Title

Los Claroscuros del Café: Socioecological Complexities in the Coffee-Biodiversity Nexus in Southern Mexico

Permalink

https://escholarship.org/uc/item/4br1x1j8

Author

Jimenez Soto, Maria E

Publication Date

2018

Peer reviewed|Thesis/dissertation

UNIVERSITY OF CALIFORNIA
SANTA CRUZ

LOS CLAROSCUROS DEL CAFÉ: SOCIOECOLOGICAL COMPLEXITIES IN THE COFFEE-BIODIVERSITY NEXUS IN SOUTHERN MEXICO

A dissertation in partial satisfaction
of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

ENVIRONMENTAL STUDIES
With and emphasis in ECOLOGY AND EVOLUTIONARY BIOLOGY

by

María Estelí Jiménez Soto

September 2018

The Dissertation of María Estelí Jiménez Soto is
Approved:

Professor Stacy M. Philpott, chair

Professor Deborah Letourneau

Professor Andrew Szasz

Professor Ingrid Parker

Lori Kletzer
Vice Provost and Dean of Graduate Studies

TABLE OF CONTENTS

LIST OF TABLES

CHAPTER 2

CHAPTER 3

LIST OF FIGURES

CHAPTER 1

CHAPTER 2

CHAPTER 3

CHAPTER 4

ABSTRACT

LOS CLAROSCUROS DEL CAFÉ: SOCIOECOLOGICAL COMPLEXITIES IN THE COFFEE-BIODIVERSITY NEXUS IN SOUTHERN MEXICO

María Estelí Jiménez Soto

Coffee is one of the most demanded commodities worldwide, supporting the livelihoods of 25 million families. Coffee has been traditionally cultivated within biodiversity hotspots, making these ideal places for biodiversity conservation. Research has pointed out that biodiverse coffee systems support biodiversity and ecosystem functions. However, less is known about the specific ecological mechanisms supporting higher biodiversity and abundance of natural enemies of coffee pests in complex agroecosystems. Resource heterogeneity could be an important factor for arthropod communities; yet, this is still an ongoing scientific exploration in coffee systems. A second area of attention in coffee studies comprises human perceptions of the associated biodiversity in coffee agroecosystems. Most studies highlight the importance of biodiverse coffee smallholdings in delivering food security and contribute to livelihoods of peasant households. However, farm workers are a marginalized sector within the coffee production chain, and much less work has examined the lived-experience of farm workers in coffee agroecosystems. I disentangle the socio-ecological complexities of coffee plantations through three disciplines: agroecology, political ecology, and multi-species ecologies. I examine coffee plantations as spaces constructed by the actions of human and non-human entities, the ecological meanings and narratives constructed from our scientific endeavors, market forces, and peoples’ everyday lived experiences. My research takes place in the Soconusco region in Mexico, a well-known coffee-producing region in the country. The methodologies I use include observations, field and laboratory experiments, ethnographic research, and participant observation in the coffee plantation system. In my work, I demonstrate how ecological mechanisms and abiotic factors drive species diversity and interactions in shaded-coffee plantations, focusing primarily on ants, an important group of natural enemies in coffee systems. I show that diversity of nesting resources drive species coexistence through niche partitioning. I demonstrate that the availability of nectar resources influence colony reproduction. I show that the availability of connectivity resources at the local scale relate to biological pest control of the coffee berry borer, the most important insect coffee pest worldwide. Finally, I present the contradictions and social struggles that arise when conservation narratives meet the everyday-lived-experience of farmworkers in organic shade-grown coffee plantations in Southeast Mexico.

DEDICATION

To all who struggle for coffee every day, in all senses possible.

A todas las que luchan por el café cada día, en todos los sentidos posibles.

El Café

Tengo tu mismo color
Y tu misma procedencia.
Somos aroma y esencia
Y amargo es nuestro sabor.
Tú viajaste a Nueva York
Con visa en Bab-el-Mandeb,
Yo mi Trópico crucé
De Abisinia a las Antillas.
Soy como ustedes semillas.
Son un grano de café.

...
Y conocimos al Peón
Con su café carretero,
Y hablando con el Obrero
Recorrimos la nación.
Se habló de revolución
Entre sorbos de café:
Cogí el machete... dudé,
¡Tú me infundiste valor
Y a sangre y fuego y sudor
Mi libertad conquisté...!
...
Tengo tu mismo color
Y tu misma procedencia,
Somos aroma y esencia
Y amargo es nuestro sabor...
¡Vamos hermanos, valor,
El café nos pide fe;
Y Changó y Ochún y Agué
Piden un grito que vibre
Por nuestra América Libre,
Libre como su café!

By Nicomedes Santa Cruz Gamarra
Poeta Peruano

ACKNOWLEDGEMENTS

I have received an incredible amount of support from family, friends, professors, and colleagues throughout my doctoral studies. I am grateful for the support and endless encouragement I have received from my parents Lorena Soto and Guillermo Jiménez, my brother Manuel Antonio Jiménez Soto, and my loving husband Aaron Augsburger. My parents have been my number one source of inspiration to become a scientist. I want to thank them for introducing me to the research in agroforestry systems, for always having an active role during my doctoral studies, and for the vibrant conversations about the future direction of coffee production and agroforestry systems in Mexico. I am thankful for the support and cheerful attitude always coming from my brother, who I always turn to for refreshing advice. My husband Aaron has been incredible in so many ways, I thank him for being present in good and tough times during my Ph.D., for always believing in me, for his company and invaluable advice during fieldwork and life in general.

Thanks to my friends, some with whom I have collaborated and created unforgettable memories that made my time in my doctoral studies pleasant: Alicia Calle, Jorge Duque, Peter Bichier, Monika Egerer, Jonathan Morris, Zach Hajian-Forooshani, Aldo de la Mora, Kaleigh Fisher, Iris Rivera-Salinas, Marcela Cely-Santos, Beatriz Otero, Senay Yitbarek, Diana Piña, Flavia Oliveira, Graeme Baird, Jenny Lovell, Paulo Quadri and Luz DeWit. Thanks to my all-time friends who although I see very little, are always my motor: Viri Escalona, Aris Gomez, Malisa Pedrero and Elvira Catena.

Several institutions that provided generous financial support that allowed me to complete my Ph.D. studies in The United States and fund my research activities and travel. I thank the El Consejo Nacional de Ciencia y Tecnologia (CONACyT), UC-MEXUS, The International Peace Scholarship through P.E.O, The Organization for Tropical Studies (OTS), and the department of Environmental Studies at the University of California Santa Cruz.

My ethnographic research would have not been possible without the openness and trust shown by the Guatemalan farmworkers who showed me the joy and pain of working in a coffee plantation. I thank them for their invaluable time and sincerity.

My agroecological research was made possible thanks to the hard work of G. Domínguez Martinez, C. Pérez, F. Rodríguez, G. López Bautista, H. U. Vazquez Perez who providing field assistance during field work.

Above all I am thankful for the scholarly support and friendship I have received from my Ph.D. advisor Stacy M. Philpott, who through kindness, thoroughness and great mentorship has inspired me to become a better scientist and mentor myself. I thank Stacy for showing me that research is exciting, collaborative, fun and stimulating. I am thankful for the support I have received from Deborah Letourneau, for her insightful ideas during the development and analysis of my research, for showing me in a humbling way the human side of the academic world. I want to thank Andrew Szasz for walking me patiently through the process of writing in the social sciences, and for being cheerful through multiple manuscript drafts. I thank Ingrid Parker for her detailed, precise and always refreshing comments on my dissertation proposal and my work with ant-plant interactions. Other professors have been key for my growth as an academic: I want to give special thanks to Ivette Perfecto and John Vandermeer, who have always been an incredible source of inspiration and support both in the field, through the development of ideas, and through upbeat scholarly conversations. I thank Madeleine Fairbairn for providing the necessary theoretical and methodological tools that form the basis of my social science research, for mentoring me through my first time teaching a course, and for being a caring, available and approachable professor and colleague. Also, thanks to Madeleine for pushing me to finish my first manuscript from my ethnographic research and for showing so much interest in my findings. I also thank Rachel Vannette, who hosted me in her lab at UC Davis and showed me the ropes of nectar analysis.

The text of this dissertation includes reprints of the following previously published material: **Jiménez-Soto, E., and S. M. Philpott. 2015. Size matters: nest colonization patterns for twig-nesting ants. Ecology and Evolution**. And **Jimenez-Soto, E., Morris, J.R., Letourneau, D., Philpott, S.M. Vegetation connectivity increases ant activity and potential for ant-provided biocontrol services in a tropical agroforest. In revisions for Biotropica**. Permission letters from may coauthors have been included as a supplementary file attached to this dissertation. Ant cartoons in chapter 4 are property of Peter Slingsby and Joe A. Macgown

Chapter 1
INTRODUCTION

Coffee, a highly demanded commodity supporting the livelihoods of more than 20 million families (Donald 2004), has been traditionally cultivated under the shade of trees (Fig. 1) within tropical and subtropical biodiversity hotspots, making it relevant for conservation, food provisioning for rural families and the delivery of ecosystem services, meaning the processes and conditions provided by natural ecosystems with the potential to sustain and fulfill human welfare (Ehrlich and Ehrlich 1981, Daily 1997, Kremen 2005, Fisher et al. 2009). Important ecosystem services in coffee plantations are pest control and pollination (Toledo and Moguel 2012). However, coffee agroecosystems continue to experience a dramatic change in their management, characterized by the reduction of shade trees and increased use of chemical inputs (Jha et al. 2014). This intensification has had severe ecological implications, including the decline of ecosystem services (Toledo and Moguel 2012, Jha et al. 2014); and social consequences like food insecurity and seasonal hunger for farming families (Bacon et al. 2008, Caswell et al. 2012).

Much research on the benefits of biodiversity in coffee agroecosystems - has pointed out that highly biodiverse habitats have the potential to sustain a number of species and interactions that support ecosystem services (Klein et al. 2003, Mendez et al. 2010, Vandermeer et al. 2010). However, less is known about the specific ecological mechanisms supporting more biodiversity and higher abundance of natural enemies of coffee pests in complex agroecosystems

(Bael et al. 2008). Previous studies have suggested that resource heterogeneity, meaning the variability of available resources through space and time (Hempson et al. 2015) and accessible refuges provided by surrounding vegetation could be important factors for arthropod communities (Rezende et al. 2014). Yet, this is still an ongoing scientific exploration in coffee systems (Pak et al. 2015).

A second area of attention in coffee studies comprises the benefits that humans perceive from the planned and associated biodiversity in coffee agroecosystems. Most of these studies have highlighted the importance of biodiverse coffee smallholdings in delivering food security and contribute to livelihoods of peasant households (Thrupp 2000). However, research has suggested that established and temporary farm workers are a highly marginalized sector of the coffee production chain (Gresser and Tickell 2002, Jha et al. 2014), which indicates that further attention needs to be put in terms of the overall lived experience– and specifically food-related experiences– of this sector.

Ecological theory provides foundations for explaining higher abundance and diversity of natural enemies in complex habitats. Two complementary hypothesis have been developed and are useful in this sense: the first one suggests that different habitat types– meaning a variety of plants, strata, microhabitats, the spatial arrangement and temporal overlap of the plants –can support greater biodiversity of predators and reduce crop damage (Andow 1991, Schmitz 2007). This hypothesis considers that an increase in resources such as floral and extrafloral nectar and provisioning of shelter through improving non-crop vegetation, favors generalist and specialist predators and parasitoids through the delivery of alternative food (Landis et al. 2000). A second hypothesis suggests that niche complementarity, which occurs when higher diversity in the system allows for a grater range of functional traits to be represented, favors a more efficient use of resources and promotes diversity at higher trophic levels (Díaz and Cabido 2001). Following these hypotheses communities of natural enemies could potentially thrive in coffee agroecosystems to the extent that these systems provide the necessary resources to survive when the main prey are not available.

My dissertation departs from two socio-ecological understandings: 1) Resource heterogeneity– expressed in temporal variation of a particular resource, differences in quality and nutritional variation of resources, or differences in microhabitats (Price et al. 2011)– is considered an important factor influencing communities. More complex habitats provide diversity of niches (food, nesting sites, etc.) and ways to exploit resources in a particular environment (Wacker et al. 2008), which in turn supports more biodiversity (Tews et al. 2004), influences the distribution and interactions of species (Tews et al. 2004) and may favor niche partitioning and species coexistence in a given environment (Ricklefs 1987). 2) Ecological diversity exists along a gradient of social complexity, allowing the co-creation of spaces. The subsistence value of biodiverse coffee systems draws upon the potential of growing and using a variety of resources other than coffee within the agroecosystem and adjacent plots (Mendez et al. 2010). There is an increase interest and awareness that biodiversity conservation can have positive effects on food production and livelihoods (Thrupp 2000). Such is the case of traditional coffee polycultures and indigenous agroforestry systems (Escamilla Prado et al. 1997). Despite benefits of highly biodiverse coffee plantations, coffee farmers frequently experience seasonal hunger and food shortages (Morris et al. 2013). Food related challenges are mostly reported from smallholdings; however a smaller but important sector of coffee production happens in large plantations, which represent a historically and currently important sector of the coffee production in Central America and issues of food security have not been explored enough.

Under this framework, this dissertation evaluates three intertwined areas. First - I examine the influence of the availability of three resources (food, nesting and connectivity resources) on ant community dynamics such as colonization, reproduction, and two species interactions: predator-prey and parasitoid-host interactions. Ants and parasitoids are important natural enemies of coffee pests and are model systems to understand the mechanisms that favor diversity in complex habitats. Second, I examine the influence of local habitat factors (habitat intensification) on community dynamics. Third, I explore the every-day lived experiences of farmworkers in coffee plantations, a scantily explored area that requires attention in coffee growing regions in Mexico.

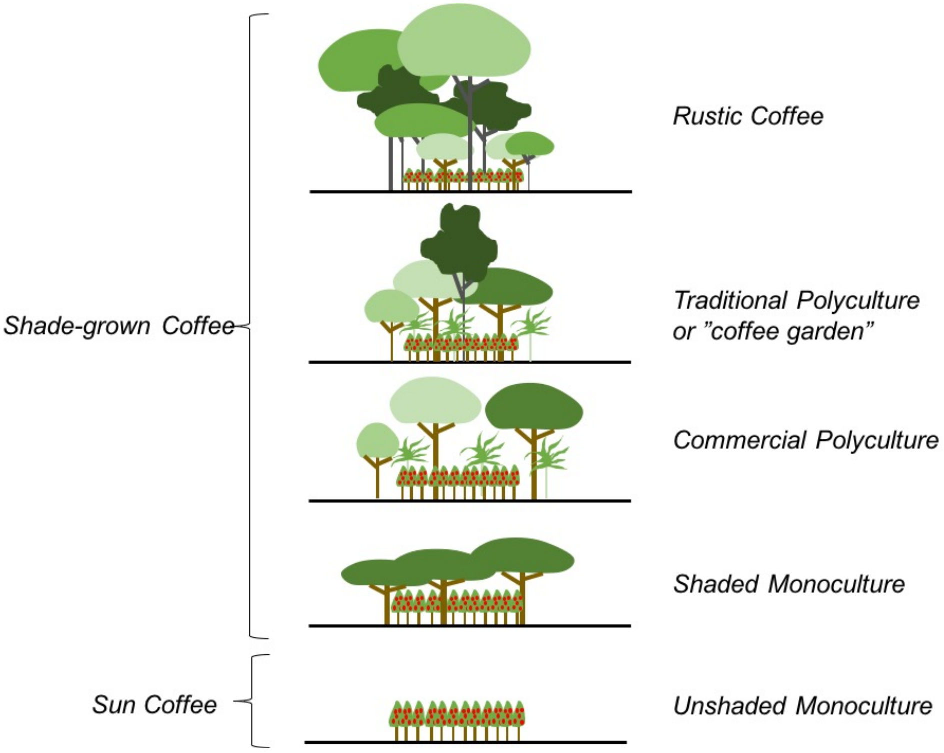


Figure 1. Different coffee growing systems described for Mexico, showing a gradient of vegetation complexity represented primarily by different levels of shade, under which coffee plants are grown. Modified from Moguel and Toledo (1999).

CHAPTER 2
NEST COLONIZATION PATTERS FOR TWIG-NESTING ANTS

Jiménez-Soto, E., and S. M. Philpott. 2015. Size matters: nest colonization patterns for twig-nesting ants. *Ecology and Evolution*.

Abstract

Different mechanisms operate at local and regional scales to influence ant species assemblages. Understanding the factors that drive ant diversity and co-occurrence in agroecosystems is fundamental given that ants influence food webs and are important predators in agroecosystems. We examined local ecological mechanisms that influence the structure of an arboreal twig-nesting ant community in coffee systems in Mexico. We investigated whether twig characteristics (nest size and diversity of nest sizes) and nest strata (shade tree or coffee shrub) affect occupation, species richness, and community composition of ants occupying twigs. We also examined whether certain ant species demonstrated nest size or strata preferences. We placed 6 artificial nests (identical bamboo twigs that differed in nest entrance size) on coffee shrubs and shade trees either in diverse (one nest of each size) or uniform (six nests of the largest size) treatments. We found 33 ant species occupying artificial nests. Strata or size treatment did not influence the percent of occupied nests or mean species richness ($F=0.75$, $P>0.05$). Community composition did differ with strata ($P=0.0001$) and between diverse and uniform nests on coffee shrubs ($P=0.0004$), but not on shade trees ($P=0.12$). A Chi-square test showed that *Camponotus atriceps*, *Camponotus striatus* and *Pseudomyrmex gracilis* are more abundant in coffee nests ($p<0.05$); and *Cephalotes basalis* and *Camponotus brettesi* on tree nests ($p<0.05$). *C. atriceps* is more abundant in uniform nests ($p<0.05$); and *C. striatus* and *P. gracilis* in diverse nests ($p<0.05$). Additionally, individual ant species preferentially occupy nests of a certain size. Our results indicate that individual ant species do respond to certain nest sizes and increases in available nesting resources but that nest size diversity and strata do not play a large role in determining the number of species in the community. These results provide insight into possible factors influencing the twig-nesting ant community in this coffee system.

Introduction

A central aim in ecology is to understand how diverse factors at local and regional scales influence community assembly. Community assembly is the process that leads to particular patterns of colonization of interacting (or not interacting) species, that may share a particular resource (HilleRisLambers et al. 2012), and a process that reflects survival of species in a particular habitat (HilleRisLambers et al. 2012). The study of communities and their assemblage processes is important for explaining community dynamics, but also because it can provide important insights into spatiotemporal factors that maintain ecosystem services in face of global change, destruction of natural biomes, and intensification of managed systems (HilleRisLambers et al. 2012; Philpott 2010). Ants are a diverse and an interesting group of insects to use for studies of community assembly and drivers of coexistence because they are found almost everywhere and in the tropics they can represent up to 80% of the animal biomass (Hölldobler 1990).

Understanding drivers of ant diversity and co-occurrence is of relevance, as ants participate in competitive, mutualistic and predatory interactions, as well as trait mediated interactions that often result in ecosystem services (Liere and Larsen 2010, Vandermeer et al. 2010, Sanabria et al. 2014, Wielgoss et al. 2014). Ants are important pollinators (de Vega et al. 2014), predators of pests in agricultural systems (Vandermeer et al. 2010), seed dispersers (Lubertazzi et al. 2010) and protectors of plants that provide resources useful for ants (Rezende et al. 2014).

Local and regional factors influence ant assemblages, however there is no single cause or dynamic that explains nest colonization patterns of entire communities of ants. Thus, recognizing that community assemblages can be structured through multiple ecological and evolutionary processes interacting synergistically is essential in community studies (Webb et al. 2002; Resetarits et al. 2005; Debout et al. 2009). By examining the community of arboreal ants that nest in hollow twigs in a coffee plantation, we investigated how availability of resources, such as diversity of nests with different sized entrances, and the vegetation strata in which nests are located influence colonization and nesting patterns for a community of twig-nesting ants. The role of cavity entrance diversity on Neotropical arboreal ants has been previously shown to strongly influence cavity colonization in a natural ecosystem (Powell et al. 2011). Although the present study shares a number of similarities with the previous study in terms of the experimental design, the novelty of our study lies in the examination of the assembly process of the arboreal ant community in an agroecosystem considering the vegetative strata (and not canopy connectivity) as a potentially significant local factor influencing ant assembly.

Other studies have also made important contributions to the understanding of the influence of resource availability, interspecific competition from dominant ants, and changes in environmental conditions on ant colonization, survival and community assembly (Philpott 2010; Ribas et al. 2003); similarly, studies have reported that niche differentiation and interspecific competition for similar resources structure ant communities (Albrecht and Gotelli 2001, Donoso 2014, Houadria et al. 2014). In the litter environment, factors such as patchiness in nest site availability (but not necessarily availability of food resources) can influence ground ants (Kaspari 1996). For other communities, however, nesting sites might not be a limiting factor, although nest-site limitation may increase with agricultural habitat intensification or disturbance (Philpott and Foster 2005). Moreover, increases in diversity of nesting sites can influence species richness and composition (Armbrecht et al. 2004). Only few studies examine factors that influence ant communities at the colonization stage, despite the importance of priority effects for community assembly (Palmer et al. 2003, Andersen 2008, Livingston and Philpott 2010, Powell et al. 2011). Recruitment limitation can affect colony density and incidence of less competitive species, thus examining initial phases of colonization may be important for understanding species coexistence (Andersen 2008). Moreover, the dispersal stage of colony formation maybe strongly influenced by community assembly mechanisms such as habitat filtering because ants must find suitable habitats (Livingston and Philpott 2010).

The present study asked the following questions: 1) Does nest strata or diversity of nest entrance sizes influence the percent of nests colonized by arboreal twig-nesting ants, 2) Does nest strata or diversity of nest entrance sizes influence the species richness of arboreal twig-nesting ants colonizing nests? 3) Does nest strata or diversity of nest entrance sizes influence the community composition of twig-nesting ants colonizing nests? 4) Are nests with certain nest entrance sizes more frequently occupied, or have a higher species richness of ants? 5) Do individual ant species more frequently occupy nests in a certain strata or nests of a certain entrance size?

Methods

Study site description

We conducted field research in a 300-ha shaded coffee farm in the Soconusco region of Chiapas, Mexico between March and June 2012. The farm is located between 900-1100 m a.s.l. Between 2006-2011, annual rainfall at the farm was between 4000-5000 mm. During the time of the research, the production style of the farm could be classified as a mix of commercial polyculture and shaded monoculture according to the system of Moguel & Toledo (1999). The farm has ~50 species of shade trees that provide 30-75% canopy cover to the coffee buses in the understory.

We studied ant occupation of nests in 44 locations (hereafter ‘sites’) on the farm. Each study site was separated by a minimum of 100 m, and consisted of two neighboring *Inga micheliana* trees of approximately the same size (separated by 10-15 m) and two coffee plants directly underneath the trees. In order to characterize the vegetation of each study site, we measured trees, canopy cover, and coffee density. For all measurements, we used the midway point between the two *Inga micheliana* trees as the center point. In a 25 m radius circle around the center, we identified and counted each tree and measured the circumference and height of all tress. We sampled canopy cover at the circle center, and 10 m to the N, S, E, and W of the circle center with a convex spherical densitometer. We counted the number of coffee plants within 5 m of each focal *Inga* tree in each site. With the vegetation data, we calculated a vegetation complexity index (VCI). To calculate the index, we divided values for each vegetation variable (mean canopy cover, tree richness, mean tree height, mean tree circumference, percent of trees in the genus *Inga*, mean number of coffee plants) by the highest observed value for each variable. For the number of coffee plants and the percent of trees in the genus *Inga*, we subtracted the product from 1 as these two factors generally negatively correlate with vegetation complexity. Then, we took the average of all values for each site to obtain a single value between 0 (low vegetation complexity) and 1 (high vegetation complexity).

Artificial nests and ant sampling

In each site, we added artificial nests to study nest colonization, following a similar methodology used by Powell et al. (2011). Artificial nests consisted of hollow bamboo twigs of the same cavity size (100 mm long, 10 mm internal diameter). We cut bamboo twigs such that the natural node blocked one end, and we plugged the other end of the bamboo with wood putty. We drilled circular holes (entrances) of the following sizes in the side of the bamboo: 1

mm^2, 2 mm^2, 4 mm^2, 8 mm^2, 16 mm^2, and 32 mm^2. The set of sizes used in the present study correspond to an exact subset of the cavity sizes used in Powell et al. (2011) – we did not use the largest size used in the previous study. We added 6 nests to each *Inga* tree and each coffee plant for a total of 24 nests added in each site, or 1056 nests added overall. In each site, we added a diverse mix of nests (one nest each of 1 mm^2, 2 mm^2, 4 mm^2, 8 mm^2, 16 mm^2, and 32 mm^2 nest entrance sizes) to one *Inga* tree and one coffee plant. On the other *Inga* tree and coffee plant we added a uniform selection of nests (six nests all of the 32 mm^2 nest entrance size). Treatments were randomly assigned to plants in each site. We attached nests to plants with twist ties and plastic string between 0.5 to 1.5 m above ground on coffee plants, and between 4 to 6 m above ground for *Inga* trees. We placed nests flush with coffee or tree branches. We placed nests between 5-7 March and harvested all nests 14 weeks later (between 14-18 June). The period of the study encompassed part of the rainy season. Rain and moisture have a significant effect on colony phenology because they regulate alate's flights in the absence of temperature variation (Kaspari et al. 2001). Although nests were placed long enough to be colonized by ants, longer time periods may have allowed us to capture colonization dynamics across time.

To determine effects of nest entrance size, entrance size diversity, and nest vegetation strata on colonization, we collected artificial nests, placed them in bags, froze them, and then cut open all nests to remove the contents. We noted whether each nest was occupied or not. We stored ants in 70% ethanol and later identified them according to the Ants of Costa Rica (Longino 2007a), and AntWeb (2014). For all species found, we obtained an approximate head width measurement from AntWeb (2014).

Data analysis

To compare whether the proportion of occupied nests differed with nest strata or the diversity of nest entrance sizes available, we used generalized linear mixed models (GLMM) with ‘glmer’ in the ‘lme4’ package in R (R-Development-Core-Team 2014). We compared two models. In the first, we included nest strata (tree or coffee), nest size treatment (diverse or uniform), and the interaction between the two as fixed factors, the vegetation complexity index (VCI) as a covariate, and site as a random factor. In the second, we removed the VCI. To select the best model, we used the Akaike's Information Criterion (AIC) computed with the ‘mass’ package (Ripley et al. 2013). For both models, we used the binomial error distribution with the logit link. Instead of using the proportion data directly, we used the ‘cbind’ function with number of nests occupied and number of nests that were not occupied as input variables.

To examine whether species richness differed with nest strata or the diversity of nest sizes available, we used two methods. First, we compared the mean species richness of ants occupying nests on a plant with GLMMs with ‘glmer’ in the ‘lme4’ package in R (R-Development-Core-Team 2014). We compared two models. In the first, we included nest strata (tree or coffee), nest size treatment (diverse or uniform), and the interaction between the two as fixed factors, the vegetation complexity index (VCI) as a covariate, and site as a random factor. In the second, we removed the VCI. To select the best model, we used the Akaike's Information Criterion (AIC) computed with the ‘mass’ package (Ripley et al. 2013). For both models, we used a Poisson error distribution with the log link. Second, we created sample-based species accumulation curves, scaled to the number of individuals, to compare richness in coffee plants vs. trees and diverse vs. uniform nest size treatment plants with EstimateS (Colwell et al. 2004). We used the number of ant colonies encountered instead of the number of individuals, as ants are social organisms and better captured by number of colonies (Longino et al. 2002). We examined curves for both observed species richness and plotted 95% confidence intervals to statistically compare species richness between treatments.

To compare whether community composition of ants differed with strata and with nest size treatment, we used two methods. We used non-metric multidimensional scaling (NMDS) and analysis of similarities (ANOSIM) in PAST (Hammer et al. 2001) to visually and statistically compare species composition of the ants occupying nests in coffee vs. shade trees and in uniform vs. diverse nest treatments. The ANOSIM compares (a) the mean distance within groups to (b) the mean distance between groups, and can statistically determine separation in species composition between the plots in different treatment groups. For the NMDS and ANOSIM we used the Bray-Curtis similarity index as the similarity measure.

