UNIVERSITY OF CALIFORNIA, SANTA CRUZ

CHANGES IN SPECIES RICHNESS, ABUNDANCE, AND COMMUNITY COMPOSITION OF ARBOREAL TWIG-NESTING ANTS ALONG AN ELEVATIONAL GRADIENT

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ABSTRACT: The distribution, diversity, and assembly of tropical insects has long intrigued ecologists, and for tropical ants, can be affected by competitive interactions, microhabitat requirements, dispersal, and availability and diversity of nesting sites. Arboreal twig-nesting ants are limited by the number of hollow twigs available, especially in intensive agricultural systems. Elevation may impact ant diversity and abundance, but no studies have examined if nest-site limitation or richness of arboreal twig-nesting ants varies with elevation. In coffee agroecosystems, there are ~40 species of arboreal twig-nesting ants. I examined communities of twig-nesting ants in coffee plants along an elevational gradient to answer the following questions: (1) Does nest-site limitation change with elevation? (2) Do species richness and colony abundance change with elevation? (3) Does community composition change with elevation? (4) Is elevation among the more important predictors of changes in the ant community and how do changes in coffee management interact with changes in elevation? I collected data in 2013 across several farms in a coffee landscape in Chiapas, Mexico. I surveyed forty-two 10 x10 m plots from 450-1550 m elevation. I sampled a total of 2211 hollow coffee twigs, 77.1% of which were occupied by one of 28 species of ants. Both the percent of hollow twigs that were occupied and species richness peaked at mid-elevations (between 800-1050 m). Among common ant species, some had higher numbers of colonies at intermediate elevations, while others were more abundant at higher or lower elevations. For example, *Pseudomyrmex simplex* was more abundant in lower elevations, *Pseudomyrmex ejectus* dominated in high elevations, and the relative abundance of *Nesomyrmex echinatinodis* peaked at mid-elevations. In sum, I found that nest-site limitation, richness, abundance, and composition of arboreal twig-nesting ants changes with elevation. These findings have important implications for understanding the role of these ants as predators in coffee agroecosystems.

KEYWORDS: coffee agroecosystems, twig-nesting ants, elevational gradients, Chiapas, Mexico, biodiversity conservation, sustainability, agroforestry

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Introduction

Empirical research supports the statement that biodiversity changes along elevational gradients (Lomolino 2001, Sanders et al. 2003, Longino & Colwell 2011, Smith et al. 2014). The study of ecological patterns along elevational gradients contributed to the general theories on the origin of species (Darwin 1859, Lomolino 2001) and continues to provide valuable insights to our understanding of ecological processes (Rahbek 2005, McCain 2009, Longino & Colwell 2011). Patterns of species richness and composition along elevational gradients are important to study, not only because they provide an understanding of species distribution, but also because these patterns can help elucidate the placement of different biotic zones that may be present throughout mountainous regions (Lomolino 2001).

Patterns of changes in diversity with changes in elevation are strongly variable. Depending on the climate and focal taxon, species richness or diversity may increase with elevational increase (moths – Brehm et al. 2003; ants – Sanders et al. 2003), decrease with elevational increase (insects – Wolda 1987; animals – Gaston 2000; plants – Kessler et al. 2001), or display a mid-elevation peak with elevation change (Olson 1994, Sanders 2002, McCain 2004, Bachman et al. 2004). These patterns have led to two main hypotheses relating to biodiversity change along elevational gradients. First, some hypothesize there is a greater species richness and diversity at lower elevations, since area, temperature, and productivity generally decrease with increasing elevation. Second, some hypothesize that there are intermediate peaks in species richness and diversity because of overlapping ecotones along elevation gradients. Many studies on elevational gradients show such intermediate

peaks, where species diversity or species richness is greatest at the intermediate elevations sampled in a given study (Shmida & Wilson 1985, Gentry & Dodson 1987, Rosenzweig & Abramsky 1993, Colwell & Hurtt 1994, Rahbek 1995, Sanders 2002). Peaks of diversity at intermediate elevations initiated the mid-domain effect (MDE) hypothesis, which is used as a null-model to interpret patterns of species richness that are influenced by geometric constraints (Colwell & Lees 2000).

