants release another pheromone which causes ants to paralyze or hide and, if close to the nest, to retreat to the safety of the nest (Vandermeer et al. 2010; Mathis 2016). It has been demonstrated that the presence of the phorids induces the TMIs within the system and can have both direct and indirect effects that cascade through the interaction network in the system (Vandermeer et al. 2010). Recently conducted work has shown that there are patterns in the intensity of phorid pressure around *A. sericeasur* nests based on their age, with younger nests having the highest parasitoid pressure (i.e. phorid density, arrival time and length of the attack periods) and older nests the lowest (Hajian-Forooshani et al. in review). This observation allows us to locate nesting sites of *A. sericeasur* with relatively high and low TMIs from the phorids.

Here we use our ability to find *A. sericeasur* nests of various ages (see method section) and presumably different intensity of TMIs to explore the impact of these interactions in structuring the competitive ant communities in the system. In line with prior theoretical work (Bailey et al. 2016), we hypothesize that sites with high phorid pressure (young *Azteca* nests), and thus with relatively high strength of TMIs (i.e. young *A. sericeasur* nests), will be associated with ant communities that are more diverse in terms of number of species than sites with low phorid pressure. Furthermore, we expect this effect to be dissipated with distance from the ant nest, with a stronger effect near the ant nest and a weaker effect farther away from the nest. Not only do these hypotheses stem from theoretical work, but they also correspond to what is known about the ability of *A. sericeasur* to exclude other ant species and the phorids' ability to disrupt that behavior.

Methods

With the aim of understanding the role of Trait Mediated Indirect Interactions (TMII) on structuring competitive communities of arboreal and leaf litter ants, we conducted surveys of arboreal and leaf litter ants around *A. sericeasur* nests with low, intermediate and high pressure of TMII by phorid flies. The study was conducted in a 45 hectare plot located in Finca Irlanda, a 300 hectare organic and shaded coffee farm is located at 1,100 MAMSL in the municipality of Tapachula, Chiapas. The shade in the system is provided by more than one hundred species of trees but more than 70% of the shade is made up by species from the genus *Inga* (Vandermeer 2002). Within the 45-ha plot, all *A. sericeasur* nests have been surveyed on a yearly basis since 2004, which allowed us to locate nests of various ages.

To be able to measure the effects on the arboreal and leaf litter ant community composition around *A. sericeasur* nests with different TMII's pressure, we located 11 *A. sericeasur* nests of different ages (N young nests = 4, N intermediate aged nests = 3, N old nests = 4), these three nest ages categories were selected based on previous results looking at the relation between age of the *A. sericeasur* nests and the density of phorids associated to them (Hajian-Forooshani et al. in review). At each nest site we sampled arboreal and leaf litter ants at various distances from the ant nest.

Arboreal ant surveys

For the arboreal ant surveys, we sampled the ants on all the coffee plants within a radius of 8-10 meters around the target ant nest. For this, we placed three tuna baits on each plant at three heights of the plant (low, medium and high). After we set up the tuna baits, we waited 20 minutes to start counting and identifying the ants on each bait. We recorded the identity and number of individuals of each ant on the bait. Additionally, we geo-located each coffee bush within the 8-10

meters radius of the nests to map the spatial distribution of ants around the *A. sericeasur* nests at each site. We did this by using the focal *A. sericeasur* nest as a focal point in the plot then measured the distance to each plant and the angle to calculate coordinates for each plant.

Leaf litter ant collection

To measure the effect of the TMIs on the community of leaf litter ants, we traced two linear transects of 7 m long starting from the nest. Using the transects, we collected 0.5 m² of leaf litter at 6 different distances from the nest (0 m, 1.0 m, 2.5 m, 4.0 m, 5.5 m and 7.0 m). Each sample was sifted through a sieve of 1 cm grid size to get just the small debris with the ants. To extract the ants from the debris, each sample was placed inside a mini-winkler extractor which was hanging above a small plastic container with 70 % alcohol where the ants were collected as the sample dried (Fisher, 1996). To be able to calculate the ant abundance and richness in each sample, all the ants in the sample were counted and identified.