Finally, we examined whether common ant species more frequently colonized nests of a certain entrance size or vegetation strata. To compare if nests with certain entrance sizes were more frequently occupied by ants we used an ANOVA followed by a Tukey’s test to compare the mean proportion of nests of each entrance size that were occupied. We only used data from the diverse treatment plants (where nests of different size entrances were equally available) to calculate differences in nest colonization. To compare if certain ant species more frequently occupied certain nest sizes or strata we performed Chi-squared analysis which is recommended for categorical data and tests the likelihood that an observed distribution is due to chance (Rao and Scott 1981) .

Results

Vegetation in the plots was somewhat variable. There were between 8 and 31 trees, 3 and 12 tree species, and 12.5 and 36.5 coffee plants in each site. Mean tree height ranged from 4.4 m to 12.7 m, canopy cover ranged from 9.4 - 86.2 %, and the VCI ranged from 0.28 to 0.74.

We recovered 1030 of the 1056 nests that were placed. Overall, we found 33 species of ants that colonized nests, and 73% of nests overall were occupied. The most common ants collected were *Camponotus atriceps* (18.72% of occupied nests), *Dolichoderus lutosus* (12.48%), *Pseudomyrmex gracilis* (6.77%), *Crematogaster sumichrasti* (6.37%), *Camponotus brettesi* (5.84%), *Crematogaster carinata* (5.44%), *Cephalotes basalis* (5.04%), *Camponotus novogranadensis* (4.9%), *Camponotus striatus* (3.98%), and *Neoponera crenata* (3.45%). Information on numbers of queens, males, workers, larvae, and pupae found for each species are presented in Table 1.

The proportion of occupied nests did not differ by nest strata or nest size treatment (Fig. 1a). The GLMM model that best predicted differences in the proportion of occupied nests included nest strata and nest size treatment as fixed factors and site as a random factor. Thus although there was a large range in values for the vegetation characteristics measured and the VCI, vegetation complexity did not improve the model fit. There was no difference in the proportion of nests occupied in different nest size treatments (diverse and uniform) ($F_{1, 43} = 2.37$, $P = 0.131$), or in different nest strata ($F_{1, 43} = 0.0112$, $P = 0.914$) and there was no significant interaction between size treatment and strata ($F_{1, 42} = 1.948$, $P = 0.170$).

Mean species richness increased with diversity of nest entrance sizes on a plant, but cumulative species richness did not differ between diverse and uniform treatment plants. The GLMM model that best predicted mean species richness included nest strata and nest size treatments as fixed factors and site as a random factor. Including the VCI did not improve model fit. The mean number of species on a plant was 20% higher on both coffee plants and shade trees with a diverse mix of nest sizes ($F_{1, 43} = 9.426$, $P = 0.004$, Fig. 1b), but there were no differences in mean species richness with nest strata ($F_{1, 43} = 0.056$, $P = 0.814$), and no significant interaction between size treatment and strata ($F_{1, 42} = 0.219$, $P = 0.643$). In contrast, species accumulation curves did not show any difference in observed or estimated species richness between the diverse and uniform nest size treatments (Fig. 2a) or for coffee vs. shade tree strata (Fig. 2b).

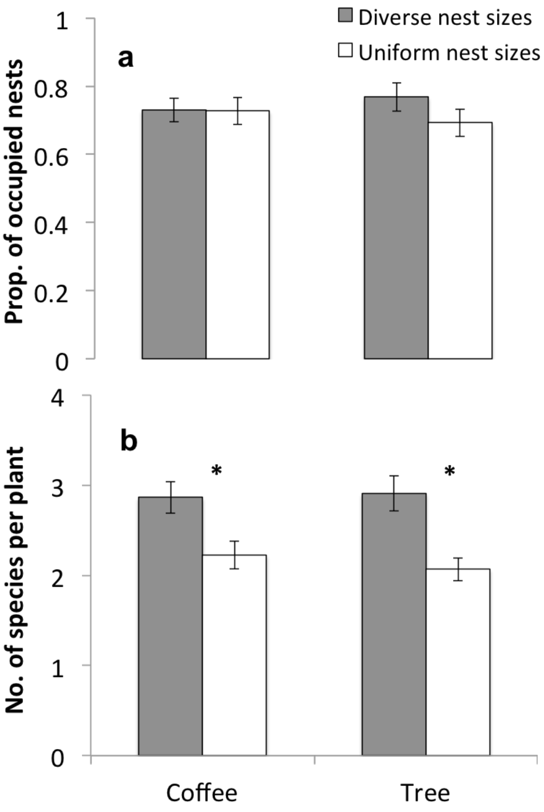


Figure 2. *Species accumulation curves comparing ant species richness in a) diverse nest size treatment nests (grey) and uniform nest size treatment nests (black) and b) coffee nests (grey) and shade tree nests (open). Thick lines show richness and thin lines (of the same color) show 95% confidence intervals for observed and estimated richness.*

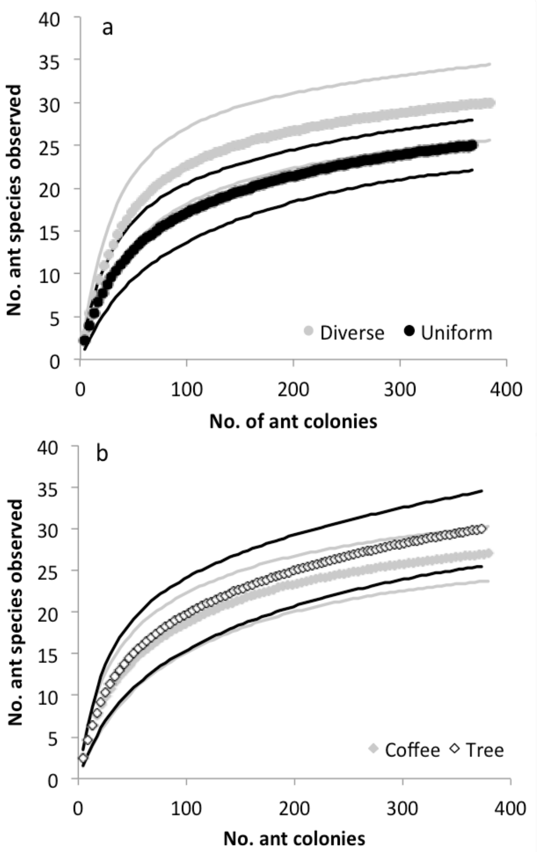


Figure 1. *Influence of nest size entrance treatment (diverse and uniform) and vegetation strata (coffee and trees) on a) the proportion of occupied nests and b) species richness of ants colonizing nests. Asterisks show significant differences between nest entrance size treatments.*

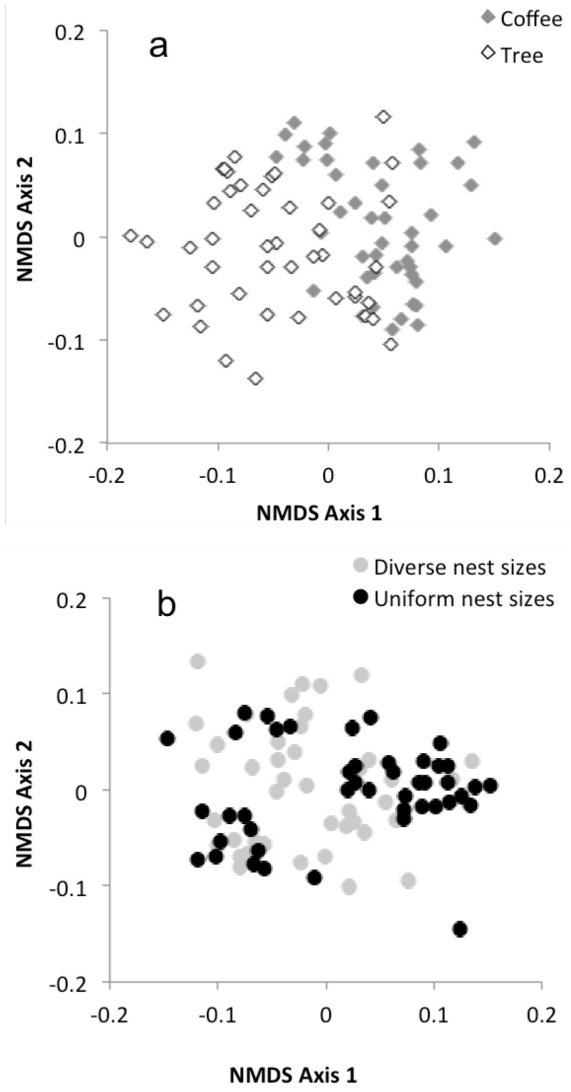


Figure 3. *Non-metric multidimensional scaling (NMDS) of the community of ants occupying a) nests placed in coffee shrubs (grey) or shade trees (black) and b) nests on plants with a diverse mix of nest entrance sizes (grey) or uniform nest entrance sizes (black).*

Ant community composition of colonizing ants differed with both nest strata and nest size treatments. The NMDS for coffee and shade tree ant communities showed marked differences between the two nest strata (Fig. 3a, stress = 0.348), and the ANOSIM demonstrated a significant difference between the two groups of ants (Global R = 0.2475, $P < 0.001$). Likewise, the NMDS showed different ant community composition in the diverse and uniform nest size treatment plants (Fig. 3b, stress = 0.3316) and the ANOSIM showed a significant difference between ants in nests on diverse and uniform treatment plants (Global R = 0.1318, $P < 0.001$).

Ants more frequently occupied nests with certain entrance sizes and richness in different sizes also differed. Of all available nest sizes, the middle sizes were more frequently occupied ($F_{5, 259} = 19.05$, $P < 0.001$, Fig. 4). There were pairwise differences in proportion of occupied nests for many pairs of entrance sizes ($P < 0.05$).

The Chi-squared analysis showed that certain ant species more frequently occupied nests with certain entrance sizes or placed in different vegetation strata (Fig. 5a, b). In particular *P. gracilis* more frequently occupied nests with 4 mm^2 entrances than nests with other entrance sizes ($X^2 = 15.09$, df = 5, N = 26, P = 0.0001; *C. basalis* more frequently occupied nests with the largest entrance size (32 mm^2, $X^2 = 12.37$, df = 5, N =10, P = 0.003), as did *C. atriceps* ($X^2 = 11.07$, df = 5, N = 20, P = 0.008). The other ant species did not more frequently occupy certain nest sizes. Likewise, half of the most common ant species found, more frequently occupied nests in one of the two nest strata (Fig 5b). Specifically, three species, *C. striatus*, *P. gracilis*, and *N. crenata* more frequently occupied nests placed on coffee shrubs (*C. striatus*, $X^2 = 6.63$, df = 1, N = 19, P = 0.01; *P. gracilis*, $X^2 = 13.56$, df = 1, N = 39, P = 0.0002; *N. crenata*, $X^2 = 15.21$, df = 1, N = 19, P<0.001). *C. bretesi* more frequently occupied nests in trees ($X^2 = 10.82$, df = 1, N = 28, P = 0.0001). *C. basalis* only occupied nests in trees ($X^2 = 22$, df = 1, N = 22, P < 0.001).

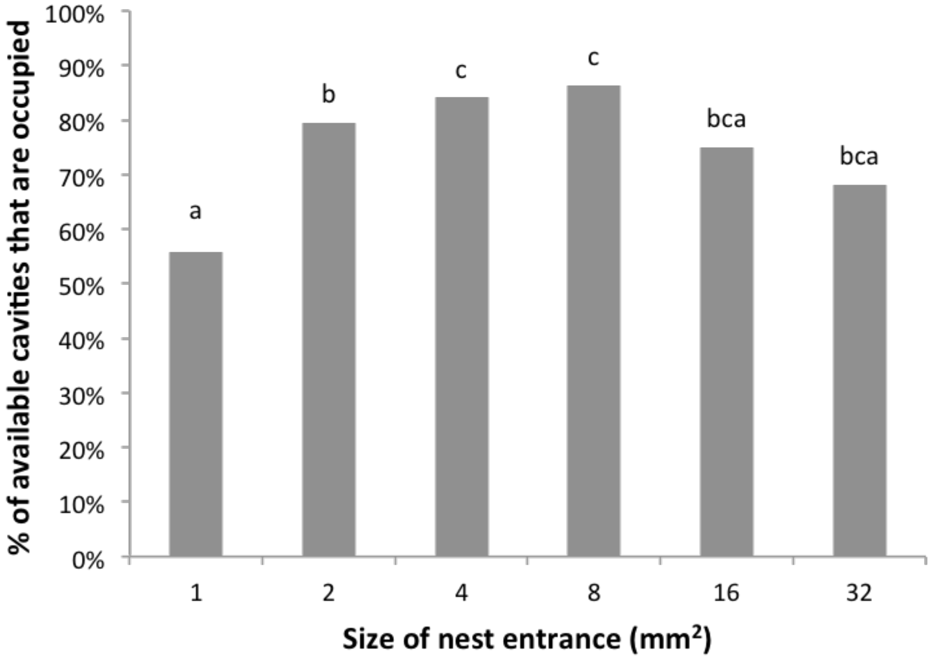


Figure 4. *The percent of nests of each nest size entrance occupied by ants on the diverse size treatment plants. The numbers above each column show richness of ants in that nest entrance size, and small letters indicate differences in percent occupation in different nest sizes according to pairwise Tukey's tests (P < 0.05).*

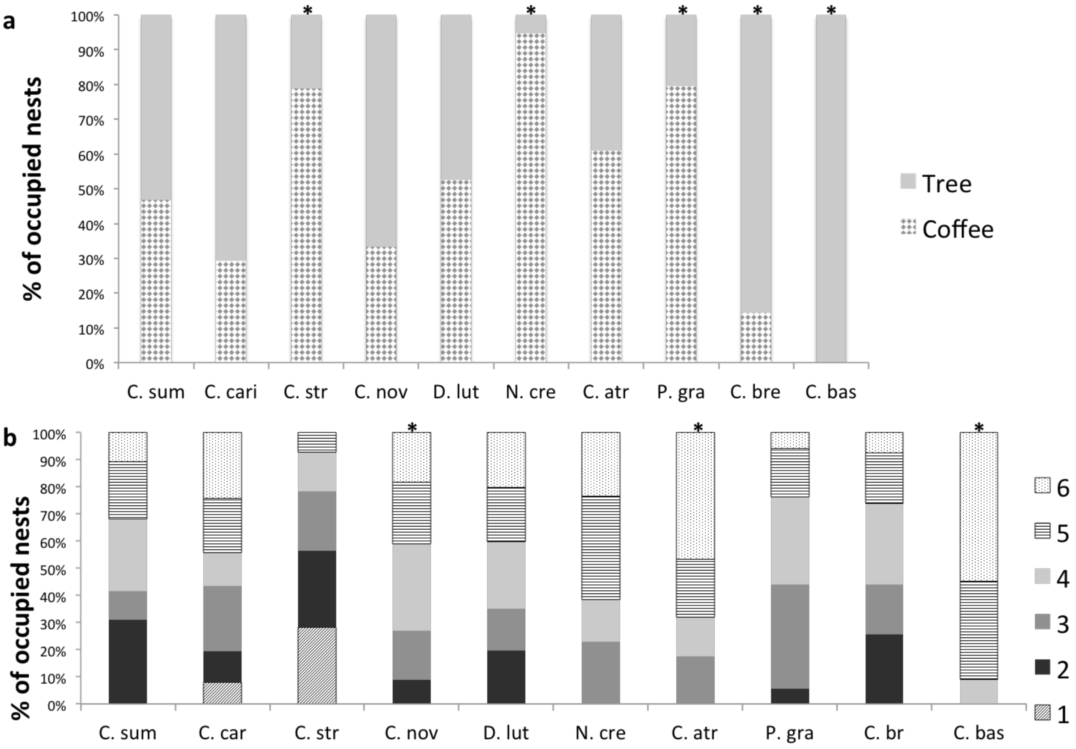


Figure 5. *The frequency with which certain ant species [Crematogaster carinata (C. cari), Camponotus striatus (C. str), Camponotus novogranadensis (C. nov), Dolichoderus lutosus (D. lut), Neoponera crenata (N. cre), Camponotus atriceps (C. atr), Pseudomyrmex gracilis (P. gra), Camponotus bretesi (C. bre), and Cephalotes basalis (C. bas)] occupy a) nests in the coffee and shade trees and b) nests of different sized entrances. Significant differences in occupation of different strata or sizes are indicated with an asterisk.*

Discussion

Ecological studies strive to understand local and regional factors that influence community assembly and species coexistence (Ricklefs 1987, Drake 1991, Huston , Chesson 2000, Hubbell 2001, Chase 2003, Foster et al. 2004, Leibold et al. 2004, Powell et al. 2011). Some factors important in for assembly of arboreal twig-nesting ants include presence of a canopy dominant species (Philpott 2010) and resource access through canopy connectivity (Powell et al. 2011). Previous studies have found that diversity of nesting resources influences the colonization process of leaf-litter twig-nesting ants (Armbrecht et al. 2004) and of tropical arboreal ants (Powell et al. 2011) and that the abundance of nesting resources may impact colonization of arboreal twig-nesting ants (Philpott and Foster 2005).

The study of assembly in ant communities in a spatial context reveals that species sorting, by which different species specialize in a particular habitat, and mass effects, in which species disperse from less to more suitable habitats, are likely important for common and rare species, respectively, in agroecosystems -- habitats embedded in landscape mosaics were local communities interact through dispersal (Leibold et al. 2004, Livingston et al. 2013). Our study is novel in that we examined colonization in a managed ecosystem looking at two factors (nest entrance size and strata) and their importance in colonization. In this study, we suggest that nesting resource utilization, specifically different frequencies of occupation of specific nest entrance sizes and specific nesting strata are important drivers of community assembly.

Overal, l we found that nesting strata (shade tree or coffee shrub) and the diversity of nest entrance sizes (uniform vs. diverse treatments) did not significantly influence the proportion of occupied artificial nests. Thus, ants use newly available cavities for colonization and nesting resources are somewhat limiting for the community of twig-nesting ants in the habitat studied. In comparison to our study, Powell et al. (2011) found that total nest occupancy was higher with higher nest cavity diversity in the Brazilian savanna (3% occupation in uniform entrance size vs. 26% in diverse entrance). It is possible that such distinct results derive from differences in overall nest availability, differences in vegetation (e.g. coffee systems with abundant woody shrubs and trees with 30-75 % canopy cover, Cerrado systems with a grass and shrub dominated ground and 30-50 % canopy cover with trees up to 8 m) and differences in the abundance of particular genera (e.g. *Cephalotes*). However, it is important to consider that the near-saturation found in the present study could be a result of adding only one cavity of each size per plant, which could mean that there were not enough nests to be colonized, once the "preferred" sizes (mainly mid-size cavities) were used on every plant —hence not available for other species to occupy. Differences in nest saturation and the proportion of nest occupation between both studies could be due to differences in the number of cavities per size used in the experiment. Thus, it is difficult to say that differences in nest limitation are due to the agroecological context, since previous studies in coffee plantations have found that the community of twig-nesting ants are limited by nesting resources (Armbrecht et al. 2006), as are ants in natural ecosystems (Kaspari 1996, Powell et al. 2011). In addition, differences in occupation dynamics of artificial nests during the colonization phase could potentially change with length of the study. A clear contrast is that the present study lasted three months, a third of the previous study, this difference in time could potentially influence competition for "preferred" cavities during colonization, as these are available for a longer period of time during the colony life cycle. Very little information is available about the reproductive phenology of arboreal twig-nesting ants. The evidence collected from our nests indicates (Table 1) that all common species were producing larvae and pupae, and that most species nests did contain alate males. Two of the common species collected from nests in the present study do experience queen flights during this time period (Table 1), but information is lacking for the other species. Thus, timing of nest placement may have affected the colonization processes, but it is important to note that many twig-nesting species expand by colony budding, and not only nuptial flights. Changes in the occupation dynamics —i.e. proportion of occupied nests, changes in diversity and species interactions—through time, could be the focus of future studies.

***Table 1** Mean number of workers, queens, larvae, pupae and males (alates) found in artificial nests, literature reports on their reproductive flight phenology of collected species. [§]Data from malaise traps in forest habitat on Barro Colorado Island (Kaspari et al. 2001). [§§]Data from pan traps in coffee habitat in Chiapas, Mexico (Philpott, unpublished data).*

Ant Species	Workers	Queens	Larvae	Pupae	Males	Reproductive flight phenology
Camponotus atriceps	25.11	0.11	10.60	21.66	0.83	
Camponotus brettesi	49.95	2.36	25.66	37.32	11.18	
Camponotus novogranadensis	55.30	0.64	15.88	21.30	2.70	
Camponotus striatus	56.70	5.07	18.43	29.20	9.43	
Cephalotes basalis	67.08	1.03	29.75	23.08	0.09	
Crematogaster carinata	247.12	0.07	74.54	60.61	0.00	
Crematogaster sumichrasti	179.23	7.13	45.77	63.67	0.42	
Dolichoderus lutosus	124.59	3.80	42.54	50.11	4.74	More alates found in Feb-June[§]
Pachycondyla crenata	11.12	1.40	4.40	7.72	0.52	
Pseudomyrmex gracilis	26.98	3.45	25.64	15.80	1.06	Queens found in March, May[§§]

Even though diversity of nest entrance sizes did not influence the percentage of occupation overall, frequency of occupation of nests by ants did differ for particular sizes. Higher occupancy was found in middle sizes (2, 4, 8 mm^2), these results are similar to Powell et al. (2011) in which middle sizes (4, 8, and 16 mm^2) were the most frequently occupied. The specificity in the use of particular sizes is important in two ways: first, the evolution of ecological specialization underlies the evolution of morphological specialization in ant soldiers, Powell (2008) showed that for different species of *Cephalotes* an increase in ecological specialization (meaning the use of cavities that matched the size of one ant head) corresponded to a higher head specialization (head morphology); in that same study *C. persimilis* uses cavities that match the size of one soldier's head and it has also evolved a highly specialized complete head-disc, while less ecologically specialized *Cephalotes* species, like *C. pusilus* (occupying cavities as big as 10 ant head sizes) have evolved a domed-head. Second, such size specialization maximizes individual nest survival and is likely to have a positive effect on overall colony reproduction as shown previously for *C. persimilis,* which more frequently nests in cavities that fit its head size (Powell 2009). On the other hand *Cephalotes* ants using cavities larger than their soldier's head, allows them to protect the nest using cooperative blocking (Powell 2009). The present study supports the former hypothesis (that ecological specialization drives a specialized morphology) (Powell 2009), in that the *Cephalotes* species present in our study (*C. basalis*), a domed-headed soldier morphotype, was more frequently found in the largest size (32 mm^2 area), an entrance size much larger than the ant's head maximum-recorded width (~3.16 mm) (Table 2, de Andrade and Baroni Urbani 1999). Other *Cepahlotes* species (e.g. *pusilis*) prefer natural nest sizes between four and up to ten times their head size (Powell 2008). If *C. basalis* shows a similar preference, and if we assume a maximum head size of ~5 mm (Powell 2008), than its preferred size might be between the 16 mm^2 and 32 mm^2 nests offered in this study.

Table 2 *Head sizes of common ant species encountered and nest entrance size that was more frequently occupied by that ant. Frequencies indicated with an asterisk were statistically significant. Species are arranged from smallest to largest.* [§]*Head size represents the widest section of the head as obtained from AntWeb (2014).* [§§]*Head size from de Andrade and Baroni Urbani (1999).*

Species	Approximate head size[§]	Nest entrance size more frequently occupied
Crematogaster sumichrasti	0.60 mm	2 mm^2
Crematogaster carinata	0.67 mm	4 mm^2
Camponotus striatus	0.75 mm	2 mm^2
Camponotus novogranadensis	0.92 mm	8 mm^2
Dolichoderus lutosus	1.25 mm	8 mm^2
Neoponera crenata	1.42 mm	16 mm^2
Camponotus atriceps	1.53 mm	32 mm$^{2\ *}$
Pseudomyrmex gracilis	1.61 mm	4 mm$^{2\ *}$
Camponotus brettesi	1.87 mm	8 mm^2
Cephalotes basalis[§§]	3.16 mm	32 mm$^{2\ *}$

Mean species richness was not different in artificial nests on coffee plants and trees, however the diversity of nest entrance sizes increased mean species richness on individual trees and coffee plants. In contrast to a previous study in which diversity of nest cavities did not significantly affect the number of ant species per tree (Powell et al. 2011), we did find that providing a diverse array of twig entrance sizes promoted local (e.g. plant level) ant species richness in both coffee shrubs and shade trees. This supports the idea that making a diversity of resources available in both strata supports a more diverse mix of arboreal twig-nesting ants. That we found more species richness per tree (and not per site, shown by the species accumulation curves) when providing a higher diversity of nest sizes could indicate that competition for resources might happen more intensively at the local scale, rather than at larger spatial scales. Diversity of nest resources is important for other twig-nesting ant communities. Namely, in a study of leaf-litter twig-nesting ants in shade coffee plantations in Colombia, 80% more species were found when providing a diverse mix of twigs rather than a monospecific collection of twigs (Armbrecht et al. 2004) showing that diversity of twig-nesting ants is influenced by other aspects of diversity of nesting resources.

We found that certain ant species more frequently occupied particular sizes and this may be in part, an explanation for why we found higher species richness on individual plants with a diversity of nest entrance sizes. Armbrecht et al. (2004) showed the importance of a diverse mix of twigs for species richness, however the driver in their study was not preference of different ant species for a different species of twigs, but rather an emergent property of a diverse mix of twigs. In our study, we provide evidence that species sorting along a size gradient likely explains the differences observed in mean species richness in uniform vs. diverse treatments. The frequency of occupation differed between sizes for certain ant species, largely following differences in ant head sizes (Table 2). As small ants can occupy a nest with a wide array of entrance sizes, larger ants can only occupy nests with entrances sizes larger than the workers. Thus providing a wider diversity of nest sizes may allow for greater niche differentiation in the ant community. This outcome might increase the overall richness of the ant community or on individual plants. In our study, larger ants seem to be more size limited than smaller ants, likely because larger ants simply cannot fit into the nests with smaller entrance sizes, and thus are directly constrained by the availability of twigs that fit their body dimensions (Kearney and Porter 2009). In vastly different systems, similar properties operate. For example, in aquatic systems, water temperatures can limit temporal and spatial distribution of certain species as morphological constraints can significantly limit species' access to suitable habitats (Kearney and Porter 2009). Alternatively, models of exploitative competition (Tilman 1990) have suggested that when two species compete for one limiting resource the result of such competition is determined by the species more capable to attain the lowest equilibrium resource concentration possible, R* (Townsend and Harper 2003). In other words, R* becomes a factor that is the lowest extent to which a certain species can survive in a certain area.

Community composition varied between plants with uniform vs. diverse nest entrance sizes, as well as in coffee plants and shade trees. Our results are consistent with previous studies that have investigated ant stratification in the rainforest, where there is a strong partitioning of ant species in the leaf litter, lower vegetation and canopy (BRÜHL et al. 1998). Likewise, tropical ant activity is often higher in the canopy than in the litter environment, and species composition differs between the canopy and litter assemblages (Yanoviak and Kaspari 2000). A study in natural ecosystems comparing forest and savanna found species richness to be affected by habitat and strata (ground and vegetation); the two environments clearly differentiated in terms of their species composition (Blüthgen and Fiedler 2004b). In our study, canopy vegetation was not a strong driver for the community of twig-nesting ants since our best models did not include a VCI. However, species compositional differences observed across both vegetation layers could be an effect of microhabitat diversity (BRÜHL et al. 1998) and canopy connectivity (Powell et al. 2011). Providing complex vegetation not only promotes ant diversity but also other organisms that facilitate ant colonization into new twigs. Presumably ants often nest in hollow branches of trees that have been previously dwelled or inhabited by beetles (Deyrup et al. 2000). Moreover diversity of trees might also provide nesting resources that are different in terms of how difficult or attractive they are to dig cavities, for example studies have found that tropical woods can be different in terms of their structure, chemistry and biology (Perez-Morales et al. 1977); this could suggest important drivers in the differentiation of ants that inhabit them.

We found a large number of arboreal twig-nesting ant species (33) in this coffee agroecosystem study supporting the notion that managed ecosystems, such as agroforestry systems in the tropics, have the potential to host a great diversity of species. A number of previous studies have provided evidence that ant diversity increases control of pests and fungal diseases (Philpott and Armbrecht 2006). We document here that increases in nest entrance size diversity on an individual tree relates to increases in ant diversity on trees. This may thus have important implications for promoting ants as biological control agents in agroforestry systems.