Insects, and in particular, ants, display large variation in their responses to elevation gradients. Some insect groups decline in species richness with increases in elevation, some increase, some show a MDE, and richness of still others does not vary with elevation changes (Hodkinson 2005). Some insects use hilltopping – a mating behavior in which certain species of insects congregate at the tops of hills – that can lead to high richness of flies, beetles, and some hymenopterans at higher elevations (Merz 2000, Alcock & Dodson 2008). Several studies examining changes in ant communities, in particular, along elevational gradients reveal peaks in species richness at intermediate elevations (Samson et al. 1997, Fisher 1998, Sanders 2002, Sabu et al. 2008, Longino & Colwell 2011, Smith et al. 2014). For example, in his study of ground-nesting ants in three western US states (Colorado, Nevada and Utah), Sanders (2002) applied the MDE to explain peaks in species richness at intermediate elevations. In contrast, species richness of ants in arid ecosystems tends to be greater at high elevations because lower temperatures and higher precipitation supports more primary production, which together provides an environment with lower levels of physiological stress (Sanders et al. 2003). It is important to note that derived patterns of species richness and diversity can be evidently impacted by the extent of the altitudinal gradient sampled (Rahbek, 2005). For example, Smith et al. (2014) studied the diversity and phylogenetic community structure of ants along an elevational gradient of three volcanoes in Costa Rica. When comparing distributions based on large-scale phylogenies, they found negative relationships between elevation and diversity on all three volcanoes. When they compared the distribution of species along extended elevational gradients, including the volcanoes and sites extending down to sea level, they observed mid-elevation peaks

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around 600 to 800 m. Although many studies examine changes in species richness and community composition along elevation gradients in natural systems, few have examined for elevational gradients in agricultural or other human-managed systems.

Coffee agroecosystems represent one habitat type that grows across a wide range of elevations in tropical landscapes. These multistrata agroforestry systems have the potential to act as model systems for sustainable agricultural production while preserving biodiversity that occurs within the agroecosystems (Perfecto et al. 1996, Philpott & Armbrecht 2006, Jha et al. 2014). Coffee grows best in elevations ranging from 600 to 1400 m (Moguel & Toledo 1999, Echevería & Gordillo 2008). Traditionally, coffee growing techniques were compatible with sustaining biodiversity and the traditional mosaic structure of coffee landscapes maintains and even improves biodiversity (Reichardt et al. 1994, Toledo et al. 1994). Yet, coffee agroecosystems vary widely in management practices. Modern techniques include reducing the shade trees and canopy cover and applying agrochemicals, and as this intensification takes place, biodiversity is lost (Vandermeer & Perfecto 1997, Moguel & Toledo 1999, Perfecto & Armbrecht 2003, Perfecto et al. 2004, Philpott et al. 2008a). Losses of canopy cover result in habitat loss and subsequent reductions of ant richness, and changes in ant community composition (Armbrecht et al. 2005, Philpott et al. 2008a). Further, reducing canopy cover increases the chances of water runoff and soil erosion (Rice 1990), and has negative impacts on the provisioning of other ecosystem services such as pollination, nutrient cycling, and predation services provided by organisms such as ants (Jha et al. 2014). Ants reduce herbivory (Rocha & Bergallo 1992, Vandermeer et al. 2002; Philpott et al. 2008b) and are important control agents of pests and fungal diseases in coffee and other agroforestry systems (Philpott & Armbrecht 2006).

One especially important group of ants in coffee agroecosystems is the arboreal twig-nesting ants. Twig-nesting ants nest in hollowed out twigs of both coffee plants and shade trees, and they can be limited by both the number and the diversity of available twigs in coffee habitats (Armbrecht et al.