Data Analyses

To quantify the differences on ant richness at young, intermediate and old *A. sericeasur* nests we counted the total number of ant species found at specific distances from the focal nest. For arboreal ants we did this by dividing the total radius sampled by 10 different distances. For leaf litter ants we did this by counting the total number of ant species found at the 6 different distances from the focal nest. To estimate the total arboreal and leaf litter ant richness at the scale of the whole site we used rarefaction curves where all the sites of the same age category were grouped.

Results

Arboreal ant surveys

Contrary to our hypothesis, rarefaction curves show that old *A. sericeasur* nests (low phorid density) have significantly higher species richness on the coffee bushes at the site level than the younger *A. sericeasur* nests (high phorid density), with the intermediate age falling slightly higher than the young nests but not significantly different (Fig. 1).

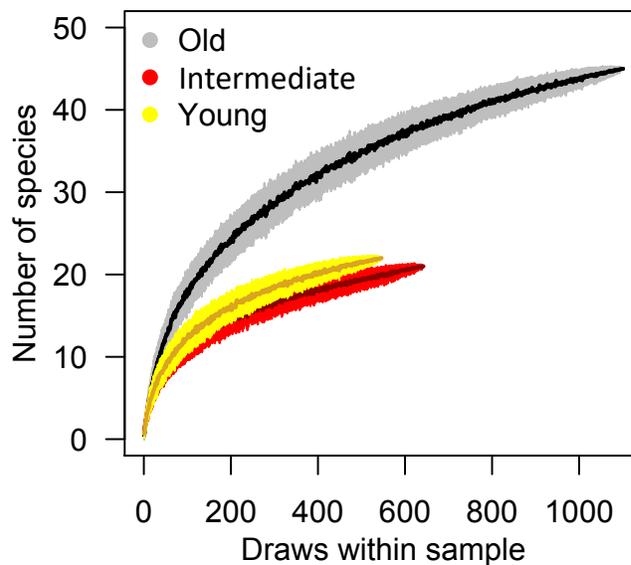


Fig. 1 Rarefaction curves for the number of arboreal ant species at sites with young age nests (high TMIIIs), intermediate age nests (intermediate TMIIIs) and old age nests (low TMIIIs).

Examining the spatial pattern of the average species richness, we find a general increase in species richness as we move away from the *A. sericeasur* nests, but no significant differences related to age of nests (Fig. 2). Additionally, when examining the proportion of baits occupied by *A. sericeasur* and other ants we find that the proportion of baits occupied by *A. sericeasur* is highest right next to the nest and decline with distance from the nest (Fig. 3 A, B & C), and conversely, the proportion of baits occupied by other ants is lowest right next to the *A. sericeasur* nest and

increases with distance from nest (Fig. 3 D, E & F). These patterns appear to be similar for young, intermediate and old nests (Fig. 3).