We conclude that the availability of a variety of nesting options (in this case different nest entrance sizes) and vegetation strata are important drivers of species diversity and support the idea that niche partitioning drives species coexistence (Chase 2003). Future studies should further investigate the competitive hierarchies of the species colonizing twigs if we want to understand how species using similar resources interact with each other; and evaluate colony fitness in face of multiple resource use, as has been done in the past for colonies of *Cephalotes persimilis* (Powell 2009). Since ants often engage in interactions that deliver ecosystem services future studies should focus on evaluating roles of different ant combinations using a diverse array of twig entrance sizes in agricultural pest control. Furthermore, we have learned from this study that the structuring of ant communities is multifactorial and that local as well as regional factors should be considered when explaining species assemblages in the tropics.

CHAPTER 3
VEGETATION CONNECTIVITY INCREASES ANT ACTIVITY AND POTENTIAL FOR ANT-PROVIDED BIOCONTROL SERVICES IN A TROPICAL AGROFOREST

Jimenez-Soto, M.E. Morris, J. R. Letourneau, D. Philpott, S.M. In revisions for *Biotropica*

Abstract

In natural and managed systems, connections between trees are important structural resources for arboreal ant communities with ecosystem-level effects. However, ongoing agricultural intensification in agroforestry systems, which reduces shade trees and connectivity between trees and crop plants, may hinder ant recruitment rates to resources and pest control services provided by ants. We examined whether increasing connectivity between coffee plants and shade trees in coffee plantations increases ant activity and enhances biological control of the coffee berry borer, the most devastating insect pest of coffee. Further, we examined whether artificial connections buffer against the loss of vegetation connectivity in coffee plants located at larger distances from the nesting tree. We used string to connect *Inga micheliana* shade trees containing *Azteca sericeasur* ant nests to coffee plants to compare ant activity before and after placement of the strings, and measured borer removal by ants on coffee plants with and without strings. Ant activity significantly increased after the addition of strings on connected plants, but not on control plants. Borer removal by ants was also three times higher on connected plants after string placement. Greater distance from the nesting tree negatively influenced ant activity on control coffee plants, but not on connected plants, suggesting that connections between coffee plants and nest trees could potentially compensate for the negative effects that larger distances pose on ant activity. Our study shows that favoring connectivity at the local scale, by artificially adding connections, promotes ant activity and may increase pest removal in agroecosystems.

Key words

Vegetation connectivity, coffee berry borer, biological control, *Azteca* ants, ant foraging, foraging behavior

Introduction

Habitat complexity is critical for the functioning of ecological communities in both terrestrial and aquatic systems. Processes such as resource foraging, colonization, and species interactions often depend on the level of heterogeneity in the configuration of physical elements in a habitat (Lassau et al. 2005). Vegetation connectivity and structure are important components of habitat complexity and can influence species interactions and community patterns at local scales. In aquatic systems, more complex habitats made up of macrophytes support communities that are more diverse and abundant, and allow for greater food capture than systems without vegetation (Crowder et al. 1998, Warfe and Barmuta 2004). In terrestrial systems, vegetation structure– such as the biomass of foliage and the variety of plant architectures– generally influences species composition, and increases species richness and abundance of numerous taxa (Andersen 1986, Halaj et al. 1998, Langellotto and Denno 2004, Adams et al. 2017). Additionally, vegetation structure can influence mobility and foraging success of vertebrates and invertebrates (Wells et al. 2004, Yanoviak and Schnitzer 2013, Arroyo-Rodríguez et al. 2015, Verdeny-Vilalta et al. 2015).

In tropical ecosystems, ants are among the most abundant and biodiverse of taxonomic groups (Longino et al. 2002), and are considered important predators, herbivores, and seed dispersers (Floren et al. 2002, Davidson et al. 2003, Camargo et al. 2016). Ants are cursorial central-place foragers – organisms that forage from a central place to which they return with food to feed with the colony (Mayo and Benabib 2009). Therefore, foraging and discovery of food resources is strongly constrained by the need to construct and follow trails along vegetation (Farji-Brener et al. 2007, Gordon 2012). This is particularly relevant for ants using the arboreal stratum as their primary foraging space (Apple and Feener Jr 2001, Hashimoto et al. 2006, Tanaka et al. 2010, Arnold et al. 2011). For instance, the availability of vegetation connections (e.g. branches, leaves, vines, lianas, bark, and moss) can maximize ants' foraging efficiency, locomotion, and velocity (Fewell 1988, Torres-Contreras and Vasquez 2004, Clay et al. 2010), as well as contribute to changes in community composition and species richness (Lassau et al. 2005, Yanoviak and Schnitzer 2013, Yanoviak et al. 2016, Adams et al. 2017). The availability of such resources can ultimately lead to differences in resource utilization by ant communities (Ozaki et al. 2000, Cogni et al. 2003).

In tropical agricultural systems, especially agroforests, ants play important ecological roles (Clausen 1940a, Leston 1973, Offenberg 2015), and management practices can strongly influence ant behavior and their potential for providing biological pest control services (Armbrecht and Gallego 2007, Teodoro et al. 2010, Abdulla et al. 2016). Indeed, one of the oldest known records of the use of ants for pest control dates to 304 A.D in citrus plantations in China. In these systems artificial connections made of bamboo were used by farmers to facilitate foraging by the Weaver Ant (*Oecophila smaragdina*) to suppress damaging phytophagous insects (Huang and Yang 1987). In that same study, Huang and Yan (1987) report anecdotal evidence that suggests equal yields in orchards that use chemicals vs. orchards that use ant bridges to control for pests. Similarly, Peng et al. (2014), report lower levels of fruit damage in cashew with the presence of weaver ants. However, as vegetation complexity declines in agroecosystems, tree density and diversity may also decrease (Moguel and Toledo 1999, Bos et al. 2007), as well as the possibility to generate connections between the arboreal vegetation, which might impact arthropod populations (Bos et al. 2007). The lack of connectivity between trees in managed systems can have a significant impact on the mobility of worker ants and their ability to control resources. This impact may be particularly marked at greater distances from the nest, where ant dominance may be lower (Ennis 2010). This in turn may influence the ecosystem services provided by ants, particularly the suppression of pest outbreaks (Ozaki et al. 2000).

Shaded coffee plantations, which maintain high levels of shade and structural complexity (Moguel and Toledo 1999) can sustain complex networks of organisms, which can result in biological pest control (Vandermeer et al. 2010). In coffee systems, ants are a functionally diverse and abundant group of ground and arboreal-nesting arthropods and are considered important biological control agents (Philpott and Armbrecht 2006, Morris et al. 2018). Ants are predators of the most devastating coffee pest, the coffee berry borer (CBB) (*Hypothenemus hampei*), a beetle that drills cavities in coffee berries and severely damages the seed (Barrera 2002, Camilo et al. 2003). Several species of arboreal ants, with nests attached to or inside tree trunks, branches, or twigs, control adult and immature stages of this pest either through direct predation or deterrence (Larsen and Philpott 2010, Gonthier et al. 2013, Morris and Perfecto 2016). Ants of the genus *Azteca* are numerically dominant in shaded coffee plantations. These ants forage intensively on coffee plants (as a result of an ant-hemipteran mutualism), and deter CBB adults by removing them from the coffee plant, therefore lowering fruit damage (Jiménez-Soto et al. 2013). In shaded coffee plantations, *Azteca sericeasur* ants nest on shade trees (Vandermeer et al. 2010) and access adjacent coffee plants through the leaf litter or available pathways, such as fallen branches, vines, and other vegetation (*personal observation*), matching the description by Longino (Longino 2007b) for this species in forest habitats. In more intensively managed coffee systems, with fewer and more distant nesting trees, connectivity may be sparse or absent and artificial connections might buffer against this loss. Vegetation structure and arboreal characteristics in coffee plantations are likely to be important factors influencing ant foraging behavior and nesting in arboreal ants (De la Mora et al. 2013, Urrutia-Escobar and Armbrecht 2013). However, the influence of vegetation connectivity on the foraging of this dominant arboreal ant, and its effect on pest removal in coffee plantations has not yet been studied.

Previous work has documented the importance of arboreal connections for ants and biological control in agricultural systems. For example, various studies and farmers' manuals suggest that connecting nests to adjacent trees using bamboo strips enables weaver ants to colonize new trees, which increases ants' efficiency in removing pests, including the pentatomid insect *Tesserarotoma papillosa* (Huang and Yang 1987, Van Mele and Vayssières 2007, Van Mele and Cuc 2007, Peng and Christian 2014). However, there is little evidence about the effect of increasing arboreal connectivity on biological control using experimental data. We report an experiment testing the influence of adding connections between shade trees and coffee plants and its effects on CBB removal on coffee plants. To our knowledge, this is the first study providing experimental data on the effect of adding connectivity on ant activity and pest removal in coffee agroecosystems. Specifically, we tested one hypothesis: connectivity affects CBB removal in this system by increasing recruitment rates of *A. sericeasur* ants to prey items; we predicted that 1) *A. sericeasur* ants use artificial connections between nesting trees and coffee plants; 2) plants with connectivity have higher ant activity than isolated plants; 3) plants with connections have grater removal rates of CBB by *A. sericeasur* ants; and 4) *A. sericeasur* activity and CBB removal rates by *A. sericeasur* ants decrease with increased distance from *A. sericeasur* nests.

Methods

Study site

We conducted the study in a 300 ha shaded coffee plantation in the Soconusco region of Chiapas, Mexico. The coffee plantation is located at 1100 m a.s.l. in the Sierra Madre de Chiapas Mountains. The natural vegetation types are high and mid-elevation perennial forest and the climate is semitropical with rainfall typically occurring between May and October (4000-5000 mm annually). The coffee plantation can be characterized as a commercial polyculture, where coffee plants grow under the canopy of shade of trees, mostly in the genus *Inga* (Fabaceae: Mimosoideae) (Moguel and Toledo 1999), providing an average canopy cover of 75% (Pak et al. 2015).

Field experiment

Within the farm, we haphazardly selected 20 non-overlapping sites located at least 10 m away from each other with one *Inga micheliana* tree containing an *A. sericeasur* carton nest on the tree trunk (referred to as the nesting tree). *A. sericeasur* is a polydomous, arboreal ant species (Longino 2007b), which occurs in ~13% of trees at our study site (unpublished data), and forages on coffee plants (Vandermeer et al. 2010). Trees were selected only if ant nests were noticeably active. In each site, we quantified ant activity on the nest tree as the number of ants crossing a single point on the main trunk during one minute. This methodology has been used in previous studies to measure overall ant activity of a nest (Perfecto and Vandermeer , Liere and Larsen). We then selected the six coffee plants nearest to the nesting tree, making sure they were not directly touching each other or the tree by removing branches and vines (Fig. 1). We then randomly assigned three of the coffee plants at each site to a connection treatment and three as controls without connections, then measured ant activity on the plants by counting the number of ants passing a point on the central trunk for one minute. We connected treatment coffee plants (from the main trunk) to the nesting tree (as near as possible to the *A. sericeasur* nest) using jute string (0.95 cm of thickness) (Fig. 1). Strings remained in the field for three days to allow for ant acclimation to disturbance and for ants to establish new foraging pathways. After three days, we returned to the sites and re-measured ant activity on the nesting tree and coffee plants. Observations took place between 10 am and 1 pm, and were immediately stopped as soon as it started raining, as this drastically decreases ant activity.

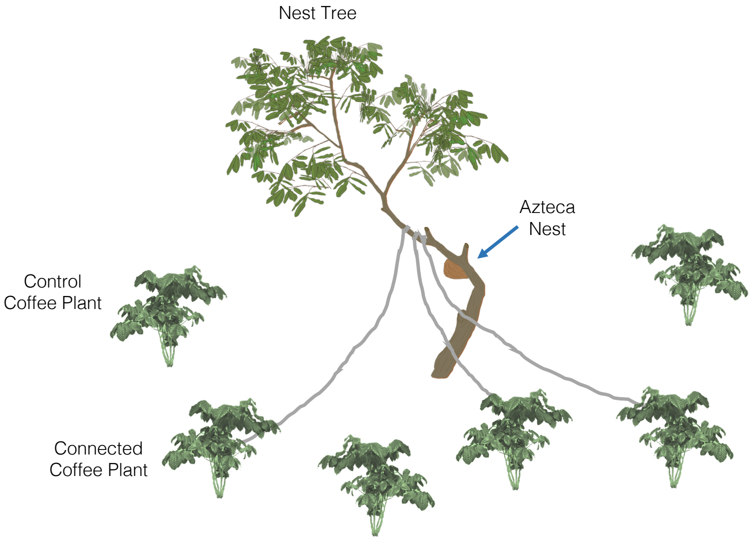


Figure 1 *Diagram of experimental setup after the placement of strings.*

To test how connectivity impacts potential biological control provided by ants, we added dead adult CBB onto connected and control coffee plants to directly assess ant removal rates. We collected CBB infested coffee berries from the field, dissected them, extracted female adult CBB individuals (only mature females bore into berries), and placed them in the freezer for up to 24 h, after which beetles were dead. Three days after placing strings and after reassessing ant activity, we placed 10 dead CBB adults on a small piece of white card on each coffee plant near the center of the trunk, left cards for 30 min, and then counted the number of CBB remaining. Cards were balanced on coffee branches and were bend slightly to keep the CBB from falling. Restricting movement of sentinel prey, either by gluing them to observation sites or freezing them is a common technique for assessing predator behavior (Armbrecht and Perfecto 2003, De la Mora et al. 2015). We used frozen (dead) sentinel prey to increase the availability and similarity of beetles on cards and to reduce the potential for live prey to escape from the arena. To assess whether CBB removal was due to ant activity, we monitored cards across the plot over a period of 30 minutes (we walked around the experiment and observed ant behavior, such as encounter and handling of CBB) and recorded any arthropods present. Only ants were observed on the cards, indicating that these were responsible for removing the CBB. Although we acknowledge that the use of dead prey may alter ant behavior, it is already well established that *A. sericeasur* both antagonizes and predates live CBB in the field, and reduces CBB infestation on plants (Gonthier et al. 2013, Jiménez-Soto et al. 2013, Morris et al. 2015, Morris et al. 2018). We used dead prey in this experiment to more readily assess ant removal rates and infer that these changes translate to changes in the biocontrol efficiency of this ant on live prey.

Immediately following each experiment, we characterized the vegetation in each site because several different environmental factors are known to influence ant foraging in coffee systems (Nestel and Dickschen 1990). We measured the percentage of canopy cover (using a spherical densiometer), coffee plant height, and distance from each coffee plant to the central *Inga* nest-tree.

Data analysis

Ant Activity on Nest Tree

To test for statistical differences in ant activity on nest trees before and after connecting trees to coffee plants, we fit our data to a generalized linear mixed model (GLMM). We included time (before and after string placement), canopy cover, and their interaction as fixed effects (Table 1a). We also modeled nest tree identity as a random effect. To assess count data (our response variable) we originally fit our model to a Poisson distribution with a log link function. However, to correct for observed over-dispersion, we modified our model to a Poisson-lognormal distribution by adding a per-observation random effect term (Elston et al. 2001).

Table 1. *Model selection table with Akaike information criterion (AIC) and ΔAIC for generalized linear mixed models (GLMMs) of (a) ant activity on nest trees, (b) ant activity on coffee plants, and (c) coffee berry borer (CBB) removal. Models were selected based on AIC comparisons, where a full model of biologically relevant terms was included, along with subsequent models of different covariate combinations and a null intercept-only model of random effects. Best fit was determined via backwards model selection compared to the full model, where the model that resulted in the lowest AIC score with ΔAIC > +2 was selected. RE indicates random effects and asterisks indicate interaction terms. The selected model is shown in bold.*

Model	df	AIC	ΔAIC
(a) Ant Activity on Nest Tree			
~Time*Canopy Cover + RE	6	315.72	0.00
~Time + Canopy Cover + RE	5	314.32	1.40
~Canopy Cover + RE	4	313.24	2.48
~Time + RE	4	312.64	3.08
~RE	**3**	**311.56**	**4.16**

(b) Ant Activity on Coffee Plant			
~Treatment*Time + Treatment*Distance + Coffee Height + Tree Activity + RE	**11**	**1123.46**	**0.00**
~Treatment*Time + Treatment*Distance + Tree Activity + RE	10	1125.87	-2.41
~Treatment*Time + Treatment*Distance + Coffee Height + RE	10	1145.70	-22.24
~Treatment*Time + Treatment*Distance + RE	9	1148.17	-24.71
~RE	4	1185.37	-61.91
(c) CBB Removal on Coffee Plant			
~Treatment*Distance + Treatment*Plant Activity + Tree Activity + Coffee Height + RE	**10**	**372.26**	**0.00**
~Treatment*Distance + Treatment*Plant Activity + Tree Activity + RE	9	372.98	-0.72
~Treatment*Distance + Treatment*Plant Activity + Coffee Height + RE	9	409.16	-36.90
~Treatment*Distance + Treatment*Plant Activity + RE	8	408.18	-35.92
~RE	3	427.46	-55.20

Ant Activity on Coffee Plants

To test for statistical differences in ant activity on coffee plants before and after establishing connections we used a GLMM. We included time (before and after string placement), treatment (connected vs. control plants), coffee plant distance to nest tree, the interaction between time and treatment, and the interaction between time and distance as fixed effects (Table 1b). We also included coffee plant height and ant activity on nest tree as covariates. Random effects were modeled with plant identity nested within site (nest tree identity) to account for the block design of the experiment (spatial non-independence) and to control for variation between our sites. To model count data and to correct for overdispersion, we used a Poisson-lognormal model with a log link function by including a per-observation random effect as described above (Elston et al. 2001).

Coffee Berry Borer Removal

We modeled CBB removal by ants using a GLMM. We included treatment (connected vs. control plants), coffee plant distance to nest tree, ant activity on coffee plants after string placement, the interaction between treatment and distance, and the interaction between treatment and ant activity on plants as fixed effects (Table 1c). We also included ant activity on nest tree and coffee plant height as covariates. Random effects were modeled with plant identity nested within site (nest tree identity) to account for the block design of the experiment (spatial non-independence) and to control for variation between our sites. To model count data in our response variable we used a Poisson distribution with a log link function.

Model Selection and Inference

We constrained model selection to include biologically pertinent terms for inference and to aid in model interpretation. A full model of these terms was tested, along with subsequent models of different covariate combinations and a null intercept-only model of random effects (Table 1). The best fit model was determined via backwards model selection compared to the full model, where the model that resulted in the lowest AIC score with ΔAIC > +2 was selected.

Overall significance in models was assessed using Wald type II Chi-squared tests. Statistical differences among treatments were compared by Wald Z tests (Table 2 & 3). In all cases, fixed effect parameters and the variance of random effects was estimated by maximum likelihood with Laplace approximation using the ‘glmer’ function in the ‘lme4’ package in R (R-Development-Core-Team 2014). To aid in data interpretation, we removed one coffee plant replicate from our analysis where measured ant activity was more than double that of any other plant measured and may have resulted from an unusually high buildup of scale insects which are tended by *A. sericeasur* on coffee. Additionally, one nest tree replicate was not included in the tree activity analysis because the data were not collected at that site. Finally, coffee plant height and distance to nest tree were centered and scaled to aid model interpretation. All analyses were performed in R (R-Development-Core-Team 2014).

Results

We observed *A. sericeasur* ants using artificial connections at all sites (Fig. 2a) and on 75% of all strings placed in the field. Other ant species such as *Cephalotes basalis* and *Pseudomyrmex simplex* co-occurred with *A. sericeasur* ants on the strings (Fig. 2b), but not on the cards.

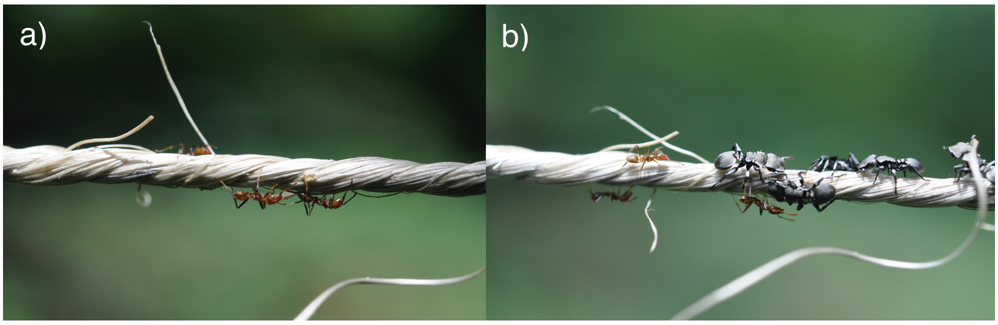


Figure 2. Azteca sericeasur *workers cross from the nesting tree to coffee plants on strings that simulate arboreal connections (a) and co-occur with other ants, such as Cephalotes basalis (b).*

Ant Activity on Nest Trees

Although there was an 18.6% increase in ant activity on nest trees after experimental set up (Fig. 3a), including time (before and after string placement) in our model did not improve its explanatory power. Canopy cover also varied from 53% to 94% among sites, however, including it as a factor did not improve model fit. The GLMM that best explained ant activity on trees was our null intercept-only model (Table 1a). Thus, we did not further assess statistical significance for our model of ant activity on nest trees.

Ant Activity on Coffee Plants

The model that best predicted ant activity on coffee plants included time (before and after string placement), treatment (connected vs. control plants), coffee plant distance to nest tree, the interaction between treatment and distance, and the interaction between treatment and ant activity on plants as fixed effects (Table 1b). This model also included coffee plant height and ant activity on nest tree as covariates.

Overall, ant activity increased in coffee plants after the placement of strings (χ^2=14.94, p<0.001, Fig. 3b). However, this effect was only significant in connected coffee plants (z=4.83, p<0.001, Table 2), which increased in activity by 163.4% after string placement, as opposed to only a 56.4% increase in control coffee plants (z=0.48, p=0.635, Table 2). The significant interaction between time (before and after string placement) and treatment (connected vs. control) in our model (χ^2=8.58, p=0.003), indicates that there was a significantly greater increase in ant activity on connected plants than on control plants after string placement (Fig. 3b).

Distance between coffee plants and nest trees varied from 0.65 to 3.5 m. Overall, ant activity significantly decreased as the distance of coffee plants from nest trees increased (χ^2=5.54, p=0.019). However, after string placement (Fig. 2) this effect was only significant in control plants (z=-3.11, p=0.002, Table 2), whereas connected plants had lower decreases in ant activity with distance (z=-

0.44, p=0.659, Table 2), as indicated by the significant interaction term between treatment and distance in our model (χ^2=4.23, p=0.040). Additionally, coffee plant height varied from 0.2 to 3.0 m and explained some of the variation in plant ant activity (χ^2=4.59, p=0.032); however, ant activity on the nest tree was not a significant covariate in our model (χ^2=3.39, p=0.066).

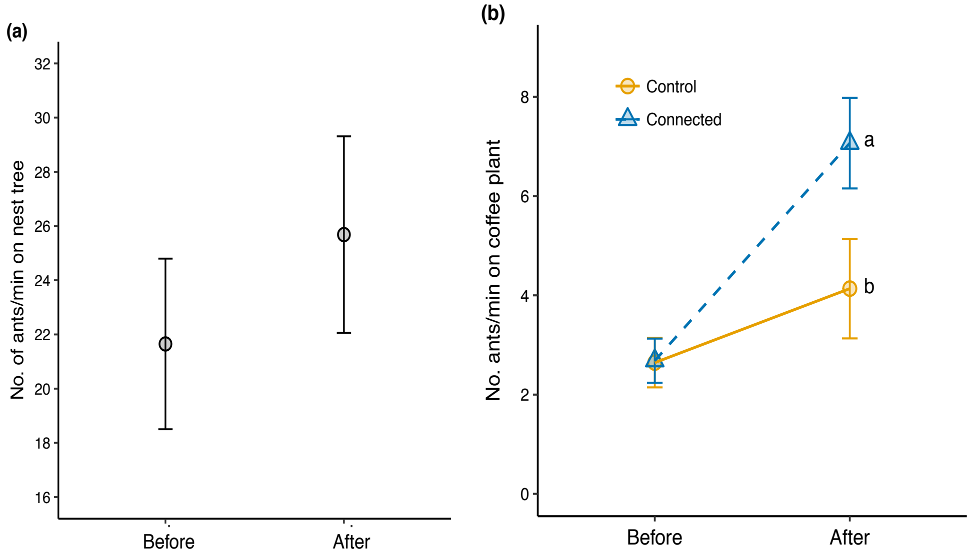


***Figure 3**. Azteca sericeasur activity on nest trees (a) and on coffee plants (b), before and after the placement of strings. In (b), different letters represent a statistically significant interaction ($p<0.05$) between treatment (control vs. connected) and time (before and after string placement), indicating a greater overall increase in activity on connected plants. Bars=Mean (± SE).*

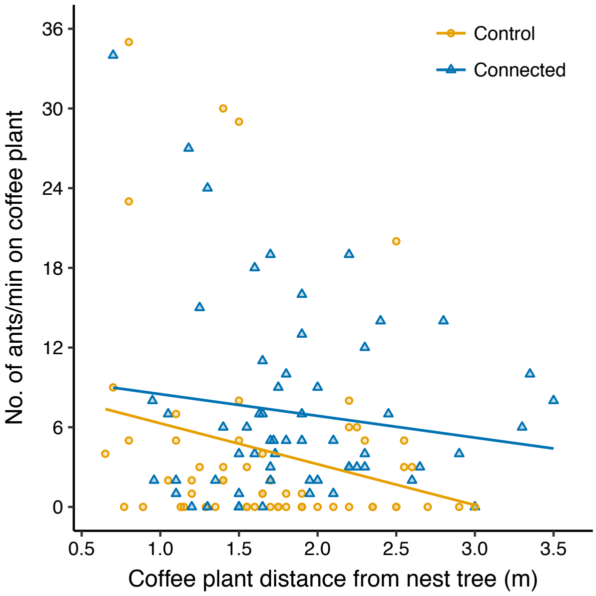


Figure 4 *Azteca sericeasur activity on coffee plants after the placement of strings as a function of distance from the nest tree. In our GLMM, ant activity significantly declined with increasing distance in control plants (z=-3.11, p=0.002), but not in connected plants (z=-0.44, p=0.659), as indicated by the significant interaction between treatment and distance (χ^2=4.23, p=0.040).*

Table 2. *Model results for our generalized linear mixed model of ant activity on coffee plants with parameter estimates (±SE), Wald Z scores, and p-values. Each output group shows the results for each possible set of references for the categorical variables treatment (connected vs. control) and time (before vs. after placement of strings). Asterisks indicate an interaction and significant (p<0.05) model terms are shown in bold.*

Parameter	Estimate (± SE)	z value	Pr(>|z|)
Reference: *Treatment (control); Time (before)*			
(Intercept)	-0.127 ± 0.277	-0.457	0.648
Treatment (connected)	0.174 ± 0.257	0.676	0.499
Time (after)	0.115 ± 0.242	0.475	0.635
Distance	**-0.472 ± 0.152**	**-3.102**	**0.002**
Tree Activity	0.014 ± 0.008	1.847	0.065
Plant Height	**0.233 ± 0.109**	**2.132**	**0.033**
Treatment(connected)*Time(after)	**0.950 ± 0.324**	**2.930**	**0.003**
Treatment(connected)*Distance	**0.409 ± 0.200**	**2.048**	**0.041**
Reference: *Treatment (control); Time (after)*			
(Intercept)	-0.010 ± 0.305	-0.032	0.975
Treatment (connected)	**1.124 ± 0.249**	**4.525**	**<0.001**
Time (before)	-0.116 ± 0.242	-0.479	0.632
Distance	**-0.474 ± 0.152**	**-3.113**	**0.002**
Tree Activity	0.014 ± 0.008	1.840	0.066
Plant Height	**0.234 ± 0.109**	**2.142**	**0.032**
Treatment(connected)*Time(before)	**-0.951 ± 0.325**	**-2.929**	**0.003**
Treatment(connected)*Distance	**0.411 ± 0.200**	**2.056**	**0.040**
Reference: *Treatment (connected); Time (before)*			
(Intercept)	0.049 ± 0.272	0.180	0.857
Treatment (control)	-0.175 ± 0.257	-0.679	0.497
Time (after)	**1.067 ± 0.221**	**4.834**	**<0.001**
Distance	-0.063 ± 0.139	-0.456	0.649
Tree Activity	0.014 ± 0.008	1.837	0.066
Plant Height	**0.233 ± 0.109**	**2.137**	**0.033**
Treatment(control)*Time(after)	**-0.951 ± 0.325**	**-2.930**	**0.003**
Treatment(control)*Distance	**-0.411 ± 0.200**	**-2.058**	**0.040**
Reference: *Treatment (connected); Time (after)*			
(Intercept)	**1.114 ± 0.278**	**4.009**	**<0.001**
Treatment (control)	**-1.125 ± 0.249**	**-4.525**	**<0.001**
Time (before)	**-1.068 ± 0.221**	**-4.835**	**<0.001**
Distance	-0.061 ± 0.139	-0.442	0.659
Tree Activity	0.014 ± 0.008	1.842	0.065
Plant Height	**0.233 ± 0.109**	**2.135**	**0.033**
Treatment(control)*Time(before)	**0.952 ± 0.325**	**2.932**	**0.003**
Treatment(control)*Distance	**-0.413 ± 0.200**	**-2.068**	**0.039**

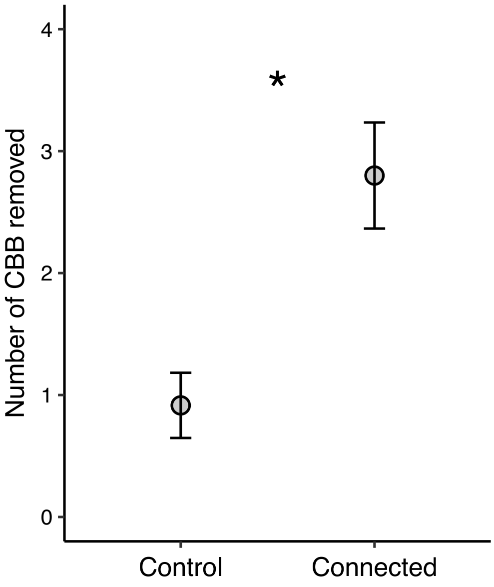
Coffee Berry Borer Removal

The GLMM that best explained CBB removal was our full model, which included treatment (connected vs. control), coffee plant distance to tree, ant activity on coffee plants after string placement, the interaction between treatment and ant activity on plants, and the interaction between treatment and coffee plant distance as fixed effects (Table 3c). This model also included coffee plant height and ant activity on the nest tree as covariates.