2004, Philpott & Foster 2005). Boring beetles (Curculionidae: Scolytinae) hollow out dead twigs (Kirkendall 1993, Ward 1991, Hulcr et al. 2007, Greco & Wright 2012). The black twig borer (*Xylosandrus compactus*) is a common pest among coffee systems of Hawaii as it causes branches of the coffee plant to die back by boring into the stem and introducing a fungus (Greco & Wright 2012). However, in the case where ants occupy hollow twigs while they are still on the coffee plants, twig-nesting ants may provide important biological control services. Twig-nesting ants are associated with reductions in attacks by other more damaging pests like the coffee berry borer (*Hypothenemus hampei*) and the coffee leaf miner (*Leucoptera coffeela*) (De la Mora et al. 2008, Larsen & Philpott 2010, Philpott et al. 2012, Gonthier et al. 2013).

Due to the importance of both elevational gradients and coffee management for ants, and the beneficial role of twig-nesting ants in biological control, I examined twig-nesting ant communities along an elevational gradient to examine how both elevation and changes in coffee shade management affect ant species richness and community composition. I specifically sought to answer the following questions: (1) Does nest-site limitation for arboreal twig-nesting ants change with elevation? (2) Do species richness and colony abundance of arboreal twig-nesting ants change with elevation? (3) Does the relative abundance of common arboreal twig-nesting species and community composition change with elevation? (4) Is elevation among the more important predictors of changes in the ant community and how do changes in coffee management interact with changes in elevation?

Methods

Site description

      I conducted my field research along an elevational gradient in coffee agroecosystems in the Soconusco Region of Chiapas, Mexico during the wet season of 2013. The study locations are about 40 km NE of Tapachula, the nearest city. The annual rainfall in this area is *ca.* 4500 mm on average (Philpott et al. 2008b). Approximately 93.7% of the land in the study area is of coffee, and the remaining 6.3% is small forest fragments (Philpott et al. 2008b). Of the coffee production, about 50% can be classified as shaded monoculture (Moguel & Toledo 1999). The majority of the shade trees belong to the genus *Inga*. Landholdings in the Soconusco are mostly are large-scale coffee farms (200-300 ha), but in all of Mexico ~70% of coffee producers have farms that are less than 2 ha (Boot 2003 in Lewis 2005).

      I established 42 study plots between 450 - 1550 m (Fig. 1). Plots occurred on several different large, estate coffee farms (Brazil, Argovia, Genova, Santa Anita, Maravillas, Irlanda, Hamburgo, and San Francisco) and on nearby smallholder farms (e.g. Ejido Sinai). Approximately every 50 m in elevation change along the gradient, I set up two 10 x 10 m plots. I established plots haphazardly in areas that did not have *Azteca sericeasur* ants. These ants were avoided due to their aggressive interactions with twig-nesting ants (Philpott 2010). Each plot was located at least 400 m from each other plot to ensure independence of the ant colonies in each plot. Both *Coffea arabica* and *Coffea canephora* are grown within this elevation range, but to be consistent, I chose sites containing only *Coffea arabica*.

Ant surveys

I surveyed ants from each coffee plant within each plot using a typical sampling method for surveying twig-nesting ants (e.g. Philpott & Foster 2005). On each coffee plant, I broke off all the dead twigs, and snapped them open to search for ants. For each coffee plant, I recorded data on (1) the total number of dry twigs, (2) the number of hollow twigs, (3) the number of occupied hollow twigs, and (4) the identity of each ant species found occupying the twigs. I collected voucher specimens of all ant species, placed them in 70% ethanol, and identified them later in the lab according to several resources (e.g. Bolton 1994, Bolton 2012, AntWeb 2013, Longino 2013). I surveyed all ants in plots during June - July 2013.