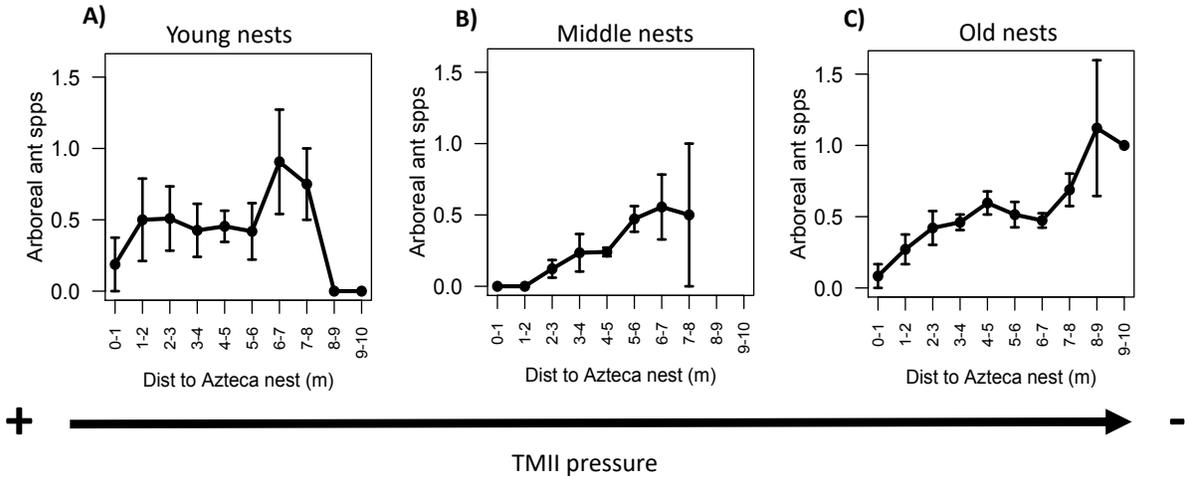


Fig. 2 Average number of arboreal ant species at specific distances from nest with high TMII's (young age nests), intermediate TMII's (middle age nests) and low TMII's (old age nests). Each nest is at TMII's pressure spectrum indicated going from higher pressure (young nests) to low pressure (old nests).

Azteca sericeasur

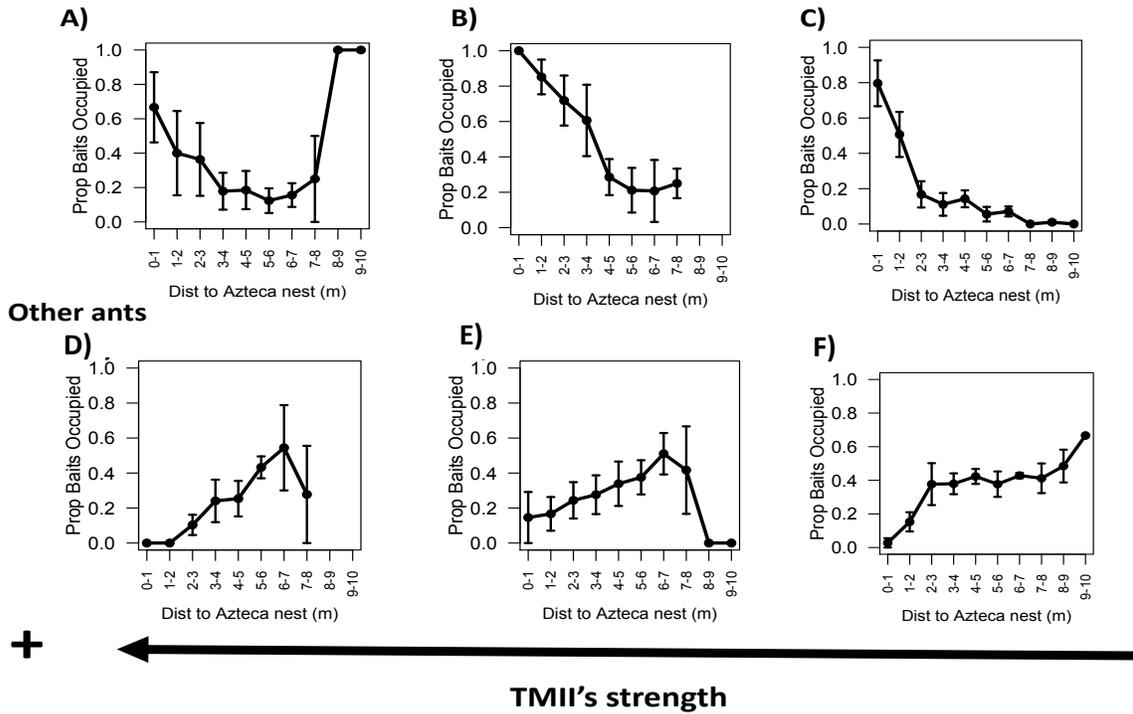


Fig. 3 Proportion of baits occupied by *Azteca sericeasur* and by other ants, at specific distances from nest. Each plot represents sites located at gradient of TMII's strength from high TMII's (A), intermediate TMII's (B) and low TMII's (C).

Leaf litter ant surveys

Similar to the results found in the surveys of arboreal ants at the site level, rarefaction curves show that old *A. sericeasur* nests (low phorid density and low TMII's) have significantly higher species richness of leaf litter and ground ants at the site level than the younger *A. sericeasur* nests (strong TMII's pressure). Species richness around nests of intermediate age was slightly lower than in young nests but not significantly so (Fig. 4).