CBB removal was nearly three times higher on connected coffee plants than on control coffee plants (χ^2=9.82, p=0.002, Fig. 5). Overall, the effect of coffee plant ant activity on CBB removal was significant (χ^2=7.91, p=0.005, Fig. 6); however, this effect was significant on control plants (z=2.35, p=0.019, Table 3), but only marginally significant on connected plants in our model (z=1.80, p=0.071, Table 3). Despite this, the interaction between treatment (control vs. connected) and ant activity on coffee plants was not significant (χ^2=0.15, p=0.699), indicating that ant activity on coffee plants and treatment independently drive CBB removal. CBB removal rate was not significantly affected by distance to the nesting tree (χ^2=0.37, p=0.545). Additionally, neither coffee plant height nor ant activity on nest tree were significant covariates in our model (Table 3). Although we chose the full model based on the lowest AIC value as explained in our methods, it should be noted that the second best model (with a ΔAIC of -0.72) does not include coffee height, which suggests that it may not be a very important variable for determining the removal rate of CBB.

Table 3. *Model results for our generalized linear mixed model of coffee berry borer removal (CBB) by ants with parameter estimates (±SE), Wald Z scores, and p-values. The two output groups show the results for both references of the categorical variable treatment (connected vs. control). Asterisks indicate an interaction and significant (p<0.05) model terms are shown in bold.*

Parameter	Estimate (± SE)	z value	Pr(>|z|)
Reference: *Treatment (connected)*			
(Intercept)	**-1.281 ± 0.605**	**-2.117**	**0.034**
Treatment (control)	**-1.481 ± 0.554**	**-2.673**	**0.008**
Distance	0.018 ± 0.263	0.067	0.947
Plant Activity	0.064 ± 0.036	1.804	0.071
Plant Height	0.397 ± 0.240	1.658	0.097
Tree Activity	0.026 ± 0.015	1.711	0.087
Treatment(control)*Distance	-0.404 ± 0.414	-0.974	0.330
Treatment(control)*Plant Activity	0.014 ± 0.047	0.292	0.771
Reference: *Treatment (control)*			
(Intercept)	**-2.742 ± 0.642**	**-4.272**	**<0.001**
Treatment (connected)	**1.540 ± 0.553**	**2.783**	**0.005**
Distance	-0.361 ± 0.326	-1.106	0.269
Plant Activity	**0.081 ± 0.035**	**2.347**	**0.019**
Plant Height	0.387 ± 0.238	1.625	0.104
Tree Activity	0.025 ± 0.014	1.777	0.076
Treatment(connected)*Distance	0.385 ± 0.412	0.934	0.350
Treatment(connected)*Plant Activity	-0.018 ± 0.047	-0.387	0.699



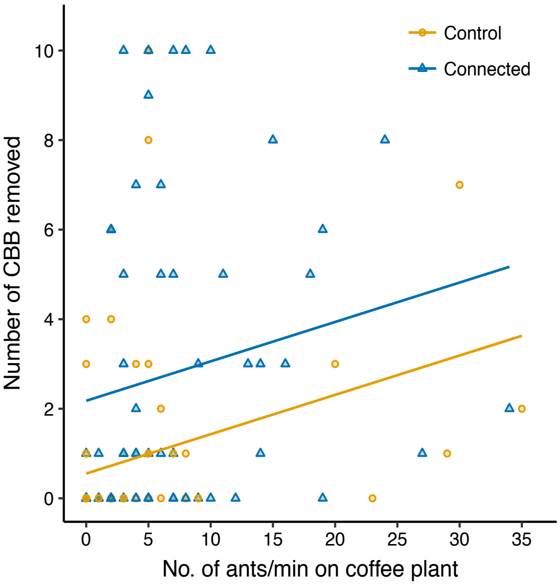


Figure 5. *Coffee berry borer (CBB) removal in control and connected coffee plants after string placement. Bars=Mean (± SE). The asterisk represents a statistically significant difference ($p<0.05$).*

Figure 6. *Number of coffee berry borers (CBB) removed after string placement as a function of ant activity on the coffee plants. In our GLMM, the effect of ant activity on CBB removal was significant on control plants ($z=2.35$, $p=0.019$), but only marginally significant on connected plants ($z=1.80$, $p=0.071$). However, the interaction between treatment and ant activity on coffee plants was not significant ($\chi^2=0.15$, $p=0.699$).*

Discussion

Our experiment demonstrates that the addition of string to connect shade trees and coffee plants in coffee agroecosystems facilitates movement for *A. sericeasur* and potentially increases ant recruitment rates. Studies in natural systems have reported increases in ant activity with arboreal connections across the arboreal stratum (Yanoviak 2015), possibly driven by the easy access these pathways provide to resources (Clay et al. 2010). Other ants, such as *Pogonomyrmex* spp. prefer linear arboreal substrates and switch to cleared routes as a mechanism to reduce the energetic costs of ant foraging (Fewell 1988), and in some cases to decrease the risk of encountering predators (Catling 1997, Yanoviak et al. 2011).

The observed increase in ant activity on connected coffee plants after the placement of strings suggests that structural connectivity can increase ant recruitment rates to foraging areas in coffee and may enhance the efficiency of movement for *A. sericeasur*. This may lead to increased foraging efficiency for ants and enhanced resource capture rates on coffee. However, this could also reflect other benefits associated with using linear arboreal substrates, such as avoiding predators, a behavior that is known to occur in *A. sericeasur* (Philpott et al. 2009). Using more efficient foraging pathways and thereby avoiding the leaf litter as a primary foraging substrate may potentially protect *A. sericeasur* workers from the attack of the phorid fly parasitoid *Pseudacteon* spp. (Philpott et al. 2009).

While ant activity only significantly increased after string placement on connected coffee plants, we also observed lesser increases in ant activity on control coffee plants and nest trees (Fig. 9). This unexpected result could mean that strings, a novel element in the environment, acted as a form of habitat modification or disturbance, which increased overall ant activity in the local area. However, if our manipulation were the cause, we would have expected the ants to attack the jute strings (e.g., Risch *et al.* 1977), a behavior that we did not observe during the experiment. Experiments in tropical forests have shown that the long-term removal of lianas can influence ant richness on trees (Yanoviak and Schnitzer 2013), and therefore may possibly also affect overall ant abundance and activity when promoted. It is also possible that other factors could potentially explain this result in control plants, such as changes in local abiotic factors that we did not measure systematically in our experiment. Future research which expands on the temporal scope of this study may be useful in assessing the long-term effects of artificial connectivity in this system.

Ant activity post string placement was negatively affected by distance to the nesting tree (Fig. 10). This result is consistent with previous studies suggesting that within 5 meters *A. sericeasur* dominance in the leaf litter decreases with distance to the nesting tree (Philpott et al. 2004, Ennis 2010). However, in our study, the effect of distance after string placement was significant only on control plants, but not on connected plants. This suggests that connections could buffer the negative effects that larger distances from the nesting tree pose to ant activity and potentially increase ant-provided biological control services in these plants.

Connected coffee plants also had significantly higher CBB removal than control plants (Fig. 11). Overall, greater ant activity on coffee plants was associated with higher CBB removal rates (Fig. 12), suggesting that ant activity directly influenced CBB removal rates. However, while this effect was significant on control coffee plants it was only marginally significant on connected plants. While we believe that these results support the hypothesis that connectivity enhances ant foraging and biocontrol services on coffee, the use of dead CBB in this experiment as a proxy to measure biocontrol may explain the only marginally significant effect of ant activity on CBB removal in connected plants. It is possible that dead prey exhibit more variable recruitment responses from ants than live prey. Despite this, it is likely that strings facilitated ant movement to coffee plants by providing a smooth, linear substrate and indirectly increased CBB removal (Clay et al. 2010). In other systems, the leaf-cutting ant *Atta cephalotes* uses fallen branches to rapidly move between areas and thereby quickly discover new food resources (Farji-Brener et al. 2007). Similarly, these resources allow scouts to return quickly to the colony, minimizing the time taken for information transfer and recruitment of other foraging workers (Farji-Brener et al. 2007). The role of trunk trails and fallen branches has received extensive attention in the leaf-cutting ant system, however, fewer studies have looked at the influence of connectivity resources on foraging behavior of predatory arboreal ants.

Surprisingly, CBB removal did not follow the same trend as ant activity with distance to the nesting tree. While control plants tended to have lower CBB removal rates than connected plants as distance to the tree increased, we did not find a significant effect of distance on CBB removal in either control or connected plant groups. Collectively, these results suggest that connections in the arboreal stratum have the potential to increase ant activity and therefore enhance plant protection from CBB attack, particularly in connected plants. Further studies should assess the effect of distance on CBB removal using plants located at distances larger than 3.5 m from the tree.

It is important to note the potential for negative impacts of enhanced ant activity on coffee plants resulting from hemipteran tending behavior. While ant activity can increase the density of green coffee scale insects, which may harm coffee plants and reduce coffee productivity, the scale are not a major pest in the region of study, and are not as economically significant as the coffee berry borer (Morris et al. 2018). A recent study evaluating the benefits associated with the indirect *Azteca*-*Coffea* mutualism, which emerges from the *Azteca*-scale mutualism, found that the protective benefit ants provide to coffee plants is positively associated with high densities of the scale (Rivera-Salinas et al. 2018). Therefore, it is possible that enhanced CBB control associated with scale-tending by ants outweighs the costs associated with scale damage. However, these interactions may be context-dependent, and still need to be fully evaluated in the field to provide a holistic understanding of the impact of connectivity on scale density and coffee yield.

Other ant species could also benefit from the addition of connections between coffee plants and shade trees, such as *Cephalotes basalis* and *Pseudomyrmex simplex*, which were observed using these connections during our study. The ant *P. simplex* has been previously reported as an important CBB biocontrol agent, acting in conjunction with other species of ants to effectively suppress CBB at various life stages (Philpott et al. 2008, Morris et al. 2018).

Therefore, this technique could support *Azteca* ants as well as other ant species that play an important role in suppressing CBB populations.

Our results support the general hypothesis that connectivity, one measure of habitat complexity, can sustain important ecological processes in natural and managed ecosystems. In aquatic systems, more complex habitats with macrophytes allow for greater food capture and maintain higher levels of diversity (Crowder et al. 1998, Warfe and Barmuta 2004). In terrestrial systems, higher complexity can influence trophic dynamics (Polis and Strong 1996, Sanders et al. 2008). In coffee agroecosystems, ants are highly sensitive to habitat change and management intensification, generally expressed as the reduction of shade, elimination of epiphytes, and use of chemical inputs (Roth et al. 1994, Armbrecht et al. 2005, Floren and Linsenmair 2005, Philpott et al. 2008). Such intensification can have a negative effect not only on vegetation connectivity and ant foraging, but may also cascade to affect ecosystem services, such as biological control. Our study supports the idea that promoting complexity at a local scale, in this case providing structural resources for ants in agroecosystems, can significantly enhance connectivity within the arboreal strata, and potentially improve biological control of coffee pests. This idea has already been successfully implemented in other agricultural systems, placing "ant bridges" made of bamboo strips or strings connecting neighboring trees in (DeBach 1964; Van Mele *et al.* 2009), and could be incorporated as a management strategy in coffee systems.

Future research should evaluate the practical feasibility of adding connections between vegetation strata to enhance biocontrol. For example, studies in timber plantations have estimated that the presence of ants increases timber production by 40%, and that ants can be maintained at lower costs by providing intra-colony host tree connections using rope, poles or lianas (Offenberg 2015). It is important that future studies in coffee also consider the costs of other CBB control methods, such as the application of the pesticide endosulfan, which can lead to the development of resistance, can negatively impact natural enemies, and can have harmful impacts on human health (Damon 2000, Jaramillo et al. 2006). Further investigation into promoting ant biocontrol with artificial connections in coffee should: 1) assess economic tradeoffs, management applicability, and farmers' perceptions of this method in large and small coffee plantations, 2) compare the cost between string placement and other management approaches (e.g. pesticides, entomopathogens), and 3) assess coffee yields on connected and not connected plants to provide management recommendations.

More broadly, incorporating conservation biocontrol strategies in combination with vegetation connectivity is consistent with criteria identified as key for the sustainability of biological control, such as increasing local habitat quality and enhancing species' dispersal ability (Perfecto et al. 1996, Tscharntke et al. 2005). Generally, the maintenance of shade trees and natural vegetation in agroforestry systems may increase vegetation complexity and natural connectivity between plants to promote ant foraging and subsequent biological pest control.

CHAPTER 4
DOES RESOURCE ACCESS MEDIATE INTERACTIONS BETWEEN TWIG-NESTING ANTS AND PARASITOID WASPS?

Abstract

The diversity and availability of resources as well as habitat complexity are important determinants of species diversity, distribution and interactions. For arboreal ant communities, hexose-dominant resources constitute an important part of their diets and often determine processes such as colonization, reproduction and species interactions. Nesting resources are also considered a key resource shaping community dynamics and even caste evolution in arboreal ants, and individually these resources can mediate species interactions. Currently, more research is needed to understand the interactive effect of food and nesting resources, with the added complexity of environmental context on the outcome of colony life and species interactions. However, given the complications associated with manipulating multiple resources and consumers, studies have focused primarily on competitive interactions around one shared resource. In this study, we examined whether colonization by twig-nesting ants– ants that nest in hollow twigs–, colony size, and parasitoid-host interactions between parasitic wasps and their ant hosts are mediated by the addition of sugar resources, the size of nest entrances and habitat complexity in a coffee agroecosystem. We experimentally manipulated the abundance of nectar resources, the availability of nests with different entrance sizes, and measured habitat complexity. Ant brood was subsequently reared in laboratory conditions to account for parasitism rates. Our study shows that nectar resources are not a limiting factor for this community of ants, and confirms that colonization is largely constrained by nest-entrance size. Although the effect of nectar addition and nest-entrance size on colony reproduction was species-specific, the effect of nest-entrance size was determined by the availability of abundant nectar resources, demonstrating an interactive effect between nesting and nectar resources, and the importance of environmental context shaping processes at the colony level. Habitat complexity varied significantly in our study sites, but it only explained the number of workers and brood in nests of some species. Parasitism was found in nests of *Solenopsis picea*, and was explained only by the number of workers in the nest. Our study suggests that nectar and nesting resources, as well as habitat complexity are important determinants of colony processes in the case of arboreal ants, and that the effect of nesting resources may change as the availability of nectar resources varies in the environment.

Keywords: Nectar resources, arboreal ants, parasitoid-host, Eucharitidae, nectar-mediated interactions

Introduction

The extent to which biotic and abiotic factors shape species interactions and their distributions has been a central focus for community ecologists (Landis et al. 2000, Landis et al. 2005, HilleRisLambers et al. 2012). Included in the wide spectrum of factors shaping community dynamics are the diversity and availability of food resources and habitat complexity; all are important determinants of species diversity, distribution and interactions (Langellotto and Denno 2004, Agrawal et al. 2007). Recent theoretical advances and empirical work in community ecology suggest that further research is needed to understand how resource availability and environmental factors shape species interactions

(HilleRisLambers et al. 2012, Camarota et al. 2015). Specifically, one research gap is in our understanding of how variation in resources along habitat complexity gradients affects species interactions (Chamberlain et al. 2014). However, empirically demonstrating how resources vary and how species respond is methodologically complicated, in the sense that the manipulation of multiple resources and consumers is not always straight forward, especially in complex systems. Consequently, studies have focused primarily on one single resource and– disproportionately– on competitive species interactions. Further, the environmental context in which resources matter is also not well understood and will gain more importance as natural and managed systems continue to experience habitat simplification (Agrawal et al. 2007).

Carbohydrate or sugar resources, predominantly from extrafloral nectaries (EFNs)– vegetative structures that secrete nectar– and hemipteran honeydew, are one of the most widely used food resources by ants and parasitoid wasps (Blüthgen and Fiedler 2004b, Koptur et al. 2015). These stable and high-quality plant and animal exudates represent an important component of ant diets (Tobin 1991, Tobin 1994, Lach et al. 2009b, Byk and Del-Claro 2011). Sugar resources can drive the formation of ant mosaics during colonization and establishment (Davidson 1997, Blüthgen et al. 2000, Blüthgen and Reifenrath 2003, Davidson et al. 2003), influence ant abundance and diversity, and determine foraging decisions (Davidson et al. 2003, Blüthgen and Fiedler 2004a, Marazzi et al. 2013). Nectar and honeydew resources also provide an important source of nutrition for parasitoid wasps and benefit parasitoid egg production, egg viability, growth, and increase lifespan (Van Emden 1963, Koptur 1991, Gentry 2003). Sugar resources can also mediate parasitoid-host interactions. For example, parasitoid wasps often use EFNs to find their hosts, or oviposit near EFNs to increase the probability of encountering hosts that visit EFNs (Koptur 1992). Parasitoid wasps in the Eucharitidae family have developed a set of morphological, chemical and behavioral adaptations that allow them to access ant brood through the use of nectar resources (Carey et al. 2012, Herreid and Heraty 2017). Adult female wasps in this family oviposit near EFNs where ants forage for food (Herreid and Heraty 2017). When planidias emerge, they find their way to ant mandibles as ants feed on EF nectar, hitchhike on ant bodies, and are thus accidentally transported to the nest. Once in the nest, adult ants transfer parasitoid planidias onto their brood during feeding (Herreid and Heraty 2017). Despite the importance of nectar resources for ants and parasitoids, research on nectar-mediated interactions has focused primarily on the benefits of mutualistic interactions to the plant rather than focusing on consumers (Marazzi et al. 2013). For instance, few studies have provided robust evidence about the benefits of nectar resources to ant colony reproduction (Lach et al. 2009a, Byk and Del-Claro 2011), or the mechanisms involved in nectar-mediated multitrophic interactions, such as parasitoid-host interactions (Koptur 1991, Herreid and Heraty). Parasitoids of ants have been previously described as “the missing link” in ant community dynamics because we know very little about how and in which contexts they shape ant communities (Wilkinson and Feener 2007).

Diversity and availability of nesting resources determine ant community structure and species co-occurrence. Nesting resources are a spatially-segregated microhabitat (Klimes et al. 2015) usually taking the form of cavities located in arboreal substrates such as twigs, branches, tree trunks and bark. These cavities can occur naturally when wood-boring beetles build galleries that are then abandoned, leaving vacant cavities suitable for ant colonization (Novais et al. 2017). In natural forests, the diversity of nest cavities available for twig-nesting ants (TNAs)– ants that nest in hollow twigs– influences colonization, the diversity of species, and colony growth (Powell et al. 2011). Similarly, in tropical agroforests a greater diversity of cavity sizes promotes niche differentiation in a community of TNAs, therefore explaining higher species diversity and species co-occurrence (Jiménez-Soto and Philpott 2015). In a similar study, Armbrecht et al. (2004) found that an array of twigs belonging to different tree species increases ant species richness. Furthermore, the close relationship between ants and their nesting resources has evolutionary implications for certain ant species. For instance, workers of *Cephalotes persimilis* choose cavities that match the size of their heads to increase individual nest survival, which has led to the evolution of a specialized head-disk that allows workers to protect their nest from other ant intruders (Powell 2008, 2009). Although it has long been established that microhabitat characteristics affect parasitism, primarily through host concealment (Gross 1993), less is known about the specific role of nesting resources used by hosts (e.g. cavity size and exposure of nests) on parasitism, particularly in social insects. It is possible that nests provide protection for parasitoids and thus constitute an attractive habitat for parasitoid wasps (Lachaud and Pérez-Lachaud 2009), leading to the development of sophisticated mechanisms that allow parasitoids to be integrated into the social life of ant colonies, as in the case of the chemical camouflage displayed by Eucharitidae wasps (Lachaud and Pérez-Lachaud 2009, Howard et al. 2014). Alternatively, characteristics of nesting resources, such as the entrance size, could determine the ability of parasitoids to access the nest. For example, a smaller nest entrance could allow ants to prevent parasitoids from getting in, if large enough to be detected.

Ants and parasitoid wasps respond differently to changes in habitat complexity (Langelloto and Denno, De la Mora et al. 2015, Pak et al. 2015, Lassau and Hochuli, Landis et al. 2000). Natural enemies are generally more abundant when habitat complexity increases, possibly because they are able to find refuge from predators and alternative food sources (Andow 1991, Langellotto and Denno 2004). Habitat complexity enhances predator mobility and colonization (Randlkofer et al. 2010), and therefore may increase host mortality by providing adequate refugia for parasitoids, as has been shown for predator-prey systems (Finke and Denno 2002). Furthermore, parasitoid-host interactions can depend on environmental contexts, as has been already suggested for predator-prey systems (Tylianakis and Romo 2010). For instance, in aquatic systems, diverse predator guilds are less effective when plant structures are more diverse (Warfe and Barmuta 2004), but also the availability of refuges can reduce intraguild predation (Finke and Denno 2002). Various scenarios are possible with parasitoid-host interactions: on the one hand, environmental context could determine the success of parasitoids to find their hosts (for some parasitoids, complex habitats can hinder their searching abilities); on the other hand, more complex habitats could provide more resources to feed when hosts are not abundant enough, allowing their persistence in the environment.

In the specific case of ants and their parasitoids, Wilkinson and Feener (2007) demonstrated that habitat complexity such as the diversity of plant architectures, allows ant hosts to escape parasitism from parasitoid flies. Although there has been considerable progress in our understanding of the role of habitat complexity on parasitoids in general, the interaction between parasitoid wasps and their ant hosts remains poorly understood.

In coffee agroecosystems, ants are considered one of the most abundant and diverse groups of natural enemies (Morris et al. 2018). Besides their relevance for agricultural management, ants are a model system to study questions in community ecology. Ants participate in a variety of species interactions (Philpott and Armbrecht 2006, De La Mora and Philpott 2010, Vandermeer et al. 2010, Gonthier et al. 2013), their abundance and diversity is often explained by the availability of food and nesting resources (Blüthgen et al. 2000, Armbrecht et al. 2006, Jiménez-Soto and Philpott), they are sensitive to habitat disturbance (Lassau et al. 2005), and are potentially regulated by top-down forces such as parasitoids (Lachaud and Pérez-Lachaud). Resource-mediated interactions, in combination with the influence of habitat complexity on both ants and parasitoids, pose an exciting opportunity to investigate whether nectar and nesting resources, and habitat complexity together, mediate important processes in the ant colony life (such as colonization, colony reproduction, and mortality).

In this study, we examined whether colonization by TNA's, colony size, and parasitoid-host interactions between parasitic wasps and their ant hosts are influenced by the addition of sugar resources, the size of nest entrances, and habitat complexity in a coffee agroecosystem. Specifically, we addressed the following questions: (1) Does the addition of nectar and nesting resources of different entrance sizes influence colonization and colony size of TNAs? (2) Does the addition of nectar resources and nest entrance size influence parasitism rates of TNAs? and (3) Is the effect of nectar resources on ant colonization, growth and parasitism context dependent?. We hypothesized that adding nectar resources would result in a higher proportion of colonized nests, larger colony size, and a "preference" for certain ant species to colonize nests of specific sizes. Further, we expected to find a higher proportion of parasitized ant pupae with nectar addition, and lower parasitism rates in nests with a smaller entrance size. Finally, we hypothesized that ant colonization, colony size, and parasitism would be higher in more complex habitats.

Methods

Study site description

This study took place within a 300 hectare organic, shaded coffee agroecosystem located at 1000 m a.s.l. in the Sierra Madre mountains of the Soconusco region in Chiapas, Mexico. The climate is semitropical with rains between May and October. The annual rainfall varies between 4000-5000 mm. The agricultural management is categorized under "commercial polyculture" with a percent canopy cover that varies from 50% to 91% (Pak et al. 2015), where trees of the genus *Inga* (Fabaceae: Mimosoideae) dominate the coffee landscape.

Within the agroecosystem, we established 20 sites, each separated from each other by 15 m. Each site consisted of two *Inga micheliana* trees that were randomly selected from a map. *I. micheliana* trees were selected making sure there were no *Azteca sericeasur* ants nesting on the selected trees or trees within 10 m. We characterized habitat complexity in each site. We measured percent of canopy cover 2 m to the N, S, E and W of each tree with a densitometer. Within 5 m of each tree, we counted the number of coffee plants, measured weed height, estimated the percent of ground covered with weeds, and measured height and circumference of all trees. We constructed a Vegetation Complexity Index (VCI) using the vegetation data. We calculated index values for vegetation surrounding each tree by dividing the values of each variable by the highest observed value across all trees for each variable. Then we took the average across the two trees within one site to obtain a single value between 0 for low vegetation complexity and 1 for high vegetation complexity.

Resource addition

To evaluate the effect of nectar and nesting resources on colonization and colony size of TNAs, we added artificial nectaries and artificial nests made of bamboo to each of the two *I. micheliana* trees in each plot. The artificial nectaries consisted of 2 bottles affixed with 4 2ml Eppendorf tubes filled with either nectar or water, and emerging cotton strings to deliver the liquid to insect visitors (Fig. 1a). The nectar solution consisted of one part of nectar (*First Nature*®, clear hummingbird nectar) and three parts of water. We randomly assigned one tree in each site to either the sugar treatment and the other to the control treatment. We added one artificial nectary device per tree at a manageable height of 3 m approximately, reachable with a standard aluminum ladder. We replenished both sugar and water solutions to 1.5 ml every two weeks and monitored ant activity on the devices. Artificial nectaries remained in the field for 3 months during the rainy season.

We added artificial nests made from bamboo to *I. micheliana* trees (Fig 1b). On each tree, we added six artificial bamboo twigs (length mm x width mm) of two different entrance sizes (three twigs had an 8 mm^2 entrance and three had a 32 mm^2 entrance which were constructed using a drill) to increase resource variability and therefore diversity of colonizing ants (Powell et al. , Jiménez-Soto and Philpott). Artificial nests remained in the field for three months.