Vegetation sampling

Because twig-nesting ants can be strongly affected by coffee management (Philpott et al. 2010), I also sampled the vegetation characteristics for each study plot. I used a convex spherical densiometer to measure the canopy cover in every site. I took five measurements per plot - one while facing north in the center of the plot and 5 m beyond the boundaries of every 10 x 10 m plot facing each cardinal direction. I took the mean value of the five measurements for each plot. I also surveyed trees and recorded the species, height, and measured the circumference at breast height (1.35 m above ground) for each tree. With that data, I examined total tree abundance, species richness, mean height, and mean circumference for each plot. Finally, I recorded the number of coffee plants and the average height of coffee plants in each plot. Because many vegetation characteristics are frequently correlated with one another, I calculated a vegetation complexity index (VCI) to generate a single vegetation value to describe the sites (see Philpott et al. 2008a, De la Mora et al. 2013). To calculate the VCI, I divided values for each variable (no. trees, no. tree species, tree height, tree circumference, coffee height, canopy cover) by the highest measured value, thereby transforming values from 0 to 1 (1 indicating more complex vegetation). For the number of coffee plants, which generally negatively

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correlates with vegetation complexity, I transformed values from 0 to 1, then subtracted from 1. I summed transformed values of each variable for each plot, and divided by 7 to obtain the VCI value.

Data Analysis

To examine the change in the proportion of occupied hollow twigs, the number of ant species, and the proportion of occupied twigs occupied by common ant species along the elevation gradient, I used generalized linear models (GLMs) with the 'lme4' package in R (Bates et al. 2009, R Development Core Team 2014). I defined common species as all species that occupied >50 nests in total. For the GLMs, I tested four different models for each of the dependent variables: 1) elevation, 2) elevation + VCI, 3) elevation + number of hollow twigs, and 4) elevation + VCI + number of hollow twigs. I ran two versions of each of these models with elevation as either a linear or quadratic predictor of the dependent variables. I compared AIC values to select the best-fit model for each of the dependent variables tested. For those dependent variables that were normally distributed (number of ant species, proportion of occupied twigs with *Pseudomyrmex simplex*), I used GLM with Gaussian family. For dependent variables that were not normally distributed (proportion of occupied twigs, proportion of twigs with *Pseudomyrmex ejectus*, proportion of twigs with *Nesomyrmex echinatinodis*, proportion of twigs with *Procryptocerus hylaeus*, proportion of twigs with *Pseudomyrmex filiformis*), I used the 'cbind' function and a GLM with binomial error and logit family.

To examine the differences in species composition of twig nesting ants along the elevation gradient, I first grouped the plots at different elevations into three elevation groups: high (1150 - 1550 m), medium elevation (850 - 1150 m), and low (450 - 850 m). I used non-metric multidimensional scaling (NMDS) and analysis of similarities (ANOSIM) in PAST (Hämmer et al. 2001) to visually and statistically compare species composition of the ants within each elevation group. The ANOSIM compares (a) the mean distance within the elevation groups to (b) the mean

distance between the elevation groups, and can statistically determine separation in species composition between the plots at different elevations. I also used a one-way PERMANOVA to examine the relative degree of clustering of plots within each elevation group. The PERMANOVA calculates the mean distance between points within each elevation group, and compares those mean values to one another. Significant differences encountered with a PERMANOVA indicate the change in species composition between plots (e.g. the species turnover) in one elevation group is less than or greater than for another elevation group. For the NMDS, ANOSIM, and PERMANOVA, I used the Bray-Curtis similarity index as the similarity measure.

Results

Vegetation Surveys

There was a large range of vegetation factors measured in the different study sites, indicating that the coffee shade management varied greatly in different plots (Table 1). The variation in tree species richness, the number of trees per plot, and the mean tree height and circumference were not correlated with changes in elevation (Table 1). While the number of coffee plants per plot increased with increasing elevation (y = 0.019x + 18.433, Table 1), the mean coffee height did not vary with elevational change. Canopy cover significantly declined with elevational increases (y = -0.0005x + 1.0336, Table 1), and overall vegetation complexity in a plot (VCI) also declined as elevation increased (y = -0.0003x - 0.5023, Table 1).