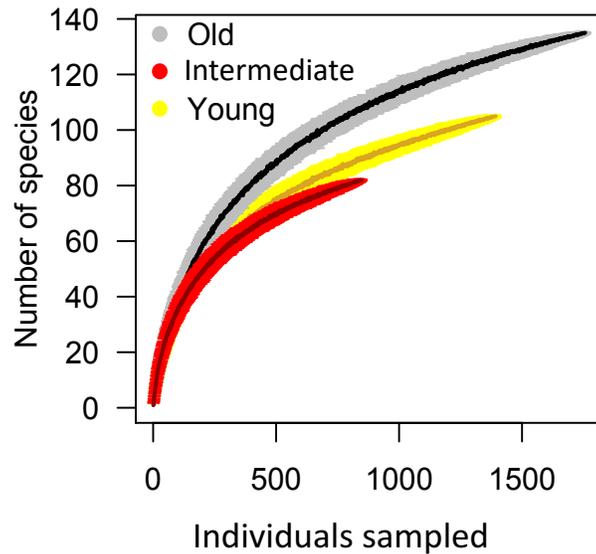


Figure 4. Rarefaction curves for the number of leaf litter and ground ant species at sites with young age nests (high TMIs), intermediate age nests (intermediate TMIs) and old age nests (low TMIs).

The spatial pattern of the average species richness of leaf litter and ground ants differ slightly for old nests as compare to intermediate and young nests (Fig. 5). While average species richness remains relatively high as the distance from the nest increases, the average species richness declines with distance for intermediate and old nests (Fig. 5).

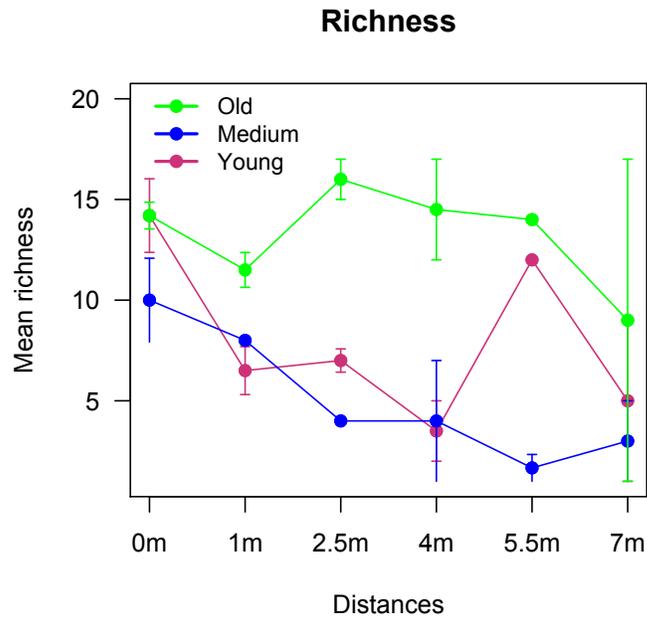


Figure 5. Average leaf litter ant richness for old, intermediate and young *A. sericeasur* nests.

Discussion

While higher-order interactions and in particular TMII's have been difficult to study empirically, here we present an example of the impact of these interactions on structuring competitive ant communities. By taking advantage of a well-studied system that includes TMII's of various strengths, we present evidence that suggest that different TMII's strength can influence the ant community richness at the site scale (species richness at the entire site) and at the local scale (species richness at various distance from nests). At the site scale we found that, contrary to our initial expectation expectations, older *A. sericeasur* nests, which have been shown to have lower phorid pressure and therefore low TMII's strength, actually have higher ant richness, than younger and intermediate-age nests, for both, arboreal (Fig. 1) and leaf litter ants (Fig. 4). At the local scale, we found something different for the arboreal ants than the leaf litter ants. There is a general trend of increase in average ant specie richness with distance from *A. sericeasur* nests, and this pattern is similar for nests in all three age categories (Fig. 2). However, for the leaf litter ant

community, we found that while there is no change with distance for ants surrounding older *A. sericeasur* nests, there is a general decline in the average species richness for intermediate and young *A. sericeasur* nests (Fig.5).