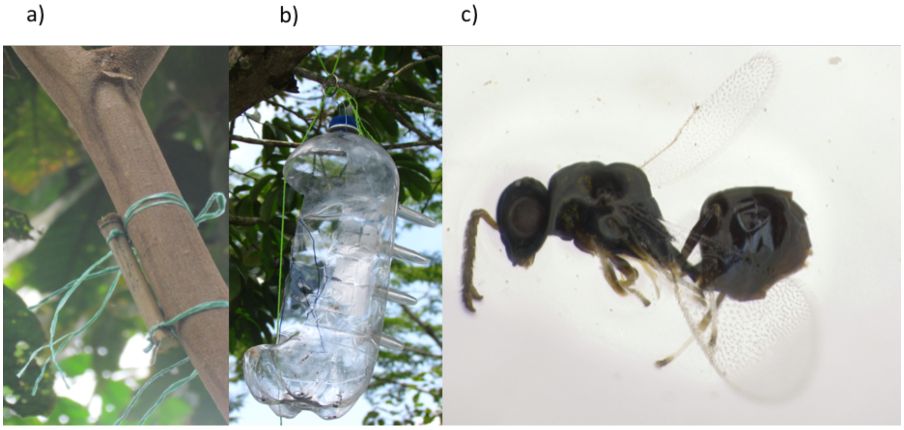


Figure 1. *Resource addition: (a) Bamboo twigs with different entrance sizes, and (b) nectar resources added with a device that slowly released either nectar or water (control solution). (c) Orasema sixaolae (Hymenoptera: Eucharitidae) (female) in lateral view. Parasitoid reared from pupae of Solenopsis picea.*

Ant colonization, colony sizes, and parasitism

To assess ant colonization and colony size, we collected artificial nests after three months. We transported artificial nests to the lab, froze them for 10 min. to decrease ant mobility, and then opened each nest to assess whether they were occupied, to identify ant occupants, and to count adults (males, workers and queens) and brood (ant larvae and pupae) in each nest.

We assessed ant parasitism by rearing all ant brood. We placed brood in plastic containers covered with a fine mesh to allow air flow. In the case of ant species without cocooned pupae (such as *Solenopsis* and *Crematogaster* species), we placed brood in containers with adults, to allow for sanitary brood care to prevent fungal infections during rearing (Tragust et al. 2013). Thus, for those species, we placed the entire nest in the plastic container, along with water and honey to allow for colony maintenance. We maintained brood for 10 days, during which time we recorded emergence of parasitoids and collected all emerged adults in plastic vials containing alcohol. After 10 days, we collected all pupae and larvae and dissected them under the microscope to account for parasitoids that did not fully develop during the rearing time. Parasitoid identification was done using the annotated keys to the genera of nearctic Chalcidoidea (Gibson et al. 1997) and Wheeler and Wheeler (1937) key to hymenopterous parasites of ants.

Data analysis

To determine if the addition of nectar resources, nest entrance size and VCI influence ant colonization (measured as ratio of occupied to unoccupied nests), we performed generalized linear mixed models (GLMM) with “glmer”, using the “lme4” package in R (Bates et al. 2014, R-Development-Core-Team

2014). We used the “cbind” function to create the dependent variable using the number of nests that were occupied and the number of nests that were not occupied, included site as a random factor, and used a Binomial error distribution. We compared two models. In the first, nest occupation was tested as a function of both nectar and artificial nest size treatments and the interaction between the two as fixed factors, with the VCI included as an additional predictor. In the second, VCI was removed. We selected the best model using the Akaike’s Information Criterion (AIC) calculated with the “MASS” package (Ripley et al. 2013).

To determine if the addition of nectar resources, nest entrance size and VCI influence colony size (measured as the number of workers, larvae and pupae inside a twig), we performed GLMM as above for each of the three most common ant species. We used site as a random factor and a Poisson error distribution. We used three dependent variables for analysis - workers and brood (larvae plus pupae). To determine the effect of both treatments, we compared two models for each dependent variable. In the first, the number of workers, larvae or pupae were tested as a function of both nectar and size treatments and the interaction between the two as fixed factors, and the VCI. In the second, VCI was removed. We chose the best model as described above.

To determine if the addition of nectar resources, nest entrance size and VCI influence ant parasitism, we used the proportion of parasitized pupaenand chose only nests from *Solenopsis picea* for the analysis, as this was the only parasitized species. In this case, generalized linear models (GLM) were performed. We constructed 25 models to test for effects on the proportion of parasitized pupae as a function of nectar treatment, nest-entrance size treatment, VCI, number of workers, and number of pupae. Models included interactions between variables. We chose the best model as described above.

Results

Vegetation complexity varied significantly among sites. Tree height varied from 4 - 12 m, tree circumference varied from 0.3 - 2.4 m, coffee density varied from 5 - 62 coffee shrubs, weed height varied from 0 - 2 m, weed density varied from 0 - 100%, canopy cover varied from 51% - 96%, and the VCI ranged from 0.30 - 0.64.

We recovered 226 (94%) of the artificial bamboo twigs. Of these, 44% were occupied by one of 16 ant species. The most common species were in the genus *Crematogaster* (38% of occupied nests), followed by *Solenopsis picea* Emery (20%), *Procryptocerus scabriusculus* Forel (7%), *Pachycondyla crenata* Roger (6%), and *Camponotus brettesi* Forel (4%).

Colonization

Ant colonization (i.e. the proportion of colonized artificial nests) varied with nest-entrance size, but did not vary with nectar addition, or with VCI. The model that best predicted ant colonization included both nectar and size treatments as fixed factors. VCI did not improve the fit of the model. Overall, there was no difference in nest occupation on nectar vs. control trees (Estimate=0.25±0.42, z=0.59, *P*=0.55, Fig. 2), but nest occupation was higher in nests with smaller entrances compared with larger entrances

(Estimate=0.87±0.42, z=2.08, *P*=0.03) (Fig. 2). The model that best predicted nest occupation for the two most common ant species (*Crematogaster* spp. and *Solenopsis picea*) did not include VCI as a covariate. *Crematogaster* spp. colonized nests with a small entrance size more frequently than large nest-entrance sizes regardless of nectar treatment (Estimate=1.84±0.87, z=-2.13, *P*=0.03). Neither nectar, nor size treatments, nor VCI explained the proportion of nests occupied by *Solenopsis picea*.

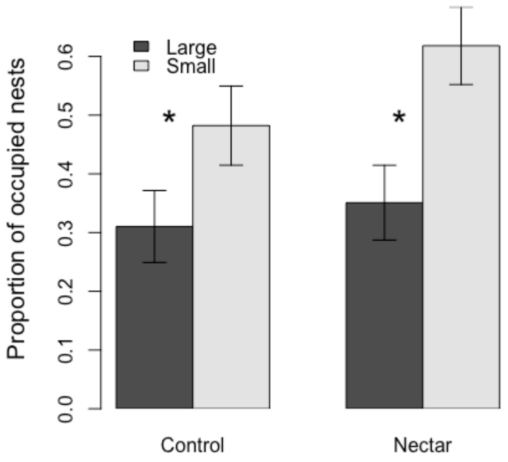


Figure 2*. Proportion of nests occupied in control and nectar treatments, and large and small nests. Asterisks represent statistically significant differences (p<0.05). Bars= Mean (SE).*

Colony size

The effect of nectar addition and twig-entrance size on the number for adults and brood was species-specific. *Crematogaster* spp. colonies had on average 88 workers, 43 larvae, and 49 pupae. The model that best predicted the number of workers of *Crematogaster* spp. included both nectar and size treatments and VCI. The mean number of workers in twigs was not significantly influenced by nectar (Estimate=-0.1±0.11, z=-1.4, *P*=0.15, Fig. 3a), but there were significantly more workers in nests with smaller entrances (Estimate=0.22±0.05, z=3.69, *P*<0.01, Fig. 3a). Surprisingly, we found fewer workers with increasing VCI (Estimate=-9.23±1.36, z=-6.74, *P*<0.01) (Fig. 4a). The model that best predicted the number of larvae of *Crematogaster* spp. included both nectar and size treatments and VCI. There was a significant interaction between nectar treatment and size (Estimate=-1.27±0.12, z=-10.12, *P*<0.01, fig. 3b), meaning that in trees with nectar addition the number of larvae decreased in nests with small entrance sizes but increased in nests with larger entrances. When looking at the individual effects, we found a higher number of larvae in the nectar treatment (Estimate=1.01±0.13, z=7.52, *P*<0.01, fig. 3b), as well as in the small twig-entrance size (Estimate=1.29±0.07, z=16.39, *P*<0.01, fig. 3b), and a significant positive effect of VCI (Estimate=6.27±1.27, z=4.92, *P*<0.01) (fig. 4b). The model that best predicted the number of pupae of *Crematogaster* spp. included nectar and nest size, but not VCI. There was a significant nectar by size interaction (Estimate=-2.30±0.12, z=-18.30, *P*<0.01 respectively) (Fig. 3c), meaning that in trees with the control treatment, small nests had a significantly greater number of pupae. When looking at the individual effects, we found a higher number of pupae in the nectar treatment compared to the control (Estimate=0.84±0.11, z=7.19, *P*<0.01, Fig. 3c), as well as in the large entrance size (Estimate=2.16±0.09, z=21.71, *P*<0.01, 3c).

The model that best predicted the number of workers, larvae and pupae of *Solenopsis picea*– the second most common species– included both nectar and size treatments as fixed factors and VCI. In control sites, large entrance nests had fewer individuals, but in nectar sites, large entrance nests had more individuals. This interaction was significant for workers (Estimate=-1.98±0.20, z=-9.55, *P*<0.01, fig. 3d), larvae (Estimate=-0.99±0.07, z=-12.67, *P*<0.01, fig. 3e), and pupae (Estimate=-0.72±0.13, z=-5.49, *P*<0.01, fig. 3f). Numbers of workers, larvae and pupae were higher in nectar treatment trees (Workers: Estimate=5.70±0.53, z=10.64, *P*<0.01; Larvae: Estimate=1.03±0.07, z=14.76, *P*<0.01; Pupae: Estimate=0.39±0.13, z=2.93, *P*=0.003), and higher in small entrance nests (Workers: Estimate=1.46±0.18, z=8.10, *P*<0.01; Larvae: Estimate=0.74±0.06, z=12.01, *P*<0.01; Pupae: Estimate=0.66±0.10, z=6.22 , *P*<0.01). Contrary to *Crematogaster* sp., the average number of workers of *S. picea* was higher with increasing VCI (Estimate=26.41±3.22, z=8.18, *P*<0.01) (Fig. 3c).

Parasitism

We found parasitism only in nests of *S. picea.* Reared parasitoids were identified as *Orasema sixaolae* Wheeler & Wheeler in the *Smithi* group (Hymenoptera: Eucharitidae) (Fig. 1c). Of all ant colonies collected, only 3% were parasitized, and within those nests, only 0.02% of pupae were parasitized. The model that best predicted the proportion of parasitized pupae included nest size and workers, and excluded nectar treatment and VCI. Parasitism did not vary significantly with nest entrance size (Estimate=0.0163 ±0.0114, z=0.0142, *P*>0.05), but was positively associated with the number of workers found in the nest (Estimate=1.69e-6 ±7.94e-5, z=2.129, *P*=0.049).

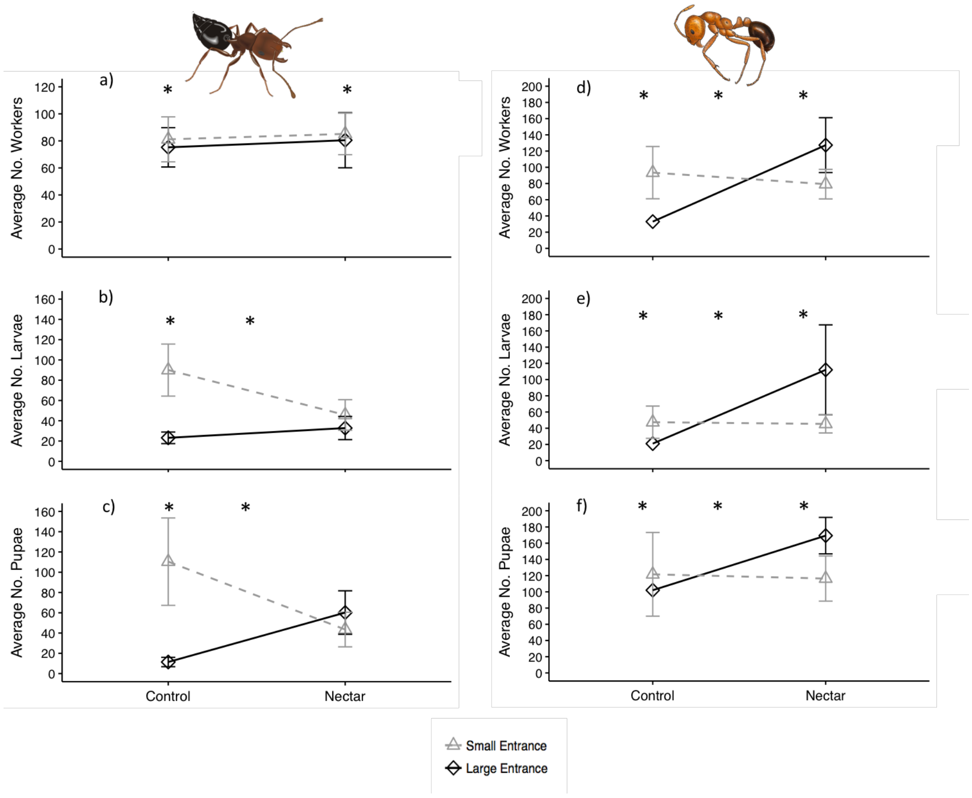


Figure 3. *Mean number of workers (a), larvae (b) and pupae (c) of Crematogaster spp. on control and nectar treatments, and large and small nests; and mean number of workers (d), larvae (e) and pupae (f) of Solenopsis picea on control and nectar treatments, and large and small nests. Asterisks represent statistically significant differences between small and large entrances (p<0.05), and statistically significant interactions when asterisks are presented between control and nectar treatment. Bars= Mean (SE).*

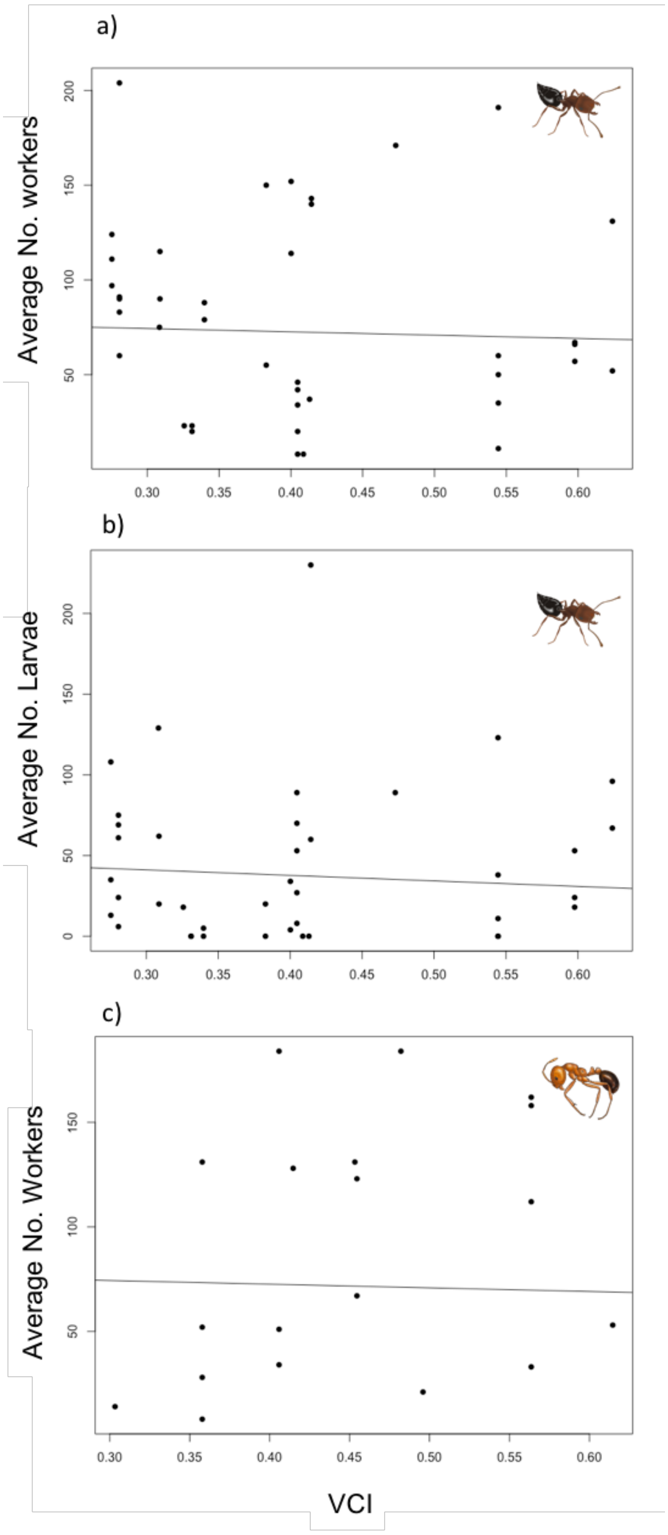


Figure 4. *Mean number of workers (a) and larvae (b) of Crematogaster spp. and workers of Solenopsis picea (c) as a function of vegetation complexity (VCI).*

Discussion

We examined the role of nectar and nesting resources, as well as habitat complexity on ant colonization, reproduction, and parasitism. Nectar availability did not influence twig-nesting ant colonization, possibly indicating that carbon-rich substances in the form of nectar are not a limiting resource for the overall community of twig-nesting ants in our study system. These results were unexpected, considering that most canopy ants feed on sugary resources available in the canopy in the form of plant exudates and honeydews (Davidson et al. 2003, Blüthgen and Fiedler 2004b, Cook and Davidson 2006, Sanders et al. 2007). This could be explained by the availability of extrafloral nectar provided by trees in the genus *Inga*, as well as honeydew from homopteran insects, making sugary resources exceptionally available in this system.

Even though this explanation might seem straightforward, the effects of sugary resources on arboreal ant communities can be variable. On the one hand, studies have suggested a strong relationship between abundance and co-occurrence of ants and sugary resources in the canopy, specifically hemipteran honeydew and extrafloral nectar, even in systems were sugar resources in the form of honeydew are highly available (Blüthgen et al. 2000), or when supplying substantial amounts of nectar in the canopy (Camarota et al. 2015). Similarly, sugar resources can regulate competitive interactions by allowing dominant ants to specialize on honeydew, while letting less dominant ant species feed on extrafloral nectar (Blüthgen and Fiedler 2004a). On the other hand, sugar resources may minimally affect ant communities, possibly because of the lack of specificity of the arboreal ant community towards the use of extrafloral nectar, and due to the temporal variability of this resource (Camarota et al. 2015). The fact that we did not observe an effect of sugar resources on ant colonization could mean that the ant species found in our study system do not maintain any strong relationship with sugary resources or do not experience intense competition over this resource, possibly suggesting that twig-nesting ants are mostly opportunistic when it comes to sugar resources (Camarota et al.). Alternatively, this may mean that the community of TNAs in this system has a generalized diet (Roeder and Kaspari 2017). Further, the high availability of nectar driven by the abundance of EFN-bearing trees in coffee systems creates a particularly carbon-rich environment where sugar is not limiting. It may also be possible that the nectar provided did not contain other important compounds such as amino acids, lipids, proteins and fatty acids, which are important for foraging decisions in addition to ant nutrition (Blüthgen and Fiedler 2004b). If so, ants may not have been drawn to colonize new twigs because the nectar provided did not contain the essential compounds that are important for certain consumers (Gardener and Gillman 2002).

Nectar availability positively influenced ant colony size, particularly of brood, suggesting that the availability of nectar has the potential to increase TNAs colony fitness after establishment, and therefore contribute to colony success beyond the colonization stage. Only a few studies have provided robust evidence that nectar resources improve ant colony survivorship (Lach et al. 2009a), reproduction, and growth (Byk and Del-Claro 2011). For instance, colonies that feed on sugar resources in the form of EF nectar have greater body weight and produce significantly more adults and progeny (Byk and Del-Claro

2011). Our study found that in the case of *Crematogaster* spp. and *S. picea*, nectar availability accounts for an increase in brood number. This result provides some evidence that sugar availability becomes important once colonies have established, specifically increasing the number of workers and brood in nests. Others have found that sugar resources increase about five times the number of individuals in colonies of *Cephalotes pusillus*, an arboreal ant that feeds on EFNs (Byk and Del-Claro 2011). However, we should note that the responses to sugar resources is species-specific and could depend on specific ants' life styles. Some species might be more responsive to amino acids, rather than to carbohydrates (González-Teuber and Heil 2009). For example, when offering sugary substances with different amino acid contents, the fire ant *Solenopsis geminata* feeds more often on the amino acid-rich substances, although *S. invicta* does not discriminate between substances (Lanza et al. 1993). Even though our study only increased carbohydrates and did not account for amino acids, it is likely that our experiment accurately represented the effect of nectar resources in the community of twig-nesting ants in our system because EF nectar resources from some *Inga* species are hexose-dominant, meaning EF nectar is primarily composed by carbohydrates, such as sucrose, fructose and glucose (Koptur 1994). However, future studies should test for species-specific preferences to artificial and naturally-occurring nectars, and account for more complex sugars and amino-acids available in EF nectar provided by *Inga* species.

Our study confirms that twig-entrance size is a limiting factor for the twig-nesting ant community during colonization (Powell et al. 2011), and that certain ant species more frequently colonize nests with a specific entrance size

(Jiménez-Soto and Philpott 2015). Both *Crematogaster* spp. and *S. picea* were more frequently found in twigs with the smallest entrance. We believe that the clear effect of entrance-size on overall colonization regardless of the nectar treatment (Figure 2) is driven mostly by the fact that we provided only two distinct entrance-sizes, as opposed to a diversity of sizes, that could have allowed for a more even occupation between the smallest and the largest size (Jiménez-Soto and Philpott 2015) and increase cavity use (Powell et al. 2011). Interestingly, the overall positive effect of small nest-entrance size on all life stages of *Crematogaster* spp. and *S. picea* in control sites changed in sites with nectar addition, as shown by significant interactions between nectar and size (Fig. 4b,c,d,e,f), except for workers of *Crematogaster* spp. (Fig. 4a). This trend showed overall more individuals (workers, larvae and pupae) in nests with a small entrance in the absence of nectar, but in the presence of nectar resources, nests with the small entrance had significantly fewer individuals than nests with a larger entrance. This effect of nectar treatment on nest-entrance size was even more dramatic for *Solenopsis picea*. Here, the addition of nectar completely inverted the positive effect of small size entrances observed in control sites. An explanation for this pattern is not straight forward. It is possible that when food resources are abundant (in this case nectar resources), there are higher recruitment and foraging rates, which could be facilitated by using nests with largest twig-entrance size. A recent study showed that in social organisms, collective clog control is vital for colony function, thus developing the right strategy to improve traffic -- for example, using nests with a large entrance size and thus increasing colony fitness -- could be important for the colony (Aguilar et al. 2018). Furthermore, in sites with abundant resources, the production of more individuals to gather resources might be important, however we did not evaluate caste structure in relation to colony fitness, which could be useful to confirm whether the observed colony structure responds to requirements set by the environment (Oster and Wilson 1979, Gordon 1996, Powell 2008).

Beyond the influence of food and nesting resources on colonization and reproduction, nectar resources may also influence the interaction between ants and their parasitoids (Herreid and Heraty 2017), an interaction that has been described as the "*missing link*" in understanding ant communities (Feener 2000). Our study aimed at understanding the significance of nectar availability on parasitism rates of TNAs by their parasitic wasps, by adding nectar on trees with EFNs. We expected that sites with nectar addition would have higher parasitism rates than control sites, because of increased foraging to the nectar source, increased probability of ants encountering their parasitoids, and higher parasitoid visitation and oviposition near sugar resources. In this system, it appears that the availability of both nectar and nesting resources benefits arboreal ants, but not ant parasitoids. These results could be explained by the extremely low parasitism rates found in our study. It is possible that placing a larger number of nests could yield higher parasitism to further explore the effect of resources on parasitoid-host interactions. In our study, parasitism was only explained by the number of workers in the colony, this positive association between colony density and parasitism has been shown for the *Azteca sericeasur–Pseudacteon* sp. system, in which attack rates of phorid flies increase at higher ant densities (Philpott et al. 2009). Other studies have found similar density dependency with the presence of species parasitized and the number of cocoons in the nest (de la Mora et al. 2015), however in our study, the number of pupae did not improve the fit of the model. These results potentially suggest density dependence in our system of study, although it is not clear whether the mechanism is behavioral (i.e parasitoid wasps are drawn to areas with a higher density of workers) or demographic (Philpott et al. 2009). Furthermore, our results suggest that parasitism is not a strong force shaping the community of twig nesting ants in this system– at least for parasitoid wasps–, contrary to the strong effect of parasitoid flies on other arboreal ants (Feener 2000). Contrary to expected, we did not find any relationship between habitat complexity and parasitism rates, in contrast to other studies that did find a positive influence of VCI on parasitism *Gnamptogenys* spp. and *Pachycondyla* spp. (De la Mora et al. 2015), as well as higher parasitism in more complex coffee agroecosystems (De La Mora and Philpott 2010). These results, however, do not rule out the possibility that the species of parasitoid wasps found in our study use EFNs to access their host. Further observations and experiments should be done on this regard, considering that females of *Orasema* (Eucharitidae: Oraseminae) have developed a highly-specialized behavior that involves the use of EFNs to access their ant hosts (Herreid and Heraty 2017). First, female wasps infiltrate the ant-plant interaction without being noticed, and lay single stalked eggs almost exclusively inside plant tissue nearby EFNs; after emergence, planidias become into contact with ants that use EFNs as feeding sites, from which they are vectored to the nest (Clausen 1940b); once in the nest, ants transfer planidias to their immature ant brood through feeding, and the wasp's life cycle continues (Herreid and Heraty

2017). This behavior has been described for the *Orasema simulatrix* and *O. wayquecha* species groups (Carey et al. 2012), *Kapala* (Eucharitinae) (Herreid and Heraty), and *Chalcura* (Schwitzke et al. 2015). However, the specific mechanism of transfer of planidia to *Solenopsis picea* nests still needs to be identified.

Collectively, our study indicates that nectar, nest-entrance size, and vegetation complexity play an important role at different stages of the ant colony life. The benefits associated with the use of a diversity of resources, could explain why ants are exceptional predators of pests in agricultural systems. We also document that it is likely that parasitoid wasps are not a strong force shaping the community of TNAs in this system. We encourage future studies to investigate potential species-specific relationships between arboreal ants and EFN-bearing trees in carbon-rich systems, as well as the specific mechanisms and factors involved in shaping the ecology of ant parasitoids, as well as parasitoid-host interactions. Finally, we encourage future studies to continue investigating the mechanisms involved in the fascinating parasitoid-EFN-ant interaction.

CHAPTER 5

THE POLITICAL ECOLOGY OF SHADED COFFEE PLANTATIONS: CONSERVATION NARRATIVES AND THE EVERYDAY-LIVED-EXPERIENCE OF FARMWORKERS

Abstract

Biodiversity conservation in coffee agroecosystems can contribute to social sustainability by improving people's livelihoods, food security, and reducing economic vulnerabilities in peasant households. This is particularly the case in smallholdings, were families are self-sustainably equipped with their means of production and use their own labor power to cultivate their land, diversify beyond coffee, and organize in cooperatives to get better prices. However, it is less clear whether conservation practices positively impact seasonal workers in labor-intensive systems. Farmworkers are one of the most vulnerable and marginalized actors within the coffee production chain facing food and labor inequalities. Through ethnographic research, I examine the tensions that arise when conservation practices and narratives meet the everyday-lived-experience of migrant farmworkers in organic shade-grown coffee plantations in Mexico. I draw attention to the ways in which conservation narratives adopted in organic shade-grown coffee plantations have material and symbolic effects on farmworkers everyday-lived-experience, and argue that they contribute to farmworkers' vulnerability and marginalization. At the same time, I recognize farmworkers as individuals with agency, and discuss the role of their peasant identity in the process of subtle resistance to unfair working conditions. The relevance of this work lies on exposing the social intricacies of coffee production and biodiversity conservation within labor-intensive systems, and questions shade-grown organic coffee as a fair and just imaginary, as we transition to more sustainable food systems.

Keywords: Political ecology, conservation narratives, shade-grown coffee, farmworkers, plantation labor

Introduction

Coffee is cultivated in a variety of ways, with varying management intensity, both socially and ecologically (Pohlenz Córdova 1979, Moguel and Toledo 1999). In terms of its ecological complexity, coffee cultivation ranges from the "rustic" coffee where coffee plants grow under the shade of trees in mature forests, to un-shaded "sun coffee" (Moguel and Toledo 1999). This gradient could be also understood as a socioecological continuum in which multiple layers of complexity interact. A vast diversity of social groups (i.e. indigenous, mestizo and plantation owners of European descent), labor intensities (i.e. with family labor or seasonal wage labor), farm sizes (i.e. from small plots to large plantations), and extent of capital accumulation, are represented and overlap within this spectrum of ecological complexity (Pohlenz Córdova 1979, Nolasco 1995). In this socio-ecologically diverse canvas, small shade-grown plots owned by peasant families may coexist along with the agro-industrial sector, primarily represented by large coffee plantations that also practice shade-grown agriculture for export[1].