Ant Surveys

Within the 42 plots, I surveyed a total of 1572 coffee plants on which I found 2211 dry, hollow twigs. On average, I found 1.41 (± 0.06 SE) hollow twigs per plant, and 52.62 (± 5.52) hollow twigs per plot. The number of available hollow twigs per plot did not change with elevation (y = - 0.029x + 81.4, R^2=0.062, F=2.63, P=0.113). Overall, 77.11% of the hollow twigs were occupied by one of the 28 arboreal twig-nesting ant species collected (Fig. 2). The most common species in my study (and the percentage of nests they occupied) were *Pseudomyrmex simplex* (37.6%)*, Pseudomyrmex ejectus* (16.95%), *Procryptocerus hylaeus* (10.6%), *Pseudomyrmex filiformis* (8.7%), and *Nesomyrmex echinotinodus* (6.01%).

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Both the proportion of hollow twigs occupied by ants and the species richness of ants occupying hollow twigs were correlated with changes in elevation as well as site characteristics. The GLM model that best predicted hollow twig occupation (for all ants) included elevation, the number of hollow twigs, and VCI. The proportion of occupied hollow twigs was significantly higher at middle elevations (Fig. 3a, Table 2). Although included in the model, VCI was not a significant predictor of the proportion of occupied nests, but the proportion of occupied hollow twigs increased linearly with the number of available hollow twigs (Fig. 3b, Table 2). Likewise, the best model for twig-nesting ant species richness included elevation, the number of hollow twigs, and the VCI. Ant species richness was highest at mid-elevations and was significantly quadratically related to elevation (Fig. 3c, Table 2). Ant species richness increased linearly with the number of available hollow twigs (Fig.3d, Table 2).

The elevational ranges for species of twig-nesting ants varied (Fig. 2) and changes in elevation correlated with the proportion of occupied twigs occupied by each of the most common species (Fig. 4, Table 2). *P. simplex* was highly abundant at lower elevations accounting for 79.5% of all occupied nests below 1000 m. The relative abundance of *P. simplex* decreased linearly with increasing elevation, and elevation was the only factor included in the best model for that species (Fig. 4a, Table 2). Similarly, *P. filiformis* occupied a wide range of elevations but occupied a higher proportion of nests at lower elevations, accounting for >20% of occupied nests below 1050 m. The model that best predicted *P. filiformis* relative abundance included elevation and VCI. Relative abundance of *P. filiformis* declined linearly with elevation (Fig. 4b) and significantly increased with VCI (Table 2). In contrast, *P. ejectus* was most abundant at higher elevations, inhabiting 56.9% of occupied nests above 1100 m. The relative abundance of *P. ejectus* increased linearly with elevation (Fig. 4c) and with the number of hollow twigs (Table 2). Abundance of *P. hylaeus* increased with elevation, but in a non-linear fashion, and relative abundance of this species decreased with an increasing number of hollow twigs in a plot (Fig. 4d, Table 2). Finally, the relative abundance of *N.*

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echinatinodis was highest at mid elevation, and declined where vegetation complexity (VCI) was higher (Fig. 4e, Table 2).

Community composition of twig-nesting ant species changed along the elevational gradient (Fig. 5). The composition of ant species within each elevation group (high, medium and low) was statistically more similar than species composition between groups (ANOSIM, R=0.217, P<0.001, Fig. 5). The composition was different between high and medium elevation plots (P=0.0006), between high and low elevation plots (P=0.0001) and between medium and low elevation plots (P=0.002). In addition, there were differences in the degree to which ant composition varied among plots in the same elevation range (PERMANOVA, F=4.16, P<0.001, Fig. 5). The mid elevation plots were most similar to each other and significantly more similar in composition than were plots within high (P=0.0008) or low (P=0.0013) elevations. Composition in low elevation plots was more similar to other low elevation plots than were high elevation plots to each other (P=0.0002). Changes in the species composition along elevation are also evident by visually examining finer scale changes in the proportion of nests occupied by different species at different elevations (Fig. 6).