A possible explanation for the higher ant species richness at sites with older *A. sericeasur* nests, is higher phorid pressure, and consequent lower TMIs presumably associated with secondary ecological interactions linked to how the keystone species, *A. sericeasur*, modifies its surrounding environment. *A. sericeasur* frequently establishes a mutualistic association with the hemipteran *Coccus viridis* (the green coffee scale) (Vandermeer and Perfecto 2006), which results in large aggregations of scale insects building up on coffee plants around their focal nesting tree. The mutualistic interaction between the two is both facultative and non-species specific, with other species tending *C. viridis* on coffee plants in the vicinity, but not too close to *A. sericeasur* nests. Thus, sites with older nests are, by definition, sites in which *A. sericeasur* nests have persisted for longer periods of time, which allows for larger aggregations of scales to be build up over time. The *A. sericeasur* nests then become a source of crawlers (scale juveniles) which disperse to other nearby plants not tended by *A. sericeasur* and provide a resource for other ant species, especially arboreally foraging ants. Thus, we suggest that the build-up of scales at a given site over time and the subsequent concentration of activity near the focal nest gives other ants the opportunity to tend scales father away from the keystone species nest which results in higher site richness (Figs. 2 and 3). Furthermore, the high scale population that builds up around older *A. sericeasur* nests also attracts a high density and variety of other insects that use the excess honeydew produced by the scale or prey on the scales (Perfecto et al. 2014). These insects and their feces and dead bodies may be a great resource for ground foraging and leaf litter ants (Shik and Kaspari 2010). The combination of these two explanations (i.e. higher scale resources for arboreal ants and higher food

resources for leaf litter and ground ants) could also explain why we see a distinct pattern in arboreal and leaf litter ants as we move away from a focal nest. While arboreal ant species richness generally increases with distance from *A. sericeasur* nests (Fig. 2), leaf litter ant richness generally declines with distance from *A. sericeasur* nest. The fact that these opposite trends are stronger for intermediate and younger nests for both the leaf litter and arboreal ant communities suggests that the bigger and older scale colonies associated with the older *A. sericeasur* nests have a higher spatial influence than in areas with intermediate and younger *A. sericeasur* nests where the influence of the *A. sericeasur* nests may be restricted to areas very close to the tree where the *A. sericeasur* nest is located.

We suggest that another way in which the age of a nest and the strength of TMIs could affect ant species richness may have to do with the changing characteristics of the nesting tree itself. It seems reasonable to assume that old *A. sericeasur* nest, which have low TMIs pressure, are often located in older trees, which may subsequently be larger and leafier resulting in higher inputs of leaf litter to the site. The larger input of leaf litter to these sites would result in more habitat for leaf litter ants and in essence increase the carrying capacity of the community (McGlynn et al. 2010). This potential mechanism can also help explain the difference in the spatial pattern observed between the old *A. sericeasur* nests and the intermediate and young nests. Although the age of the trees may be a complicating factor when disentangling the patterns in our data, we believe that it is not totally confounding since the system is very actively managed. Frequent pruning of the canopies of shade trees in the coffee agroecosystem is a part of standard management of the system and results in a generally uniform amount of shade distributed across the farm.

The scale dependent patterns of the system, where we see different patterns at both the very local and site level scale, highlights how space may play an important role in understanding the dynamics of the system. The dynamics of the clustered spatial pattern formation of *A. sericeasur* has been studied in detail and thought to emerge from the predator-prey interaction between *A. sericeasur* and its principal natural enemy the phorid flies (Vandermeer et al. 2008). The specific patterns of parasitization via the phorids, and thus distribution of TMIIIs, has a particular spatial pattern in which youngest nests on the periphery of clusters are attacked more frequently (thus higher TMII) than older nests at the center of clusters (Hajian- Forooshani et al. in review). This suggests that patterns of community richness may emerge at even larger landscape scales which we know are relevant to the dynamics of the pattern formation of *A. sericeasur*. We suggest that future work take a broader spatial scale approach when trying to understand the role of the TMIIIs in structuring community dynamics, as we know it may be spatially contingent.