---

[1] It is important to point out that not all shade-grown coffee systems are the same sociologically speaking. In this article, I discuss conservation narratives only in

Shade-grown coffee often resembles the appearance of native forests (Moguel and Toledo 1999), offering the possibility to conserve biodiversity, ecosystem services, and to improve households' food security (Perfecto et al. 1996). Indeed, several studies since the conservation boom of the 1980's in Latin America (Zimmerer 2011) have addressed the ecological benefits associated with biodiversity conservation within shade-grown coffee agroecosystems. For example, pollination, pest control, reduced soil erosion, water conservation and improved scenery (Greenberg et al. 2000, Roubik 2002, Perfecto et al. 2004, Armbrecht and Gallego 2007, Méndez et al. 2009, Johnson et al. 2010, Vandermeer et al. 2010, Philpott et al. 2012).

In terms of coffee as a global commodity, the possibility for biodiversity conservation in shade-grown systems (through the implementation of environmentally-friendly management practices) and the participation in alternative market niches (e.g. organic, shade grown, bird friendly and eco/agro-tourism) have been part of a successful marketing strategy appealing to green and socially conscious consumers in the global north. In the global market, shade-grown coffee is often advertised using particular imagery, which is meant to remind us of "conserved natural forests" or places with vast natural resources, rather than agricultural systems where both humans and non-humans play an important role in processes of commodity production. The result has been the construction of a coffee imaginary that paints shade-grown coffee plantations as

---

the context of a plantation system, and acknowledge that these narratives and their effect on peoples may be different in peasant systems, were families are self-sustainably equipped with their means of production and use their own labor power to cultivate their land, diversify beyond coffee, and organize to get better prices.

lush gardens with tropical birds, jaguars, and foraging tapirs. Although an attractive and marketable vision of the coffee landscape, this imaginary is an inaccurate representation of the social reality of these spaces.

At the core of this coffee imaginary is a *conservation narrative*[2] that places responsibility of environmental degradation and species extinctions on exploitation by humans, and growing human populations (Campbell 2002c). As a result, humans are excluded from places and the use of natural resources commonly used for social reproduction and the sustenance of human livelihoods. This conservation narrative incorporates some aspects of the "protected-area" discourse of conservation, emphasizing the maintenance of critical ecosystem functions and structures (Berdej et al. 2015). Although this conservation narrative is based on strong scientific evidence, it is often presented under a framework of "crisis" (Campbell 2002c, Berdej et al. 2015), which potentially dehumanizes places and intensifies the human-nature dichotomy through the exclusion of the human experience (Berdej et al. 2015).

The impact of this conservation narrative on human communities has been explored in the context of exclusionary practices around protected areas, such as national parks, coral reefs, and fisheries (Campbell 2002c, b, Bardej et al., 2015, von Heland and Clifton, 2015). However, despite the prevalence of this conservation narrative in organic shade-grown coffee plantations, no studies have explored its impact on plantation workers, and whether the embodiment of

---

[2] In the broader literature, other authors refer to this conservation narrative as *traditional conservation narrative,* in the sense that it is a long-standing approach (Campbell 2002c). However, in this article I exclude the word *traditional*, as it might be confused with shade-grown coffee management in its traditional sense.

such narrative through potentially exclusionary practices further marginalizes vulnerable peoples. This is particularly relevant for three reasons: first, seasonal workers in labor-intensive systems are one of the most vulnerable and marginalized actors within the coffee production chain (Jha et al. 2014). Research suggests that about 30% of the coffee currently consumed worldwide comes from large plantation systems (between 25 and 741 acres), where seasonal workers face food and labor inequalities (Gresser and Tickell 2002, Renard 2011). Second, although literature on organic agriculture suggests that organic markets and price premiums from certifications can potentially support livelihoods in rural areas, farmworkers continue to suffer inequalities and forced labor (Guthman 2014, Shennan et al. 2017). In fact, the priorities of such eco-labeling initiatives focus primarily on certification criteria and privilege ecological goals while paying scarce attention to social processes and labor issues (Bray et al. 2002, Shreck et al. 2006), and fail to question inequalities experienced by farmworkers (Allen and Sachs 1993). And third, although shade-grown coffee has been a critical system for conservation efforts (Perfecto et al. 1996) and in some cases, supports peasant households (Méndez 2004, Bacon 2005, Mendez et al. 2010), it is possible that the conservation narrative in organic shade-grown coffee plantations helps construct a coffee imaginary that misrepresents the human experience.

This chapter examines the tensions that arise when conservation narratives meet the everyday-lived-experience of migrant farmworkers in organic shade-grown coffee plantations in Soconusco, Mexico. I draw attention to the ways in which conservation narratives embodied in organic shade-grown coffee plantations have material and symbolic effects on farmworkers' everyday-lived-experience, and argue that they contribute to farmworkers' vulnerability and marginalization. The relevance of this work lies in exposing the social intricacies of coffee production and biodiversity conservation within this labor-intensive system as I demystify coffee production as a fair and just imaginary. First, I address the labor aspect of coffee plantations in the Soconusco region. Second, I discuss conservation narratives in the context of organic shade-grown coffee plantations, and the ways in which conservation narratives are embodied in organic shade-grown coffee plantations. Finally, I discuss the implications of these conservation narratives on the everyday-lived-experience of migrant farmworkers.

Fieldwork in a coffee plantation

In order to understand conservation narratives in coffee plantations and how they are perceived and contested by farmworkers, I carried out ethnographic research in an organic shade-grown coffee plantation in the Soconusco region. The extension of this plantation is approximately 300ha and can be categorized as a mix between traditional and commercial polyculture, with hired wage labor, both permanent and temporary. The epistemological basis of my research is rooted in the interpretivist tradition of anthropology using a phenomenological approach, which emphasizes the importance of symbols and experiences as well as individual opinions, values and categories to understand societies (Scott 1986, Geertz 1994, Orne and Bell 2015). This methodological approach allowed me to capture meaningful experiences of farmworkers, as well as to understand how farmworkers perceive themselves in the plantation.

During the harvest season between October 2015-January 2016, I picked coffee with 15 families of migrant farmworkers. I also lived in their shacks and joined them in daily activities such as collecting edible wild plants, hunting, and preparing meals. My research consisted of participant observation and informal interviews that took place while picking coffee during the day, in the evenings over meals, and while performing other activities. Along with my interlocutors I experienced the physical struggles of picking coffee and, in return for their time, I contributed my (small) portion of harvested coffee at the end of each day to their totals. The population of migrant farmworkers with which I carried out my research were mestizo from Guatemala, although indigenous laborers also work in the plantation during the earliest part of the harvest season.

I complemented my ethnographic research with interviews of three coffee plantation owners which allowed me to understand their engagement with conservation narratives, as well as their own struggles as coffee growers in a highly competitive market. Farm owners are often blamed for the social conditions experienced in their farms, yet we should not assume that owners can automatically change this reality (Holmes 2013). Therefore, research about farmworkers should also consider the experiences of the growers themselves. As suggested by Holmes "The fact that the perspectives of farm management are generally overlooked, inadvertently encourages the assumption that growers may be wealthy, selfish, or unconcerned" (2013:52). This may reinforce a superficial understanding of the reality of farmworkers, and therefore the fact that the complexity of their struggles and structural challenges are not often recognized.

Due to my interest in analyzing how conservation narratives weave with the popular public perception of shade-grown coffee, I also visited coffee plantation lodges along the touristic *Ruta del Café* (Coffee Route), where I collected written comments representing the public discourse surrounding shade-grown coffee plantations.

Placing labor in the imaginary of shade-grown organic coffee

Plantations are highly specialized, large-scale agricultural operations, which are characterized by their intensive use of capital investments, as well as the exploitation of wage labor (Young 1970). Although plantations are primarily concerned with the production of agricultural products grown on land, in scale and method of operation plantations are more akin to a modern factory or industrialized agriculture than they are to a small-scale family farm (Myrdal 1968, Young 1970). The plantation model of agriculture has affected the ecologies of place, including the interaction between humans, non-humans, and their environment, as it embodies both the control of *nature* and of people.

The essence of plantations–with defined social stratification and a controlling character, full labor control, and the transmission of agricultural management instructions from top to bottom (Young 1970)– continues to have a presence in agricultural production in Latin America. In its origins, plantation economies were entirely controlled by foreign capital, and labor would be primarily imported, but profits would be invested overseas. Knowledge and technology were also imported from abroad, often by sending the owner's offspring to their country of origin to study, as part of the colonial emulation of the plantation economy (Young 1970). The primal organizational aspects of plantations slowly disappeared in most places in Latin America, giving way to communal land and small holdings that followed land reforms and land grabs lead by displaced peasants. However, in some places plantations continue to shape the landscape and the lives of people that live in, of and around plantations. This is the case in the Soconusco region of Chiapas, Mexico.

Coffee production in the Soconusco region– one of the most important coffee producing regions in Mexico– is particularly interesting, as it played a key historical role in incorporating the state into the global capitalist market (Pohlenz Córdova and Córdova 1979, Lurtz 2016). By the end of the XIX Century, factors such as the economic policies of the Mexican government (lead by Porfirio Diaz), strong foreign capital (primarily German) and adequate ecological conditions, allowed the expansion of coffee plantations in the Soconusco region (Renard 2011). In its expansion, the coffee plantation economy became not only a powerful mode of production, but also a way of life for both plantation owners and laborers (Toledo Tello 2002), which remains an integral part of the cultural identity of Soconusco.

The expansion of German plantations (also called "*fincas*") in this region was characterized by the adoption of a production system that did not fall too far from the *hacienda* system of the pre-revolutionary period (De Vos 2002). Coffee production in large volumes was done primarily by these large plantations, which had access to commercialization routes and the required capital investments (Bartra 1996). Today, the subsistence peasant economy coexists alongside the export-oriented economy of coffee plantations, generating a rich cultural, social and economic rural patchwork (Martinez-Torres 2006).

Plantations in Soconusco maintain a social organization based on a centralized political structure and the employment of wage labor (both permanent and temporary). At the center of this organization is the *Patron*, or owner of the plantation who often lives outside of the plantation; followed by an administrator; a sideman or *mayordomo*; a set of foremen or *caporales* in charge of crews of laborers; and the laborers themselves (Lopez-Echeverria and 2007). Although labor has been historically sourced from the highlands of Chiapas, most laborers today are currently seasonal migrants that come from Guatemala, primarily during the harvest season (October-January). The increasing migration of labor from Central and South America directly to the United States has generated a labor shortage in the region of Soconusco (Renard and Breña 2010), which in turn has promoted alternative strategies of labor recruitment, including the provisioning of temporary visas and permits granted by the patrons of large operations, extended for up to five years of work (Renard and Breña 2010). Such permits are only legally granted to individuals and not to entire families, meaning that only one or two family members are legally represented in the migratory destination (Renard and Breña 2010). This situation only exacerbates the already vulnerable position of migrant laborers in coffee plantations, where living and working conditions are overwhelmingly unfair[3]. Once migrating, the

---

[3] Working and living conditions of plantation laborers are often unacceptable,

vulnerabilities that come with illegal status and high dependency from the contractors increase the stress experienced by farmworkers (Gresser and Tickell 2002). Additionally, the barriers to transnational mobility limits the ability of farmworkers to claim better labor conditions and wages (Renard and Breña 2010). Issues of migration, illegal status, and poor working conditions are accompanied by differences among farmworkers in terms of their ethnicity, farming abilities, and their permanency in the farms, as has been shown for other agricultural systems that rely heavily on migrant labor (Holmes 2011).

In coffee plantations, multiple ecological knowledges and imaginaries meet farmworkers' experience, which makes farmworkers important actors for providing meaning to these spaces (Besky 2013) despite the fact they are often overlooked in the coffee production cycle. The harsh reality of laborers in coffee plantations contrasts with the coffee imaginary of shade-grown organic coffee and fails to show its reality, therefore obscuring the lives of people (West 2012). Additionally, the social sustainability of organic agriculture can be widely questioned for the contradictions posed to laborers. On the one hand, organic agriculture provides a safer space to laborers in terms of limiting the exposure to pesticides (Shennan et al. 2017), while on the other hand, it does not address structural inequalities, occupational injuries, and other health related concerns

---

lacking basic living requirements like clean water and healthy food (Gresser and Tickell 2002, Renard 2010). Commonly farmworkers can't unionize to negotiate wages, and women get a lower pay for the same amount of work (30% less in Honduras according to Gresser and Tickell 2002). Moreover, occupational injuries from bending for long periods of time, climbing or lifting are common, but lack the necessary medical attention (Villarejo and Baron 1999).

common in the community of farm laborers (Shreck et al. 2006). In an ideal world, the benefits of organic shade-grown coffee should be perceived not only through the conservation of biodiversity, but also through improving social justice and human livelihoods. Yet, as Guthman argues, "the organic movement has fallen woefully short of addressing the social justice issues that are often assumed to be part and parcel of organic farming" (2014:3).

The embodiment of conservation narratives in coffee plantations

The Soconusco region is famous for its *Ruta del Café*, repeatedly advertised as a "magical destination on the coast of Chiapas". Plantation-style lodges embedded in the tropical perennial forest overlook what is hard to not categorize as a dreamlike landscape for the avid nature lover: a mosaic of greens, the coffee within the dense natural forest, the sound of the river, and the singing of the birds. Woven into the panorama of colors and the smell of wet soil is the social contrast shaped by the division between private property and communal lands, or *ejidos*, which often depend on the commercialization routes, and infrastructure owned by the larger estates. Situated within the landscape is the human life of the plantation: the often unseen bodily pain of the workers, the stories of migration, the joy and the soreness of the harvest season, and the longing of what has been left behind. This marks a striking contrast with the luxurious experience advertised in plantation resorts: the heavenly countryside in the heart of a tropical atmosphere, a hidden treasure in the jungle of Chiapas.

La Ruta del Café emphasizes the coffee terroir and confers coffee with symbolic attributes in terms of the historic, cultural and ecological backgrounds of the region (Lyon 2013). Printed in a lustrous package, the description of this region's coffee reads: "this wonderful coffee comes from the slopes of the Sierra Madre de Chiapas, Mexico's finest coffee-growing region, where high altitudes and rich, volcanic soil create ideal growing conditions. This coffee is cultivated under a canopy of shade trees that protect a diversity of wildlife– foraging tapirs, colorful quetzals, the sleek jaguar–, by farmers who are committed to producing something exceptional. Chiapas' coffee is crisp and nutty with hints of cocoa".

Along with the economic benefits associated with ecotourism activities, the region is notorious in the alternative coffee market, particularly through biodiversity-friendly initiatives, such as organic, shade-grown, and bird friendly. Today, these *fincas* export their product in specialty coffee markets to Europe, the United States, and more recently Japan, primarily to accommodate their product in an increasingly competitive environment and overflowed market. Additionally, coffee plantations in this region have had an important presence in the history of alternative agriculture. In fact, the region is portrayed as the first to export biodynamic coffee internationally, and many plantations have been in the spotlight of scientific research.

Some *finqueros* (plantation owners) have adopted biodiversity conservation practices such as increasing tree diversity, shade cover, promoting ground cover vegetation, and not applying agrochemicals. These practices are regularly accompanied by strict regulations in relation to the use of natural resources within the plantations. For example, farmworkers are instructed to not cut trees, and it is common to find signs that say: *prohibido la caceria*; *cuida los bosques y selvas, no esta permitido cazar, extraer flora y fauna silvestre, o tirar* *arboles* (hunting prohibited, protect the forests, it is not permitted to hunt, extract flora and fauna, or to cut trees).

These signs meant to enforce conservation practices are based on a narrative of crisis, one that emphasizes the maintenance of ecosystems and their conditions (Campbell 2002a), and prioritize limiting or prohibiting the use or extraction of natural resources in the name of conservation (Campbell 2002a). The narrative is reminiscent of the traditional protected area discourse of conservation, in which the threat of wildlife populations is directly caused by human exploitation, rather than systemic problems (Campbell 2002a). In the context of shade-grown coffee plantations in this region, the exclusionary narrative of conservation assumes farmworkers are careless actors who do not value biodiversity: *"they* [farmworkers] *do not know better, they must be taught*". For example, one *finquero* illustrates this point:

> *"Here there are monkeys, cuatusas, deer, anteaters, –how about tapirs? – no, there are no more tapirs here" … "[Here in my finca] it is prohibited to hunt, whoever I catch hunting I'll burry him in jail."*

These conservation narratives prevalent in organic shade-grown coffee plantations are used to present a marketable vision of the coffee landscape to consumers. They represent a myth which is repeated and advertised in various ways, and maintained through a narrative of exclusion. As Slater argues: "[These narratives] are representations of a natural or seemingly natural landscape in terms that consciously– or, more often, unconsciously– evoke the biblical account of the Eden…. They highlight stories of nostalgia for a perfect past or deep fears about continuing loss" (1996:115). In this sense, Slater continues, "biodiversity also may serve as the focus of an ecocentric story in which human beings find themselves forced to play an ambiguous or unaccustomed supporting role" (1996:116). Conservation narratives also resonate in the popular discourse. For example, visitors to plantation resorts describe these places as a "heavenly paradise within the rainforest", a "back to nature experience with luxury", "who knew paradise would smell of coffee?". Slater's analysis of the implication of these narratives in the Amazon, as well as their manifestation in the public discourse, helps us appreciate how exclusionary narratives of biodiversity conservation promote a skewed and often exaggerated vision of the space, which ultimately obscures people's lives (Slater 1996).

The journey of *los tapiscadores* and the process of *la cosecha*

In this section I lay out the lived experience of farmworkers in relation to living and working conditions in the coffee plantation. Here, I highlight food-related experiences, the suffering and joy characteristic of the harvest season, and the injustices perceived by farmworkers, which become central when discussing conservation narratives and the normalization of poverty and violence surrounding farmworkers.

Every year, entire families from Guatemala prepare for a journey across the border to work in *la cosecha de café* (the coffee harvest season). Back at home, *los tapiscadores* (coffee pickers) are *campesinos* (peasants) who own small plots of land where they grow *milpa*– a traditional intercropping system with corn, beans, squash, and chile–, *hortalizas* (vegetables), and engage in animal husbandry, primarily raising pigs and chickens. This rural semiproletariat constitutes one of the primary labor fluxes in this region since the XX Century (Martinez-Velasco 1994, Angeles 2011). Although exact numbers are not reported, almost 12,400 migrants (from Guatemala and Belize) crossed the border in 2017 to work in Mexico. Of those, the majority work in the agricultural sector, and about 42% specifically in the coffee industry.[4] Due to labor shortages in Soconusco, the region benefits from this influx of migration from Guatemala, and at the same time, this allows *tapiscadores* to reproduce and sustain their peasant living back at home (Castillo and Casillas R 1988, Isakson 2009), as wages from coffee picking allow them to buy seeds, fertilizer, and home goods after the coffee harvest season is over.

The journey of *los tapiscadores* lasts about 4 months following the path of Arabica coffee maturation: from the Soconusco highlands at an altitude between 900 and 1100msl, to the highlands of Jaltenango, in the Frailesca region in Chiapas at 1600msl. For many of them, the journey starts in the border village of Chanjulé, in the municipality of Tacaná in Guatemala. Families pack burlap sacks full of clothes, cooking pans, and foods from their own plots, such as potatoes (at least three varieties: white, yellow, and purple), *Calabazas*, *chilacayota*s (Mexican varieties of squash), and *tomates de arbol* (a variety of tomato). They also pack blankets and other goods like radios and machetes. The

---

[4] “Trabajadores Fronterizos: Guatemaltecos y Beliceños en la Frontera Sur”. 2017. Secretaria de Gobernacion, SEGOB. This source only reflects individuals that have presented a Tarjeta de Visitante de Trabajador Fronterizo on their arrival to the border. “Illegal” entries are not included in these statistics. http://www.politicamigratoria.gob.mx/es_mx/SEGOB/TFyVR_FronteraSur

contractor, who is from Guatemala and often a family member of the *tapiscadores*– and hired for this job by the plantation– charges ~$200 Mexican pesos (one way) per family to transport them in an old *camion de redila* (similar to a flatbed truck) to the coffee plantation. The journey lasts about eight hours, furrowing major migration checkpoints at the border. Near the entrance, people are received by a sign that says: "welcome home, respect nature".

Upon arrival, families and single *tapiscadores* are assigned to their shacks. Families are given small rooms with bunk beds made of wood or concrete. Each room has two bunk beds, and may host a family of up to eight people. Single *tapiscadores* (usually male) are assigned to the singles' shack, a long room with more than 20 wooden bunkbeds. No mattresses, pillows or blankets are provided. The rooms are dark and the odor of sweat mixes with the humidity impregnated in the wood and the moldy walls. During my research, I am also assigned my own shack neighboring about 20 other rooms that are part of a recently renovated living area. My shack smells like newer concrete, and has a laminated roof that gets hot during the day and amplifies the sound of rain at night. I am also given a *ficha de alimentacion* (similar to a food stamp), which I can use to pick up breakfast and lunch at the communal kitchen. I am also given a basket to pick coffee, which I can fasten to my waist using a *mecapal*– a belt made of plastic or leather.

A distant bell rings at 4 am, my neighbor's lights turn on, a radio starts playing *banda* music, a child cries in a neighboring shack, and the sound of an industrial tortilla maker is in the background. Farmworkers (mostly men) start gathering at the kitchen to pick up the breakfast ration with their *ficha de* *alimentacion*: coffee, tortillas, and beans. The men bring the food back to a separate communal kitchen with *fogones* (wood stoves), where women are preparing other foods to mix with the basic food ration. They cook eggs bought at the plantation store and boil or fry plants collected during the previous day. As I later came to discover, there are about thirteen species of plants used around the plantation to complement their daily ration.[5] With them, women sometimes prepare tamales and mix them with frijoles, cheese, or eggs, and eat them with tortillas, which they pack in plastic bags and cloths to take with them to the field.

The work of harvesting coffee begins as soon as the sun comes up, at about 5:30 am. Families of farmworkers carry their baskets and burlap sacks, which they will later use to separate the green coffee from the red, kneeling on the side of dirt roads in the plantation. Most of them are wearing sandals, and very few are wearing rubber boots. I am at the end of a long line of workers walking up a muddy trail in the plantation, following the sound made by the horn of *el caporal*.[6] Workers are making jokes or talking about how bad the coffee is this year, and often I hear about the fear of *la migra* (immigration officers), who visit plantations to take people's children away from their parents. Despite the fear, children of all ages are running around playing, shooting birds and squirrels

---

[5] Some of the plants used by farmworkers in the coffee plantation include: Pacaya, Flor de Izote, Hierba Mora, Pata de Paloma, Hongo Blanclo de Izote, Hongo Oreja, Verdolaga, Berro, Tepejilote, Hierba Buena, Quilete, and Capote. Many of these plants are gathered in or around the coffee plantation while at work, and are used to mix with frijoles, boiled or fried with eggs, inside of tamales and mixed with pork, chicken, or inside of soups.

[6] The *Caporal* is a worker in charge of crews of farmworkers. He carries a horn-like instrument made of plastic, which produces a sound similar to a trumpet, and it is used to assign sections of land that need to be harvested. This horn is also used to let farmworkers know it is time for breakfast, or time for a break to drink water.

in the trees using their handmade slingshots. Children also contribute to the coffee harvest, they are– as Zapata-Martelo and colleagues (2012) point out– “invisible contributors” of the coffee harvest, as they neither get paid nor receive food stamps, but do help their parents pick coffee, and represent– to some extent– a monetary benefit for the plantation. In this sense, minors in coffee plantations find themselves in a highly vulnerable position, as they depend on their parents for food, and for medical attention (Zapata-Martelo et al. 2012).

At the end of the day, full burlap sacks are left on the side of the muddy plantation roads, marked with a colorful ribbon to identify each farmworker. A large truck picks up the burlap sacks and deposits them in the *beneficio* (the processing facility) for *la entrega de café* (the coffee delivery). Immediately after, farmworkers deposit their coffee in large wooden measuring boxes, which according to some are rigged to increase plantation gains. Farmworkers are then handed a *ficha* (token) by the plantation administrator or *mayordomo,* which then they return to the administration in order to keep track of their monthly harvest records. Farmworkers get paid at the end of the month, although it is common for owners to delay the pay day, to keep farmworkers from leaving the plantation earlier. In this regard, a man in a family of four tells me that, “*it is hard to harvest coffee, if they don’t pay us we are going to strike, we are not toys*”. Other work-related abuses are common in the plantation. For example, workers report having ongoing debt in the plantation store, which not only charges an excessive amount for the products, but also subtracts what is owed from the monthly paycheck. Furthermore, health care and transportation to the nearest hospital is not necessarily provided to people in need.

La cosecha is a physically demanding task. It requires carrying a basket full of coffee tied to the waist, and is rough on the hands as it scratches palms and fingers. If not careful, a branch full of coffee can hit you in the face with a whiplash effect, leaving the eye sore for days to come. The long and strenuous working hours carrying heavy weight, kneeling, and walking through rough terrain is reflected in the sore backs and generalized body aches of the workers. Throughout my time with the farmworkers, food and the lack of leisure time were recurrent topics of conversation. In a conversation with a young woman, she said to me that "*in reality, we suffer for food when we come here, but also, there is no money there* [referring to Guatemala], *so we have to come here to buy food, like oil and sugar*." Her mother in law, a recent widowed woman who lost her husband from pesticide poisoning, adds, "*it is boring here because we only get beans and rice*". Her daughter-in-law continues: "*yes, what we miss the most is to rest and to eat various things. Back in our village we have milpa, frijol, varieties of squash, and vegetables*." On a different occasion, while harvesting coffee with a couple, the man told me "*we live on corn, and if there is corn there will always be something to eat, but we need to come here to earn some money too, some centavitos, because the milpa is not enough*".

Despite the harsh conditions lived during this time in the plantation, the harvest season is an opportunity to earn money. Farmworkers get paid based on "piece rate" (quantity of coffee harvested), rather than per day or task performed. Each basket of coffee– also called an *octavo*– earns $15 pesos (~0.8 USD), and a full burlap sack requires eight baskets and has a final payout of $120 pesos. During productive days, families can harvest up to four burlap sacks of coffee.

The contradictions of organic shade-grown coffee: the fear of what hides beneath the *hojarasca*

I have laid out the living and working conditions of farmworkers in a coffee plantation. In this section, I highlight the ways in which conservation narratives meet these everyday experiences of farmworkers. I argue that the social reality in this labor-intensive system contrasts sharply with what is presented in the organic shade-grown coffee imaginary. Further, I question whether biodiversity conservation can offer benefits to farmworkers, where systemic vulnerabilities (Holmes 2013), and food insecurities (Quandt et al. 2004) are a major concern. From my position as an agroecologist, I reflect on the effects of the conservationist narrative on this system: what we as scientists see as an opportunity to explore questions in ecology and conservation, and what eco-tourists and nature lovers see as a "heavenly paradise amid the rainforest", is not necessarily perceived in the same way by plantation workers. To a certain extent, the conservation narrative prevalent in organic shade-grown coffee plantations relies on the exclusion of farmworkers, because it represents shade-grown coffee plantations as places of social and ecological wellbeing that, if acknowledged, would make those narratives less idyllic. In this sense, the conservation narratives laid out above that sustain such an imaginary are at odds with the farmworker lived experience in the coffee plantation.

One of the most evident contradictions of organic shade-grown coffee is the fear of snakes and stinging ants that hide in the dense vegetation. In shade-grown coffee plantations, the dense shade– which is sometimes managed inadequately–, is often accompanied by a dense pad of *hojarasca* (leaf litter), which is substantially important for nutrient cycling in an organic system. The trees, which are in their majority leguminous species (*Inga* spp.), supplement coffee plants with Nitrogen, a highly limiting nutrient for coffee production. Farmworkers express their fear of what lies beneath the *hojarasca*: snakes, spiders, and stinging ants. For instance, a woman harvesting coffee in a highly-shaded area told me: "*when there is shade there is a lot of leaf litter and it is frightening because there are snakes, it is also frightening to go into the dense vegetation"*. Moreover, although the lack of herbicide application in conventional plantations might represent a benefit to farmworkers, some compare the organic shade-grown coffee plantation with the conventional regime, where "*the ground is clean*": "*it is easier to work* [in the conventional plantation] *because it is well weeded and you can work well, or you can even just go take a walk, but here I am afraid because there are some very big snakes, because the weeds are very tall"*. While picking coffee in a steep and densely vegetated area, another woman said to me: *"It is hard to pick coffee here, and worse when the weeds are tall like here* [looking down at the vegetation that reaches beyond her waist]. *The coffee is very scarce. We barely pick any … then when one goes to deliver the coffee, they take a bit more from you, because they fix the boxes"*.