By providing an empirical study of the role of higher-order interactions in structuring community dynamics in two distinct but associated competitive ant communities, we have highlighted the complexities of which higher-order interactions may play out in real ecological communities. We don't suggest we have a definite resolution to the sometimes contradictory claims made by the theory developed to study the role of higher-order interactions, but hope to highlight areas of further consideration. The importance of spatial scale in understanding our results suggests that space may be an important component to consider moving forward. From trait-mediated indirect interactions between predatory Odonata larvae and fishes (Werner and McPeck 1994; Werner and Anholt 1996) to higher-order interactions between competing plant communities (Levine et al. 2017) there is inevitable a spatial component that is frequently ignored in theoretical attempts to understand the dynamics of such systems. Additionally, we suggest that

more empirical work needs to be conducted to study the diverse types of higher-order interaction that exist in nature, with TMIs being just one of those.

References

Anholt, Bradley R., Earl Werner, and David K. Skelly. "Effect of food and predators on the activity of four larval ranid frogs." *Ecology* 81, no. 12 (2000): 3509-3521.

Bairey, Eyal, Eric D. Kelsic, and Roy Kishony. "High-order species interactions shape ecosystem diversity." *Nature communications* 7 (2016): 12285.

Beckerman, Andrew P., Maria Uriarte, and Oswald J. Schmitz. "Experimental evidence for a behavior-mediated trophic cascade in a terrestrial food chain." *Proceedings of the National Academy of Sciences* 94, no. 20 (1997): 10735-10738.

Dáttilo, Wesley, Armando Aguirre, Pedro Luna De la Torre, Lucas A. Kaminski, Juan García-Chávez, and Víctor Rico-Gray. "Trait-mediated indirect interactions of ant shape on the attack of caterpillars and fruits." *Biology letters* 12, no. 8 (2016): 20160401.

Fisher, Brian L. "Ant diversity patterns along an elevational gradient in the Reserve Naturelle Integrale d'Andringitra, Madagascar." *Fieldiana Zoology* (1996): 93-108.

Gause, Georgii Frantsevitch. "Experimental analysis of Vito Volterra's mathematical theory of the struggle for existence." *Science* 79, no. 2036 (1934): 16-17.

Jiménez-Soto, Estelí, Juan A. Cruz-Rodríguez, John Vandermeer, and Ivette Perfecto. "Hypothenemus hampei (Coleoptera: Curculionidae) and its interactions with *Azteca instabilis* and *Pheidole synanthropica* (Hymenoptera: Formicidae) in a shade coffee agroecosystem." *Environmental entomology* 42, no. 5 (2013): 915-924.

Hajian-Forooshani, Zachary, Iris Saraeny Rivera Salinas, Estelí Jiménez-Soto, Ivette Perfecto, and John Vandermeer. "Impact of regionally distinct agroecosystem communities on the potential for autonomous control of the coffee leaf rust." *Journal of Environmental Entomology* (2016): nvw125.

Levine, Jonathan M., Jordi Bascompte, Peter B. Adler, and Stefano Allesina. "Beyond pairwise mechanisms of species coexistence in complex communities." *Nature* 546, no. 7656 (2017): 56.

Lotka, A. J. "Elements of physical biology. Williams and Wilkins." *Baltimore, Md* (1925).

Mathis, Kaitlyn A., Stacy M. Philpott, and Rayane F. Moreira. "Parasite lost: chemical and visual cues used by *Pseudacteon* in search of *Azteca instabilis*." *Journal of insect behavior* 24, no. 3 (2011): 186-199.

Mathis, Kaitlyn A., and Neil D. Tsutsui. "Cuticular hydrocarbon cues are used for host acceptance by *Pseudacteon* spp. phorid flies that attack *Azteca sericeasur* ants." *Journal of chemical ecology* 42, no. 4 (2016): 286-293.

MacArthur, Robert, and Richard Levins. "The limiting similarity, convergence, and divergence of coexisting species." *The American Naturalist* 101, no. 921 (1967): 377-385.

McCann, Kevin, Alan Hastings, and Gary R. Huxel. "Weak trophic interactions and the balance of nature." *Nature* 395, no. 6704 (1998): 794.

McGlynn, Terrence P., Ryan M. Fawcett, and Deborah A. Clark. "Litter biomass and nutrient determinants of ant density, nest size, and growth in a Costa Rican tropical wet forest." *Biotropica* 41, no. 2 (2009): 234-240.

May, Robert M. "Will a large complex system be stable?." *Nature* 238, no. 5364 (1972): 413.

May, Robert M. "Qualitative stability in model ecosystems." *Ecology* 54, no. 3 (1973): 638-641

Morris, Jonathan R., John Vandermeer, and Ivette Perfecto. "A keystone ant species provides robust biological control of the coffee berry borer under varying pest densities." *PloS one* 10, no. 11 (2015): e0142850.

Neill, William E. "The community matrix and interdependence of the competition coefficients." *The American Naturalist* 108, no. 962 (1974): 399-408.

Peacor, Scott D., and Earl E. Werner. "Trait-mediated indirect interactions in a simple aquatic food web." *Ecology* 78, no. 4 (1997): 1146-1156.

Peacor, Scott D., and Earl E. Werner. "How dependent are species-pair interaction strengths on other species in the food web?." *Ecology* 85, no. 10 (2004): 2754-2763.

Perfecto, Ivette, John Vandermeer, and Stacy M. Philpott. "Complex ecological interactions in the coffee agroecosystem." *Annual Review of Ecology, Evolution, and Systematics* 45 (2014): 137-158.

Perfecto, Ivette., and John, Vandermeer. *Coffee agroecology: a new approach to understanding agricultural biodiversity, ecosystem services and sustainable development*. Routledge, 2015.

Philpott, Stacy M. "Trait-mediated effects of parasitic phorid flies (Diptera: Phoridae) on ant (Hymenoptera: Formicidae) competition and resource access in coffee agro-ecosystems." *Environmental Entomology* 34, no. 5 (2005): 1089-1094.

Reese, Katlynd M., and Stacy M. Philpott. "Environmental and habitat drivers of relative abundance for a suite of *Azteca*-attacking *Pseudacteon* phorid flies." *Environmental entomology* 41, no. 5 (2012): 1107-1114.

Rivera-Salinas, Iris Saraeny, Zachary Hajian-Forooshani, Esteli Jiménez-Soto, Juan Antonio Cruz-Rodríguez, and Stacy M. Philpott. "High intermediary mutualist density provides consistent biological control in a tripartite mutualism." *Biological Control* 118 (2018): 26-31.

Schmitz, Oswald J., Andrew P. Beckerman, and Kathleen M. O'Brien. "Behaviorally mediated trophic cascades: effects of predation risk on food web interactions." *Ecology* 78, no. 5 (1997): 1388-1399.

Shik, Jonathan Z., and Michael Kaspari. "More food, less habitat: how necromass and leaf litter decomposition combine to regulate a litter ant community." *Ecological Entomology* 35, no. 2 (2010): 158-165.

Vandermeer, John H. "The competitive structure of communities: an experimental approach with protozoa." *Ecology* 50, no. 3 (1969): 362-371.

Vandermeer, J., M. A. Evans, P. Foster, T. Höök, M. Reiskind, and M. Wund. "Increased competition may promote species coexistence." *Proceedings of the National Academy of Sciences* 99, no. 13 (2002): 8731-8736.

Vandermeer, John, and Ivette Perfecto. "A keystone mutualism drives pattern in a power function." *Science* 311, no. 5763 (2006): 1000-1002.

Vandermeer, John, Ivette Perfecto, and Stacy M. Philpott. "Clusters of ant colonies and robust criticality in a tropical agroecosystem." *Nature* 451, no. 7177 (2008): 457

Vandermeer, John, Ivette Perfecto, and Stacy Philpott. "Ecological complexity and pest control in organic coffee production: uncovering an autonomous ecosystem service." *BioScience* 60, no. 7 (2010): 527-537.

Volterra, Vito. "Variations and fluctuations of the number of individuals in animal species living together." *ICES Journal of Marine Science* 3, no. 1 (1928): 3-51.

Werner, Earl E., and Mark A. McPeck. "Direct and indirect effects of predators on two anuran species along an environmental gradient." *Ecology* 75, no. 5 (1994): 1368-1382.

Werner, Earl E., and Bradley R. Anholt. "Predator-induced behavioral indirect effects: consequences to competitive interactions in anuran larvae." *Ecology* 77, no. 1 (1996): 157-169.