Another contradiction in shade coffee is that conserving biodiversity can promote natural pest control, but organisms that control pests may also pester humans. For example, ants have had considerable attention in the ecological literature, as they are important natural enemies of major coffee pests (Morris et al. 2018). Despite the attention placed on the beneficial effect of these organisms, much less attention has been given to potential disservices and social tradeoffs associated with their conservation in coffee systems. This, as well as the fear associated with the dense vegetation, poses an important contradiction to management and conservation. The tropical fire ant (*Solenopsis geminata*) is the most feared ant species, it nests on the ground close to coffee plants and has a very powerful sting. Farmworkers often advise their children about ants, because many of them wear sandals or go barefoot to the field, as they cannot afford to buy rubber boots. Other species of ants are less harmful, but harvesting coffee in plants that host ant nests is not considered a pleasant experience. While harvesting coffee among ants, it is common to be bitten by the aggressive *Azteca* ant. I asked a family "*what do you do when you find a plant with this many ants*?". They replied, "*Nothing, if we don't harvest all the coffee the caporal scolds us*". The conflict here is twofold. On the one hand, the farmworker wishes to harvest coffee in a "clean" space, free of snakes and the nuisance of ants, as this evidently adds stress and anxiety to the everyday working experience. On the other hand, management practices in coffee production in general, necessitate that all fruits are harvested, because leaving ripe fruits in the field is an important source of pests. This contradiction poses an important challenge for coffee management, and for the conservation discourse.

The experience of farmworkers in this labor-intensive system, as well as the experience in relation to ecological attributes of the organic shade-grown coffee plantation, is accentuated by strict regulations surrounding the use of natural resources. Particularly, farm owners and administrators emphasize the prohibition around hunting. Although these regulations sustain a fundamental aspect of the conservation discourse in organic shade-grown coffee plantations, hunting allows farmworkers to diversify their diets. From the perspective of the farmworkers, the illegality of this practice presents a barrier to improving their living conditions. Migrant farmworkers are not allowed to bring dogs to the plantation, but borrow hunting dogs from their families or friends that are established farmworkers. The practice is so common among farmworkers, that there is chatter about who has the best hunting dog. At night, farmworkers gather in the lowlands of the plantation and hunt for hours in the hopes of finding armadillo, andasolo, tlacoache, and tepezcuintle. At the end of the harvest season, when the seasonal farmworkers prepare to return home, established workers sell their good hunting dogs for up to $1000 pesos (~53 USD) to migrant workers who purchase them using the earnings from the harvest season.

Challenges and visions of *los finqueros*

In the process of describing the everyday-lived-experience of farmworkers, is important to also recognize that the experience of the *finqueros* themselves is often overlooked, which in turn encourages a shallow understanding of the complexity of the problems faced by migrant workers in coffee plantations. Similar to what Holmes (2013) describes in the case of migrant farmworkers in US agriculture, the increasingly corporatized market "squeezes growers such that they cannot easily imagine increasing the pay of the pickers or improving the labor camps without bankrupting the farm" (2013:52). As he continues, "perhaps instead of blaming the growers, it is more appropriate to understand them as human beings doing the best they can in the midst of an unequal and harsh system" (2013:53).

The struggle in coffee plantations is experienced on its own way by the *finqueros*, who find themselves "squeezed" between the pressure of the market, increasing indebtedness and the social stigma that accompanies large plantations in this region. The *finqueros* I interviewed for this work were generally concerned about the living conditions of their workers and expressed future plans to improve mostly infrastructure, but find themselves with their hands tied in the face of low prices and few economic benefits from the premiums offered by the specialty market.

On the one hand *finqueros* most catch up with current trends that include roasting their own coffee, which requires special infrastructure, special training, as well as high investments. On the other hand, growers have also had to incorporate the touristic aspect of their plantations, create and recreate the colonial stories that forged these places, build attractive bungalows and spas, and sell coffee as a whole new "experience of the senses", that includes biodiversity conservation at its center and the recasting of colonial narratives (Lyon 2013). As one of them puts it: "el turismo hace maravillas" (tourism makes wonders). In addition, in order to increase economic gain, *finqueros* have also started to diversify their income, not only through tourism, but also through the production of ornamentals, cardamom, timber, and medicinal plants, which marketable value increases when being planted along with coffee.

Low and unstable coffee prices, in combination to a changing climate and disease outbreaks, add to the struggle of coffee growers, which blends with the problem of low productivity of their shade-grown coffee plantations, and labor shortages for this region[7], a problem that is not new to the region (Renard 2011). To add to this problematic, Renard (2011) points out: " The liberalization of the international coffee market combined with a sharply reduced state intervention engendered the control over coffee production by a few transnational companies and the collapse of the economy of small producers. Combined with natural disasters whose effects were not addressed by the neoliberal state, this situation caused the region to be bypassed by Guatemalan labor that now prefers direct migration to the United States" (2011:147).

Moreover, in the past decade, finqueros in Soconusco and Central America were also challenged by two important coffee leaf rust disease outbreaks caused by the fungus *Hemileia vastatrix*, that practically swept entire coffee plantations in the region in 2008 and 2013 (Avelino et al. 2015). This disease is highly associated with climate change (Morris et al. 2016), another important environmental challenge that is projected to increase climatic variability and the intensity of rain for this region (Knutson et al. 2010).

---

[7] Farmworkers and finqueros expressed their concern about low exchange rates between Mexican pesos and Guatemalan Quetzales, which encourages labor shortages in coffee plantations. A large number of farmworkers mention that many of them prefer to look for work in Guatemala or migrate to The United States.

Conclusion: acknowledgement of the farmworkers experience

The Soconusco region is often presented in the popular discourse as a magical region with vast biodiversity. At the center of the imaginary is the shade-grown coffee farm, which is offered to the world as a steward of the land, a guardian of endangered species, a place for retreat within lush gardens overlooking a seemingly natural, remote land. However, within the wrinkles and creases of this portrait lies the experience of farmworkers laboring in the fields, the struggles, the joys, and the stories that give meaning to this place.

Considering that various visions, knowledge, and experiences converge within the coffee plantation, we can begin to understand it as a co-produced space, one that is constructed through the ecological views and social relations of diverse actors that produce this space (Besky 2013): the market and the consumers, the workers and their everyday labor experiences, the owners with their own struggles and desires, and dominant conservation narratives. In some ways, the convergence of ecological knowledges in the coffee plantation, the alternative market boom, and the conservation narrative sold in "First World" cafeterias, has created a particular coffee tropical imaginary. In this sense, coffee produced on shaded and biodiverse plantations is often targeted toward a specific environmentally conscious, upper class consumer that engages with these narratives by both directly buying the coffee as commodity, and through eco-tourist vacations to coffee plantations. Shaded plantation coffee is also presented as a luxurious commodity associated with a type of tropical imaginary that, in actuality, is produced at the expense of farmworkers' living and working conditions.

This work questions the practices and narratives surrounding biodiversity conservation in the context of farmworkers' lives. Farmworkers in coffee plantations are a highly vulnerable sector in the coffee production chain. In these labor-intensive systems, they not only suffer unfair living and working conditions, but also face fears and anxieties posed by conservation practices and discourses: the need to harvest coffee in the dense vegetation or abundant leaf litter, and the strict regulation around the use of resources to supplement their daily diets.

Multiple imaginaries have shape this landscape dominated by coffee. On the one hand, neoliberal market trends in coffee production– which have brought the multiple certification schemes we can find in the supermarket– have imposed dogmatic regimes around the production of coffee (West 2012), which– as I have shown– are at odds with people's needs and desires. On the other hand, scientists have often promoted an imaginary around shade-grown coffee production, which reminds us of a natural or seemingly natural portrait, in which humans are non-existent (Slater 1996). These imaginaries, supported by an exclusionary narrative of biodiversity conservation, obscure the lived experience of farmworkers.

I also bring attention to an important problem in organic production, which is the fact that it does not question social conditions, particularly of farmworkers, despite presenting itself as a label with social responsibility. Issues such as poor wages, structural violence, social segregation, and racism are aspects of the daily lives of farmworkers in systems that depend heavily on migrant labor (Holmes 2013). However, there is a strong emphasis on ecological sustainability goals, that ignore such issues. The social implications of these labels and discourses about conservation in a labor-intensive system are striking. Therefore, in the practice of questioning our current food regime, we must reflect and recognize how narratives of conservation might reinforce farmworkers' marginalization.

A change of paradigm in the conservation narrative in shaded coffee plantations should acknowledge workers' experiences, but not only the ways in which farmworkers experience injustices in the plantation, such as prohibitions, unequal pay, forced labor, bodily pain, and unfair living conditions; also, the potential subtle and creative ways of contesting them, which challenges a potential passive and subjugated vision that their experiences might provoke on the reader. For example, disregarding hunting prohibitions, using the work in coffee plantations to reproduce the peasant living back at home, appropriating land in abandoned areas of the plantation, and gossiping and character assassination of powerful figures within the hierarchy of the plantation (Scott 2008), all as an act of autonomy or "everyday resistance". Similarly, I acknowledge the fact that plantation owners also find themselves squeezed in various narratives: the push to be more ecologically sustainable, the unforgiving reputation that many of them receive by the media and the adjacent ejidos, the push to be more productive in a competitive market while being socially just, all within a reality of low coffee prices, and increasing indebtedness to international buyers and powerful corporations, such as Nestle and Starbucks. In some way, *finqueros* benefit from the conservation narratives and the imaginary of shade grown coffee plantations, as they are able to accommodate their coffee with much more identity and value in the market.

Finally, this research invites all of us as scientists, tourists, and coffee consumers to rethink our political actions as we construct the spaces that we visit, study, and imagine. In a time of increasing violence towards immigrants, and a food regime increasingly dominated by corporations, it is pertinent to ask how our actions change and perpetuate current neoliberal models, that are ultimately detrimental to the lives of people that live with and from coffee.

CONCLUSION

Coffee is an important agricultural system for Latin America, supporting millions of farmers and national economies. A large portion of coffee in Latin America is produced under the shade of forests, making this habitat important for the conservation of biodiversity and ecosystem functions, as well as the sustenance of human livelihoods. Through the analysis of species interactions and human lived-experiences I provide a glimpse to the social and ecological complexities of organic shade-grown coffee plantations. Shaded coffee plantations are complex socioecological systems constructed through our scientific understandings of ecological interactions, insects and other organisms, as well as by the experience of people making a living in these spaces. My work contributes to our understanding of complexity through the lens of humans and non-humans, and paints a portrait of shade grown coffee that shows *Los claroscuros del café*, or the disambiguation of this space. On the one hand, my research contributes to our understanding of the mechanisms that maintain species diversity and complex interactions in complex agroecosystems. From an agroecological perspective, resource heterogeneity, and the availability of a diverse suit of resources, including food, nesting and connectivity resources can promote species richness and biological pest control in coffee systems. My research highlights the importance of conserving specific resources for insects in the face of increasing agricultural simplification. From a political ecology perspective, my research brings attention to an overlooked aspect of shaded-coffee systems, which is the lived experience of farmworkers, and indirectly invites all of us to rethink our political actions as we construct the spaces that we study.

REFERENCES

Abdulla, N. R., G. M. Rwegasira, K. M. V. Jensen, M. W. Mwatawala, and J. Offenberg. 2016. Control of mango seed weevils (Sternochetus mangiferae) using the African Weaver Ant (Oecophylla longinoda Latreille) (Hymenoptera: Formicidae). Journal of Applied Entomology **140**:500-506.

Adams, B. J., S. A. Schnitzer, and S. P. Yanoviak. 2017. Trees as islands: canopy ant species richness increases with the size of liana-free trees in a Neotropical forest. Ecography **40**:1067-1075.

Agrawal, A. A., D. D. Ackerly, F. Adler, A. E. Arnold, C. Cáceres, D. F. Doak, E. Post, P. J. Hudson, J. Maron, and K. A. Mooney. 2007. Filling key gaps in population and community ecology. Frontiers in Ecology and the Environment **5**:145-152.

Aguilar, J., D. Monaenkova, V. Linevich, W. Savoie, B. Dutta, H.-S. Kuan, M. Betterton, M. Goodisman, and D. Goldman. 2018. Collective clog control: Optimizing traffic flow in confined biological and robophysical excavation. Science **361**:672-677.

Albrecht, M., and N. J. Gotelli. 2001. Spatial and temporal niche partitioning in grassland ants. Oecologia **126**:134-141.

Allen, P., and C. Sachs. 1993. Sustainable agriculture in the United States: Engagements, silences, and possibilities for transformation. Food for the future: Conditions and contradictions of sustainability:139-167.

Andersen, A. N. 1986. Diversity, seasonality and community organization of ants at adjacent heath and woodland sites in southeastern Australia. Australian Journal of Zoology **34**:53-64.

Andersen, A. N. 2008. Not enough niches: non-equilibrial processes promoting species coexistence in diverse ant communities. Austral Ecology **33**:211-220.

Andow, D. A. 1991. Vegetational diversity and arthropod population response. Annual review of entomology **36**:561-586.

Apple, J., and D. Feener Jr. 2001. Ant visitation of extrafloral nectaries of Passiflora: the effects of nectary attributes and ant behavior on patterns in facultative ant-plant mutualisms. Oecologia **127**:409-416.

Armbrecht, I., and M. C. Gallego. 2007. Testing ant predation on the coffee berry borer in shaded and sun coffee plantations in Colombia. Entomologia Experimentalis et Applicata **124**:261-267.

Armbrecht, I., and I. Perfecto. 2003. Litter-twig dwelling ant species richness and predation potential within a forest fragment and neighboring coffee plantations of contrasting habitat quality in Mexico. Agriculture, Ecosystems & Environment **97**:107-115.

Armbrecht, I., I. Perfecto, and E. Silverman. 2006. Limitation of nesting resources for ants in Colombian forests and coffee plantations. Ecological Entomology **31**:403-410.

Armbrecht, I., I. Perfecto, and J. Vandermeer. 2004. Enigmatic biodiversity correlations: ant diversity responds to diverse resources. Science **304**:284-286.

Armbrecht, I., L. Rivera, and I. Perfecto. 2005. Reduced Diversity and Complexity in the Leaf-Litter Ant Assemblage of Colombian Coffee Plantations. Conservation biology **19**:897-907.

Arnold, M., B. Powell, P. Shanley, and T. Sunderland. 2011. Editorial: Forests, biodiversity and food security. International Forestry Review **13**:259-264.

Arroyo-Rodríguez, V., N. Asensio, J. Dunn, J. Cristóbal, and A. González-Zamora. 2015. Ecology of Lianas.

Avelino, J., M. Cristancho, S. Georgiou, P. Imbach, L. Aguilar, G. Bornemann, P. Läderach, F. Anzueto, A. J. Hruska, and C. Morales. 2015. The coffee rust crises in Colombia and Central America (2008–2013): impacts, plausible causes and proposed solutions. Food Security **7**:303-321.

Bacon, C. 2005. Confronting the coffee crisis: can fair trade, organic, and specialty coffees reduce small-scale farmer vulnerability in northern Nicaragua? World Development **33**:497-511.

Bacon, C. M., V. Ernesto Mendez, M. E. F. Gomez, D. Stuart, and S. R. D. Flores. 2008. Are sustainable coffee certifications enough to secure farmer livelihoods? The millenium development goals and Nicaragua's Fair Trade cooperatives. Globalizations **5**:259-274.

Bael, S. A. V., S. M. Philpott, R. Greenberg, P. Bichier, N. A. Barber, K. A. Mooney, and D. S. Gruner. 2008. Birds as predators in tropical agroforestry systems. Ecology **89**:928-934.

Barrera, J. 2002. La Broca del café: Una plaga que llegó para quedarse. Tres Plagas del Café en Chiapas. . El Eolegio de la Frontera Sur:17-20.

Bartra, A. 1996. El México bárbaro: plantaciones y monterías del sureste durante el porfiriato. El Atajo.

Bates, D., M. Maechler, B. Bolker, S. Walker, R. H. B. Christensen, H. Singmann, B. Dai, and G. Grothendieck. 2014. Package 'lme4'. R foundation for statistical computing, Vienna **12**.

Berdej, S., M. Andrachuk, and D. Armitage. 2015. Conservation narratives and their implications in the Coral Triangle Initiative. Conservation and Society **13**:212.

Besky, S. 2013. The Darjeeling distinction: Labor and justice on fair-trade tea plantations in India. Univ of California Press.

Blüthgen, N., and K. Fiedler. 2004a. Competition For Composition: Lessons From Nectar-Feeding Ant Communities. Ecology **85**:1479-1485.

Blüthgen, N., and K. Fiedler. 2004b. Preferences for sugars and amino acids and their conditionality in a diverse nectar-feeding ant community. Journal of Animal Ecology **73**:155-166.

Blüthgen, N., and K. Reifenrath. 2003. Extrafloral nectaries in an Australian rainforest: structure and distribution. Australian Journal of Botany **51**:515-527.

Blüthgen, N., M. Verhaagh, W. Goitía, K. Jaffé, W. Morawetz, and W. Barthlott. 2000. How plants shape the ant community in the Amazonian rainforest canopy: the key role of extrafloral nectaries and homopteran honeydew. Oecologia **125**:229-240.

Bos, M. M., P. Höhn, S. Saleh, B. Büche, D. Buchori, I. Steffan-Dewenter, and T. Tscharntke. 2007. Insect diversity responses to forest conversion and agroforestry management. Pages 277-294 Stability of Tropical Rainforest Margins. Springer.

Bray, D. B., J. L. P. Sanchez, and E. C. Murphy. 2002. Social dimensions of organic coffee production in Mexico: lessons for eco-labeling initiatives. Society &Natural Resources **15**:429-446.

BRÜHL, C. A., G. GUNSALAM, and K. E. LINSENMAIR. 1998. Stratification of ants (Hymenoptera, Formicidae) in a primary rain forest in Sabah, Borneo. Journal of Tropical Ecology **14**:285-297.

Byk, J., and K. Del-Claro. 2011. Ant–plant interaction in the Neotropical savanna: direct beneficial effects of extrafloral nectar on ant colony fitness. Population Ecology **53**:327-332.

Camargo, P. H., M. M. Martins, R. M. Feitosa, and A. V. Christianini. 2016. Bird and ant synergy increases the seed dispersal effectiveness of an ornithochoric shrub. Oecologia **181**:507-518.

Camarota, F., S. Powell, H. L. Vasconcelos, G. Priest, and R. J. Marquis. 2015. Extrafloral nectaries have a limited effect on the structure of arboreal ant communities in a Neotropical savanna. Ecology **96**:231-240.

Camilo, J. F., F. F. Olivares, and H. A. Jiménez. 2003. Phenology and reproduction of the coffee borer (Hypothenemus hampei Ferrari) during the fruit growth. Agronomía Mesoamericana **14**:59-63.

Campbell, L. 2002a. Conservation Narratives in Costa Rica: Conflict and Co-existence.

Campbell, L. M. 2002b. Conservation narratives and the" received wisdom" of ecotourism: case studies from Costa Rica. International Journal of Sustainable Development **5**:300-325.

Campbell, L. M. 2002c. Conservation narratives in Costa Rica: conflict and co-existence. Development and Change **33**:29-56.

Carey, B., K. Visscher, and J. Heraty. 2012. Nectary use for gaining access to an ant host by the parasitoid Orasema simulatrix (Hymenoptera, Eucharitidae). Journal of Hymenoptera Research **27**:47-65.

Castillo, M. Á., and R. Casillas R. 1988. Características básicas de la migración guatemalteca al Soconusco chiapaneco. Estudios demográficos y urbanos:537-562.

Caswell, M., V. E. Méndez, and C. M. Bacon. 2012. Food security and smallholder coffee production: current issues and future directions.

Catling, P. M. 1997. Influence of aerial Azteca nests on the epiphyte community of some Belizean orange orchards. Biotropica **29**:237-242.

Chamberlain, S. A., J. L. Bronstein, and J. A. Rudgers. 2014. How context dependent are species interactions? Ecology Letters **17**:881-890.

Chase, J. M. 2003. Community assembly: when should history matter? Oecologia **136**:489-498.

Chesson, P. 2000. General theory of competitive coexistence in spatially-varying environments. Theoretical Population Biology **58**:211-237.

Clausen, C. P. 1940a. Entomophagous insects. McGraw Hill Book: London.

Clausen, C. P. 1940b. The oviposition habits of the Eucharidae (Hymenoptera). Journal of the Washington Academy of Sciences **30**:504-516.

Clay, N. A., M. Bauer, M. Solis, and S. P. Yanoviak. 2010. Arboreal substrates influence foraging in tropical ants. Ecological Entomology **35**:417-423.

Cogni, R., A. V. Freitas, and P. S. Oliveira. 2003. Interhabitat differences in ant activity on plant foliage: ants at extrafloral nectaries of Hibiscus pernambucensis in sandy and mangrove forests. Entomologia experimentalis et applicata **107**:125-131.

Cook, S. C., and D. W. Davidson. 2006. Nutritional and functional biology of exudate-feeding ants. Entomologia Experimentalis et Applicata **118**:1-10.

Crowder, L., E. MColeum, and T. Martin. 1998. Changing perspectives on food web interactions in lake littoral zones. . In: Jeppesen E, Sondergaard M, Sondergaard M, Christoffersen K, Eds.

Daily, G. 1997. Nature's services: societal dependence on natural ecosystems. Island Press.

Damon, A. 2000. A review of the biology and control of the coffee berry borer, Hypothenemus hampei (Coleoptera: Scolytidae). Bulletin of entomological research **90**:453-465.

Davidson, D. W. 1997. The role of resource imbalances in the evolutionary ecology of tropical arboreal ants. Biological Journal of the Linnean Society **61**:153-181.

Davidson, D. W., S. C. Cook, R. R. Snelling, and T. H. Chua. 2003. Explaining the abundance of ants in lowland tropical rainforest canopies. Science **300**:969-972.

De la Mora, A., J. A. García-Ballinas, and S. M. Philpott. 2015. Local, landscape, and diversity drivers of predation services provided by ants in a coffee landscape in Chiapas, Mexico. Agriculture, Ecosystems & Environment **201**:83-91.

De la Mora, A., C. Murnen, and S. Philpott. 2013. Local and landscape drivers of biodiversity of four groups of ants in coffee landscapes. Biodiversity and conservation **22**:871-888.

De La Mora, A., and S. M. Philpott. 2010. Wood-Nesting Ants and Their Parasites in Forests and Coffee Agroecosystems. Environmental Entomology **39**:1473-1481.

de Vega, C., C. M. Herrera, and S. Dötterl. 2014. Floral volatiles play a key role in specialized ant pollination. Perspectives in Plant Ecology, Evolution and Systematics **16**:32-42.

De Vos, J. 2002. Una tierra para sembrar sueños: historia reciente de la Selva Lacandona. Ciesas.

Deyrup, M., L. Davis, and S. Cover. 2000. Exotic ants in Florida. Transactions of the American Entomological Society:293-326.

Díaz, S., and M. Cabido. 2001. Vive la difference: plant functional diversity matters to ecosystem processes. Trends in ecology & evolution **16**:646-655.

Donald, P. F. 2004. Biodiversity impacts of some agricultural commodity production systems. Conservation biology **18**:17-38.

Donoso, D. A. 2014. Assembly mechanisms shaping tropical litter ant communities. Ecography **37**:490-499.

Drake, J. A. 1991. Community-assembly mechanics and the structure of an experimental species ensemble. American Naturalist:1-26.

Ehrlich, P. R., and A. H. Ehrlich. 1981. Extinction: the causes and consequences of the disappearance of species. Random House New York.

Elston, D. A., R. Moss, T. Boulinier, C. Arrowsmith, and X. Lambin. 2001. Analysis of aggregation, a worked example: numbers of ticks on red grouse chicks. Parasitology **122**:563-569.

Ennis, K. K. 2010. A thesis entitled: Ground-foraging ant diversity and the role of an aggressive ant (Azteca instabilis) in coffee agroecosystems. University of Michigan.

Escamilla Prado, E., E. Garcia Perez, R. Mosqueda Vazquez, V. H. Santoyo Cortes, and J. E. Pacheco Velasco. 1997. Evaluation of coffee production systems in Veracruz State. Publicacion especial (Mexico).

Farji-Brener, A. G., G. Barrantes, O. Laverde, C. Fierro, xf, K. n, Bascop, xe, F., xf, and A. pez. 2007. Fallen Branches as Part of Leaf-Cutting Ant Trails: Their Role in Resource Discovery and Leaf Transport Rates in Atta cephalotes. Biotropica **39**:211-215.

Feener, J., Donald H. 2000. Is the assembly of ant communities mediated by parasitoids? Oikos **90**:79-88.

Fewell, J. H. 1988. Energetic and time costs of foraging in harvester ants, Pogonomyrmex occidentalis. Behavioral Ecology and Sociobiology **22**:401-408.

Finke, D. L., and R. F. Denno. 2002. Intraguild predation diminished in complex-structured vegetation: implications for prey suppression. Ecology **83**:643-652.

Fisher, B., R. K. Turner, and P. Morling. 2009. Defining and classifying ecosystem services for decision making. Ecological economics **68**:643-653.

Floren, A., A. Biun, and E. K. Linsenmair. 2002. Arboreal ants as key predators in tropical lowland rainforest trees. Oecologia **131**:137-144.

Floren, A., and K. E. Linsenmair. 2005. The importance of primary tropical rain forest for species diversity: an investigation using arboreal ants as an example. Ecosystems **8**:559-567.

Foster, B. L., T. L. Dickson, C. A. Murphy, I. S. Karel, and V. H. Smith. 2004. Propagule pools mediate community assembly and diversity-ecosystem regulation along a grassland productivity gradient. Journal of Ecology **92**:435-449.

Gardener, M. C., and M. P. Gillman. 2002. The taste of nectar–a neglected area of pollination ecology. Oikos **98**:552-557.

Geertz, C. 1994. Thick description: Toward an interpretive theory of culture. Readings in the philosophy of social science:213-231.

Gentry, G. 2003. Multiple parasitoid visitors to the extrafloral nectaries of Solanum adherens. Is S. adherens an insectary plant? Basic and Applied Ecology **4**:405-411.

Gibson, G. A., J. T. Huber, and J. B. Woolley. 1997. Annotated keys to the genera of Nearctic Chalcidoidea (Hymenoptera). NRC Research Press.

Gonthier, D. J., K. K. Ennis, S. M. Philpott, J. Vandermeer, and I. Perfecto. 2013. Ants defend coffee from berry borer colonization. BioControl **58**:815-820.

González-Teuber, M., and M. Heil. 2009. The role of extrafloral nectar amino acids for the preferences of facultative and obligate ant mutualists. Journal of chemical ecology **35**:459-468.

Gordon, D. M. 1996. The organization of work in. Nature **380**:14.

Gordon, D. M. 2012. The dynamics of foraging trails in the tropical arboreal ant Cephalotes goniodontus. PLoS One **7**:e50472.

Greenberg, R., P. Bichier, A. C. Angon, C. MacVean, R. Perez, and E. Cano. 2000. The impact of avian insectivory on arthropods and leaf damage in some guatemalan coffee plantations. Ecology **81**:1750-1755.

Gresser, C., and S. Tickell. 2002. Mugged: Poverty in your coffee cup. Oxfam.

Gross, P. 1993. Insect behavioral and morphological defenses against parasitoids. Annual review of entomology **38**:251-273.

Guthman, J. 2014. Agrarian dreams: The paradox of organic farming in California. Univ of California Press.

Halaj, J., D. W. Ross, and A. R. Moldenke. 1998. Habitat structure and prey availability as predictors of the abundance and community organization of spiders in western Oregon forest canopies. Journal of Arachnology:203-220.

Hammer, Ø., D. Harper, and P. Ryan. 2001. PAST-Palaeontological statistics. www. uv. es/~ pardomv/pe/2001_1/past/pastprog/past. pdf, acessado em **25**:2009.

Hashimoto, Y., Y. Morimoto, E. S. Widodo, and M. Mohamed. 2006. Vertical distribution pattern of ants in a Bornean tropical rainforest (Hymenoptera: Formicidae). Sociobiology **47**:697-710.

Hempson, G. P., A. W. Illius, H. H. Hendricks, W. J. Bond, and S. Vetter. 2015. Herbivore population regulation and resource heterogeneity in a stochastic environment. Ecology **96**:2170-2180.

Herreid, J. S., and J. M. Heraty. 2017. Hitchhikers at the dinner table: a revisionary study of a group of ant parasitoids (Hymenoptera: Eucharitidae) specializing in the use of extrafloral nectaries for host access. Systematic Entomology **42**:204-229.

HilleRisLambers, J., P. B. Adler, W. S. Harpole, J. M. Levine, and M. M. Mayfield. 2012. Rethinking Community Assembly through the Lens of Coexistence Theory. Annual Review of Ecology, Evolution, and Systematics **43**:227-248.

Hölldobler, B. 1990. The ants. Harvard University Press.

Holmes, S. 2013. Fresh fruit, broken bodies: Migrant farmworkers in the United States. Univ of California Press.

Holmes, S. M. 2011. Structural vulnerability and hierarchies of ethnicity and citizenship on the farm. Medical anthropology **30**:425-449.

Houadria, M., A. Salas-Lopez, J. Orivel, N. Bleuthgen, and F. Menzel. 2014. Trophic functions, a structuring trait for tropical ant assemblages.*in* 17th Congress of the International Union for the Study of Social Insects (IUSSI), Cairns, Australia, 13-18 July 2014. IUSSI.

Howard, R., G. Pérez-Lachaud, and J.-P. Lachaud. 2014. Cuticular hydrocarbons of Kapala sulcifacies (Hymenoptera: Eucharitidae) and its host, the ponerine ant Ectatomma ruidum (Hymenoptera: Formicidae). Annals of the Entomological Society of America **94**:707-716.

Huang, H., and P. Yang. 1987. The ancient cultured citrus ant. BioScience **37**:665-671.

Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography (MPB-32). Princeton University Press.

Huston, M. A. 1999. Local processes and regional patterns: appropriate scales for understanding variation in the diversity of plants and animals. Oikos:393-401.

Isakson, S. R. 2009. No hay ganancia en la milpa: the agrarian question, food sovereignty, and the on-farm conservation of agrobiodiversity in the Guatemalan highlands. The Journal of Peasant Studies **36**:725-759.

Jaramillo, J., C. Borgemeister, and P. Baker. 2006. Coffee berry borer Hypothenemus hampei (Coleoptera: Curculionidae): searching for sustainable control strategies. Bulletin of entomological research **96**:223-233.

Jha, S., C. M. Bacon, S. M. Philpott, V. E. Méndez, P. Läderach, and R. A. Rice. 2014. Shade Coffee: Update on a Disappearing Refuge for Biodiversity. BioScience **64**:416-428.

Jiménez-Soto, E., J. A. Cruz-Rodríguez, J. Vandermeer, and I. Perfecto. 2013. <i>Hypothenemus hampei</i> (Coleoptera: Curculionidae) and its Interactions With <i>Azteca instabilis</i> and <i>Pheidole synanthropica</i> (Hymenoptera: Formicidae) in a Shade Coffee Agroecosystem. Environmental Entomology **42**:915-924.

Jiménez-Soto, E., and S. M. Philpott. 2015. Size matters: nest colonization patterns for twig-nesting ants. Ecology and Evolution:n/a-n/a.

Johnson, M., J. Kellermann, and A. Stercho. 2010. Pest reduction services by birds in shade and sun coffee in Jamaica. Animal conservation **13**:140-147.

Kaspari, M. 1996. Testing Resource-Based Models of Patchiness in Four Neotropical Litter Ant Assemblages. Oikos **76**:443-454.

Kaspari, M., J. Pickering, and D. Windsor. 2001. The reproductive flight phenology of a neotropical ant assemblage. Ecological Entomology **26**:245-257.

Kearney, M., and W. Porter. 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. Ecology letters **12**:334-350.

Klein, A. M., I. Steffan-Dewenter, and T. Tscharntke. 2003. Pollination of Coffea canephora in relation to local and regional agroforestry management. Journal of Applied Ecology **40**:837-845.

Klimes, P., P. Fibich, C. Idigel, and M. Rimandai. 2015. Disentangling the diversity of arboreal ant communities in tropical forest trees. PloS one **10**:e0117853.

Knutson, T. R., J. L. McBride, J. Chan, K. Emanuel, G. Holland, C. Landsea, I. Held, J. P. Kossin, A. K. Srivastava, and M. Sugi. 2010. Tropical cyclones and climate change. Nature Geoscience **3**:157.

Koptur, S. 1991. Extrafloral nectaries of herbs and trees: modelling the interaction with ants and parasitoids. Huxley, C, R,, Cutler, D, F ed (s). Ant-plant interactions. Oxford Univ. Press: Oxford, etc:213-230.

Koptur, S. 1992. Interactions between insects and plants mediated by extrafloral nectaries. CRC series on insect/plant interactions **4**:85-132.

Koptur, S. 1994. Floral and extrafloral nectars of Costa Rican Inga trees: a comparison of their constituents and composition. Biotropica:276-284.

Koptur, S., I. M. Jones, and J. E. Peña. 2015. The influence of host plant extrafloral nectaries on multitrophic interactions: an experimental investigation. PloS one **10**:e0138157.

Kremen, C. 2005. Managing ecosystem services: what do we need to know about their ecology? Ecology letters **8**:468-479.

Lach, L., E. Hobbs, and E. Majer. 2009a. Herbivory-induced extrafloral nectar increases native and invasive ant worker survival. Popul Ecol **51:237–243**.

Lach, L., R. J. Hobbs, and J. D. Majer. 2009b. Herbivory-induced extrafloral nectar increases native and invasive ant worker survival. Population Ecology **51**:237-243.

Lachaud, J.-P., and G. Pérez-Lachaud. 2009. Impact of natural parasitism by two eucharitid wasps on a potential biocontrol agent ant in southeastern Mexico. Biological Control **48**:92-99.

Landis, D. A., F. D. Menalled, A. C. Costamagna, and T. K. Wilkinson. 2005. Manipulating plant resources to enhance beneficial arthropods in agricultural landscapes. Weed Science **53**:902-908.

Landis, D. A., S. D. Wratten, and G. M. Gurr. 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. Annual review of entomology **45**:175-201.

Langellotto, G. A., and R. F. Denno. 2004. Responses of invertebrate natural enemies to complex-structured habitats: a meta-analytical synthesis. Oecologia **139**:1-10.

Lanza, J., E. L. Vargo, S. Pulim, and Y. Z. Chang. 1993. Preferences of the fire ants Solenopsis invicta and S. geminata (Hymenoptera: Formicidae) for amino acid and sugar components of extrafloral nectars. Environmental Entomology **22**:411-417.

Larsen, A., and S. M. Philpott. 2010. Twig-Nesting Ants: The Hidden Predators of the Coffee Berry Borer in Chiapas, Mexico. Biotropica **42**:342-347.

Lassau, S. A., D. F. Hochuli, G. Cassis, and C. A. Reid. 2005. Effects of habitat complexity on forest beetle diversity: do functional groups respond consistently? Diversity and distributions **11**:73-82.

Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. Chase, M. Hoopes, R. Holt, J. Shurin, R. Law, and D. Tilman. 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecology letters **7**:601-613.

Leston, D. 1973. The ant mosaic-tropical tree crops and the limiting of pests and diseases. PANS Pest Articles & News Summaries **19**:311-341.

Liere, H., and A. Larsen. 2010. Cascading trait-mediation: disruption of a trait-mediated mutualism by parasite-induced behavioral modification. Oikos **119**:1394-1400.

Livingston, G., S. M. Philpott, and A. de la Mora Rodriguez. 2013. Do Species Sorting and Mass Effects Drive Assembly in Tropical Agroecological Landscape Mosaics? Biotropica **45**:10-17.

Livingston, G. F., and S. M. Philpott. 2010. A metacommmunity approach to co-occurrence patterns and the core-satellite hypothesis in a community of tropical arboreal ants. Ecological research **25**:1129-1140.

Longino, J. 2007a. Ants of costa rica. http://academic. evergreen. edu/projects/ants/AntsofCostaRica. html.

Longino, J. T. 2007b. A taxonomic review of the genus Azteca (Hymenoptera: Formicidae) in Costa Rica and a global revision of the aurita group. Magnolia Press Longwood, FL.

Longino, J. T., J. Coddington, and R. K. Colwell. 2002. The Ant Fauna of a Tropical Rain Forest: Estimating Species Richness Three Different Ways. Ecology **83**:689-702.

Lopez-Echeverria, M. E., and 2007. Las Fincas Cafetaleras Alemanas en el Soconusco: más de 150 años de experiencia. Universidad Autonoma de Chiapas, facultad de contaduria y administracion. Tuxtla Gutierrez, Chiapas, Mexico.

Lubertazzi, D., M. A. A. Lubertazzi, N. McCoy, A. D. Gove, J. D. Majer, and R. R. Dunn. 2010. The ecology of a keystone seed disperser, the ant Rhytidoponera violacea. Journal of Insect Science **10**.

Lurtz, C. M. 2016. Insecure Labor, Insecure Debt: Building a Workforce for Coffee in the Soconusco, Chiapas. Hispanic American Historical Review **96**:291-318.

Lyon, S. 2013. Coffee tourism in Chiapas: recasting colonial narratives for contemporary markets. Culture, Agriculture, Food and Environment **35**:125-139.

Marazzi, B., J. L. Bronstein, and S. Koptur. 2013. The diversity, ecology and evolution of extrafloral nectaries: current perspectives and future challenges. Annals of Botany **111**:1243-1250.

Martinez-Torres, M. E. 2006. Organic coffee: sustainable development by Mayan farmers. Ohio University Press.

Mayo, A., and M. Benabib. 2009. Testing Central Place Foraging Theory in the Ant Genus Pogonomyrmex: a review of the literature from 1977 through 2008.

Méndez, V. E. 2004. Traditional shade, rural livelihoods and conservation in small coffee farms and cooperatives of western El Salvador. University of California, Santa Cruz.

Mendez, V. E., C. M. Bacon, M. Olson, K. S. Morris, and A. Shattuck. 2010. Agrobiodiversity and Shade Coffee Smallholder Livelihoods: A Review and Synthesis of Ten Years of Research in Central America*. The Professional Geographer **62**:357-376.

Méndez, V. E., E. N. Shapiro, and G. S. Gilbert. 2009. Cooperative management and its effects on shade tree diversity, soil properties and ecosystem services of coffee plantations in western El Salvador. Agroforestry Systems **76**:111-126.

Moguel, P., and V. M. Toledo. 1999. Biodiversity conservation in traditional coffee systems of Mexico. Conservation biology **13**:11-21.

Morris, J. R., E. Jiménez-Soto, S. M. Philpott, and I. Perfecto. 2018. Ant-mediated (Hymenoptera: Formicidae) biological control of the coffee berry borer: diversity, ecological complexity, and conservation biocontrol. Myrmecological News **26**:1-17.

Morris, J. R., and I. Perfecto. 2016. Testing the potential for ant predation of immature coffee berry borer (Hypothenemus hampei) life stages. Agriculture, Ecosystems & Environment **233**:224-228.

Morris, J. R., J. Vandermeer, and I. Perfecto. 2015. A keystone ant species provides robust biological control of the coffee berry borer under varying pest densities. PloS one **10**:e0142850.

Morris, K. S., V. E. Mendez, and M. B. Olson. 2013. 'Los meses flacos': seasonal food insecurity in a Salvadoran organic coffee cooperative. The Journal of Peasant Studies **40**:423-446.

Morris, K. S., V. E. Méndez, M. van Zonneveld, A. Gerlicz, and M. Caswell. 2016. Agroecology and climate change resilience: In Smallholder Coffee Agroecosystems of Central America.

Myrdal, G. 1968. Asian drama, an inquiry into the poverty of nations. Asian drama, an inquiry into the poverty of nations.

Nestel, D., and F. Dickschen. 1990. The foraging kinetics of ground ant communities in different Mexican coffee agroecosystems. Oecologia **84**:58-63.

Nolasco, M. 1995. Migración indígena a las fronteras nacionales.

Novais, S. M., W. D. DaRocha, N. Calderón-Cortés, and M. Quesada. 2017. Wood-boring beetles promote ant nest cavities: extended effects of a twig-girdler ecosystem engineer. Basic and Applied Ecology **24**:53-59.

Offenberg, J. 2015. Ants as tools in sustainable agriculture. Journal of Applied Ecology **52**:1197-1205.

Orne, J., and M. Bell. 2015. An invitation to qualitative fieldwork: a multilogical approach. Routledge.

Oster, G. F., and E. O. Wilson. 1979. Caste and ecology in the social insects. Princeton University Press.

Ozaki, K., S. Takashima, and O. Suko. 2000. Ant predation suppresses populations of the scale insect Aulacaspis marina in natural mangrove forests. Biotropica **32**:764-768.

Pak, D., A. L. Iverson, K. K. Ennis, D. J. Gonthier, and J. H. Vandermeer. 2015. Parasitoid wasps benefit from shade tree size and landscape complexity in Mexican coffee agroecosystems. Agriculture, Ecosystems & Environment **206**:21-32.

Palmer, T. M., M. L. Stanton, and T. P. Young. 2003. Competition and coexistence: exploring mechanisms that restrict and maintain diversity within mutualist guilds. The American Naturalist **162**:S63-S79.

Peng, R., and K. Christian. 2014. Weaver ant role in cashew orchards in Vietnam. Journal of economic entomology **107**:1330-1338.

Perez-Morales, J. V., L. M. Pinzon-Picaseno, and R. Echenique-Manrique. 1977. Laboratory test on natural resistance of tropical mexican woods to wood rotting fungi. Boletin de la Sociedad Mexicana de Micologia:99-110.

Perfecto, I., R. A. Rice, R. Greenberg, and M. E. Van der Voort. 1996. Shade coffee: a disappearing refuge for biodiversity. BioScience:598-608.

Perfecto, I., and J. Vandermeer. 2006. The effect of an ant-hemipteran mutualism on the coffee berry borer (Hypothenemus hampei) in southern Mexico. Agriculture, Ecosystems & Environment **117**:218-221.

Perfecto, I., J. H. Vandermeer, G. L. Bautista, G. I. Nunez, R. Greenberg, P. Bichier, and S. Langridge. 2004. Greater predation in shaded coffee farms: the role of resident neotropical birds. Ecology **85**:2677-2681.

Philpott, S. M. 2010. A canopy dominant ant affects twig-nesting ant assembly in coffee agroecosystems. Oikos **119**:1954-1960.

Philpott, S. M., W. J. Arendt, I. Armbrecht, P. Bichier, T. V. Diestch, C. Gordon, R. Greenberg, I. Perfecto, R. Reynoso-Santos, L. Soto-Pinto, C. Tejeda-Cruz, G. Williams-Linera, J. Valenzuela, and J. M. Zolotoff. 2008. Biodiversity Loss in Latin American Coffee Landscapes: Review of the Evidence on Ants, Birds, and Trees

Pérdida de Biodiversidad en Paisajes Cafetaleros en Latinoamérica: Revisión de la Evidencia en Hormigas, Aves y Árboles. Conservation biology **22**:1093-1105.

Philpott, S. M., and I. Armbrecht. 2006. Biodiversity in tropical agroforests and the ecological role of ants and ant diversity in predatory function. Ecological Entomology **31**:369-377.

Philpott, S. M., and P. F. Foster. 2005. Nest-site limitation in coffee agroecosystems: artificial nests maintain diversity of arboreal ants. Ecological Applications **15**:1478-1485.

Philpott, S. M., J. Maldonado, J. Vandermeer, and I. Perfecto. 2004. Taking trophic cascades up a level: behaviorally-modified effects of phorid flies on ants and ant prey in coffee agroecosystems. Oikos **105**:141-147.

Philpott, S. M., G. L. Pardee, and D. J. Gonthier. 2012. Cryptic biodiversity effects: importance of functional redundancy revealed through addition of food web complexity. Ecology **93**:992-1001.

Philpott, S. M., I. Perfecto, J. Vandermeer, and S. Uno. 2009. Spatial scale and density dependence in a host parasitoid system: an arboreal ant, Azteca instabilis, and its Pseudacteon phorid parasitoid. Environmental Entomology **38**:790-796.

Pohlenz Córdova, J. 1979. Dependencia y desarrollo capitalista en una región agrícola, las plantaciones cafetaleras de la Sierra Madre de Chiapas.

Pohlenz Córdova, J., and J. P. Córdova. 1979. Dependencia y desarrollo capitalista en una región agrícolaLas plantaciones cafetaleras de la Sierra Madre de Chiapas.

Polis, G. A., and D. R. Strong. 1996. Food web complexity and community dynamics. The American Naturalist **147**:813-846.

Powell, S. 2008. Ecological specialization and the evolution of a specialized caste in Cephalotes ants. Functional Ecology **22**:902-911.

Powell, S. 2009. How ecology shapes caste evolution: linking resource use, morphology, performance and fitness in a superorganism. Journal of evolutionary biology **22**:1004-1013.

Powell, S., A. N. Costa, C. T. Lopes, and H. L. Vasconcelos. 2011. Canopy connectivity and the availability of diverse nesting resources affect species coexistence in arboreal ants. Journal of Animal Ecology **80**:352-360.

Price, P. W., R. F. Denno, M. D. Eubanks, D. L. Finke, and I. Kaplan. 2011. Insect ecology: behavior, populations and communities. Cambridge University Press.

Quandt, S. A., T. A. Arcury, J. Early, J. Tapia, and J. D. Davis. 2004. Household Food Security among Migrant and Seasonal Latino Farmworkers in North Carolina. Public Health Reports **119**:568-576.

R-Development-Core-Team. 2014. A language and environment for statistical computing. R Development Core Team, Vienna, Austria. Available at http://www.R- project.org.

Randlkofer, B., E. Obermaier, M. Hilker, and T. Meiners. 2010. Vegetation complexity—the influence of plant species diversity and plant structures on plant chemical complexity and arthropods. Basic and Applied Ecology **11**:383-395.

Rao, J., and A. Scott. 1981. The analysis of categorical data from complex sample surveys: chi-squared tests for goodness of fit and independence in two-way tables. Journal of the American Statistical Association **76**:221-230.

Renard, M.-C. 2011. Chapter 5 Free trade of coffee, exodus of coffee workers: The case of the Southern Mexican border region of the state of Chiapas. Pages 147-165 Globalization and the Time–Space Reorganization. Emerald Group Publishing Limited.

Renard, M.-C., and M. O. Breña. 2010. The Mexican Coffee Crisis. Latin American Perspectives **37**:21-33.

Rezende, M. Q., M. Venzon, A. L. Perez, I. M. Cardoso, and A. Janssen. 2014. Extrafloral nectaries of associated trees can enhance natural pest control. Agriculture, Ecosystems & Environment **188**:198-203.

Ricklefs, R. E. 1987. Community diversity: relative roles of local and regional processes. Science **235**:167-171.

Ripley, B., B. Venables, D. M. Bates, K. Hornik, A. Gebhardt, D. Firth, and M. B. Ripley. 2013. Package 'mass'. CRAN Repos. Httpcran R-Proj. OrgwebpackagesMASSMASS Pdf.

Rivera-Salinas, I. S., Z. Hajian-Forooshani, E. Jiménez-Soto, J. A. Cruz-Rodríguez, and S. M. Philpott. 2018. High intermediary mutualist density provides consistent biological control in a tripartite mutualism. Biological Control **118**:26-31.

Roeder, K. A., and M. Kaspari. 2017. From cryptic herbivore to predator: stable isotopes reveal consistent variability in trophic levels in an ant population. Ecology **98**:297-303.

Roth, D. S., I. Perfecto, and B. Rathcke. 1994. The Effects of Management Systems on Ground-Foraging Ant Diversity in Costa Rica. Ecological Applications **4**:423-436.

Roubik, D. W. 2002. Tropical agriculture: the value of bees to the coffee harvest. Nature **417**:708-708.

Sanabria, C., P. Lavelle, and S. J. Fonte. 2014. Ants as indicators of soil-based ecosystem services in agroecosystems of the Colombian Llanos. Applied Soil Ecology **84**:24-30.

Sanders, D., H. Nickel, T. Grützner, and C. Platner. 2008. Habitat structure mediates top–down effects of spiders and ants on herbivores. Basic and Applied Ecology **9**:152-160.

Sanders, N. J., G. M. Crutsinger, R. R. Dunn, J. D. Majer, and J. H. C. Delabie. 2007. An Ant Mosaic Revisited: Dominant Ant Species Disassemble Arboreal Ant Communities but Co-Occur Randomly. Biotropica **39**:422-427.

Schmitz, O. J. 2007. Predator diversity and trophic interactions. Ecology **88**:2415-2426.

Schwitzke, C., B. Fiala, K. E. Linsenmair, and E. Curio. 2015. Eucharitid ant-parasitoid affects facultative ant-plant Leea manillensis: top-down effects through three trophic levels. Arthropod-Plant Interactions **9**:497-505.

Scott, J. 1986. Everyday forms of peasant resistance. The Journal of Peasant Studies **13**:5-35.

Scott, J. C. 2008. Weapons of the weak: Everyday forms of peasant resistance. yale university Press.

Shennan, C., T. J. Krupnik, G. Baird, H. Cohen, K. Forbush, R. J. Lovell, and E. M. Olimpi. 2017. Organic and Conventional Agriculture: A Useful Framing? Annual Review of Environment and Resources **42**:317-346.

Shreck, A., C. Getz, and G. Feenstra. 2006. Social sustainability, farm labor, and organic agriculture: Findings from an exploratory analysis. Agriculture and Human Values **23**:439-449.

Slater, C. 1996. Amazonia as edenic narrative. Uncommon ground: Rethinking the human place in nature:114-131.

Tanaka, H. O., S. Yamane, and T. Itioka. 2010. Within-tree distribution of nest sites and foraging areas of ants on canopy trees in a tropical rainforest in Borneo. Population Ecology **52**:147.

Teodoro, A., L. Sousa-Souto, A.-M. Klein, and T. Tscharntke. 2010. Seasonal contrasts in the response of coffee ants to agroforestry shade-tree management. Environmental Entomology **39**:1744-1750.

Tews, J., U. Brose, V. Grimm, K. Tielbörger, M. Wichmann, M. Schwager, and F. Jeltsch. 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. Journal of biogeography **31**:79-92.

Thrupp, L. A. 2000. Linking Agricultural Biodiversity and Food Security: The Valuable Role of Sustainable Agriculture. International Affairs (Royal Institute of International Affairs 1944-) **76**:265-281.

Tilman, D. 1990. Mechanisms of plant competition for nutrients: the elements of a predictive theory of competition. Mechanisms of plant competition for nutrients: the elements of a predictive theory of competition.:117-141.

Tobin, J. 1991. A neotropical rainforest canopy, ant community: some ecological considerations. Ant-plant interactions:536-538.

Tobin, J. E. 1994. Ants as primary consumers: diet an dabundance in the Formicidae. Nourishment and evolution in insect societies:279-307.

Toledo Tello, S. 2002. Fincas, poder y cultura en Simojovel, Chiapas.

Toledo, V. M., and P. Moguel. 2012. Coffee and sustainability: the multiple values of traditional shaded coffee. Journal of Sustainable Agriculture **36**:353-377.

Torres-Contreras, H., and R. Vasquez. 2004. A field experiment on the influence of load transportation and patch distance on the locomotion velocity of Dorymyrmex goetschi (Hymenoptera, Formicidae). Insectes Sociaux **51**:265-270.

Townsend, C., and J. Harper. 2003. Michael Begon, Essentials of Ecology. Blackwell Science.

Tragust, S., L. V. Ugelvig, M. Chapuisat, J. Heinze, and S. Cremer. 2013. Pupal cocoons affect sanitary brood care and limit fungal infections in ant colonies. BMC evolutionary biology **13**:225.

Tscharntke, T., A. M. Klein, A. Kruess, I. Steffan-Dewenter, and C. Thies. 2005. Landscape perspectives on agricultural intensification and biodiversity–ecosystem service management. Ecology letters **8**:857-874.

Tylianakis, J. M., and C. M. Romo. 2010. Natural enemy diversity and biological control: Making sense of the context-dependency. Basic and Applied Ecology **11**:657-668.

Urrutia-Escobar, M. X., and I. Armbrecht. 2013. Effect of Two Agroecological Management Strategies on Ant (Hymenoptera: Formicidae) Diversity on Coffee Plantations in Southwestern Colombia. Environmental Entomology **42**:194-203.

Van Emden, H. 1963. Observations on the effect of flowers on the activity of parasitic Hymenoptera. Entomol. Mon. Mag **98**:265-270.

Van Mele, P., and J.-F. Vayssières. 2007. Weaver ants help farmers to capture organic markets. Appropriate Technology **34**:22.

Van Mele, P. L. J., and N. T. T. Cuc. 2007. Ants as friends: improving your tree crops with weaver ants. CABI.

Vandermeer, J., I. Perfecto, and S. Philpott. 2010. Ecological Complexity and Pest Control in Organic Coffee Production: Uncovering an Autonomous Ecosystem Service. BioScience **60**:527-537.

Verdeny-Vilalta, O., M. Aluja, and J. Casas. 2015. Relative roles of resource stimulus and vegetation architecture on the paths of flies foraging for fruit. Oikos **124**:337-346.

Villarejo, D., and S. L. Baron. 1999. The occupational health status of hired farm workers. Occupational medicine (Philadelphia, Pa.) **14**:613-635.

Wacker, L., O. Baudois, S. Eichenberger-Glinz, and B. Schmid. 2008. Environmental heterogeneity increases complementarity in experimental grassland communities. Basic and Applied Ecology **9**:467-474.

Warfe, D. M., and L. A. Barmuta. 2004. Habitat structural complexity mediates the foraging success of multiple predator species. Oecologia **141**:171-178.

Wells, K., M. Pfeiffer, M. B. Lakim, and K. E. Linsenmair. 2004. Use of arboreal and terrestrial space by a small mammal community in a tropical rain forest in Borneo, Malaysia. Journal of Biogeography **31**:641-652.

West, P. 2012. From modern production to imagined primitive: The social world of coffee from Papua New Guinea. Duke University Press.

Wheeler, G. C., and E. W. Wheeler. 1937. New hymenopterous parasites of ants (Chalcidoidea: Eucharidae). Annals of the Entomological Society of America **30**:163-175.

Wielgoss, A., T. Tscharntke, A. Rumede, B. Fiala, H. Seidel, S. Shahabuddin, and Y. Clough. 2014. Interaction complexity matters: disentangling services and disservices of ant communities driving yield in tropical agroecosystems. Proceedings of the Royal Society B: Biological Sciences **281**:20132144.

Wilkinson, E. B., and D. H. Feener. 2007. Habitat complexity modifies ant–parasitoid interactions: implications for community dynamics and the role of disturbance. Oecologia **152**:151-161.

Yanoviak, S., and M. Kaspari. 2000. Community structure and the habitat templet: ants in the tropical forest canopy and litter. Oikos **89**:259-266.

Yanoviak, S. P. 2015. Effects of lianas on canopy arthropod community structure. Ecology of Lianas:343-361.

Yanoviak, S. P., Y. Munk, and R. Dudley. 2011. Evolution and ecology of directed aerial descent in arboreal ants. Integrative and comparative biology:icr006.

Yanoviak, S. P., and S. A. Schnitzer. 2013. Functional roles of lianas for forest canopy animals. Pages 209-214 Treetops at Risk. Springer.

Yanoviak, S. P., C. Silveri, A. Y. Stark, J. T. Van Stan, and D. F. Levia. 2016. Surface roughness affects the running speed of tropical canopy ants. Biotropica.

Young, R. C. 1970. The plantation economy and industrial development in Latin America. Economic Development and Cultural Change **18**:342-361.

Zapata-Martelo, E., A. Nazar-Beutelspacher, B. Suárez-San Román, M. del Rosario Ayala-Carrillo, N. J. Cárcamo-Toalá, N.-B. S.-S. Zapata-Martelo, and A. Román. 2012. Contribución invisible: trabajo infantil y adolescente en los cafetales del Soconusco, México. Colegio de Postgraduados.

Zimmerer, K. S. 2011. " Conservation booms" with agricultural growth. Sustainability and shifting environmental governance in Latin America **2011**:82-114.