Discussion

This research indicates that arboreal twig-nesting ant communities shift with changes in elevation in coffee agroecosystems. I documented significant changes in both the occupation of hollow twigs (i.e. nest-site limitation) and species richness of ants with changes in elevation, such that both occupation and richness peak at mid elevations. Second, I demonstrate that the relative abundance of individual ant species shifted along the elevation gradient – at low elevations, nests were commonly occupied by *P. simplex* and *P. filiformis,* and at high elevations nests were commonly occupied by *P. ejectus*. These individual changes also resulted in large shifts in community composition with changes in elevation. Finally, I documented that elevation was a consistent predictor of changes in ant communities, and that other management factors did have some influence.

Ants and elevation

When studying the richness and abundance of species in natural ecosystems the most common pattern found is MDE (*ca.* 50%) (Rahbek 2005). In my study, both twig-nesting ant species richness and the proportion of hollow twigs occupied peaked at mid-elevations. These results were not initially expected since productivity tends to be higher in lower elevations, and many have documented that richness declines with increasing elevation (MacArthur 1972, Brown 1988, Begon et al. 1990, Stevens 1992, Rahbek 1995). For ants, however, most elevation studies have found mid-elevation peaks in richness, abundance or diversity (Samson et al. 1997, Fisher 1998, Sanders 2002, Sabu et al. 2008, Smith et al. 2014). Thus, my results are consistent with other studies that have

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examined species richness and abundance of ants along elevational gradients. The hump-shaped

MDE pattern is hypothesized to be caused by a variety of factors including habitat disturbance,

overlapping ecotones, climatic severity, temperature, resource availability, predation, and/or

competition (Rahbek 2005). Thus, when discussing the causes of variation along elevational

gradients, it is important to consider the multiple mechanisms that contribute to the pattern.

It may be the case that MDE patterns are entirely natural, or that some of these patterns are

influenced by humans. In this human-modified landscape, where forest fragments may be more

prevalent at higher elevations, it may be possible that MDE patterns are related to relatively stronger

human modification of landscapes at low elevations landscapes (Tejeda-Cruz & Sutherland 2004).

For example, Fisher (1998) found MDE for ant diversity along an elevational gradient in

Madagascar, and he concluded that the pattern was probably affected by habitat disturbances in low

elevation areas. Yet, in contrast, in the arid ecosystems of Nevada, where ant diversity showed a

positive correlation with elevation along two transects, but peaked at mid-elevations along the third

transect, Sanders et al. (2003) concluded that the disturbance associated with a city at the high

elevations of the third transect was likely the contributor of diversity reduction and the mid-domain

pattern. Thus human disturbance has been invoked as a driver of MDE in different ways. The type of

habitat or habitat management may affect the patters with elevation. Hence, because of human

influences in agricultural systems, we may find a different pattern along elevation gradients than that

of unmanaged ecosystems.

Ants and vegetation management

The fact that elevational gradients are many times representative of other environmental

gradients, and correlated with other habitat characteristics makes testing for patterns associated with

elevation itself problematic (Rahbek 2005). Beyond the effects of elevation, changes in habitat due to

the variety of land management practices along the elevational gradient influenced twig-nesting ant communities. In this study, elevation increase correlated with increases in number of coffee plants, and decreases in canopy cover and vegetation complexity (Table 1). This suggests a positive correlation between elevation and agricultural intensification in this particular region. Temperatures are generally cooler with increasing elevation. As coffee production and quality is highly sensitive to temperature conditions (Lin et al. 2008), coffee farmers at higher elevations may reduce shade to increase temperature and provide coffee plants with more sunlight. In the study area, the high elevation farmers are positioned near the top end of a valley that brings increases in fog and cloud cover, which could increase the humidity. Farm owners often argue that reductions in canopy cover are necessary to reduce humidity that increases their susceptibility to fungal diseases (Jha et al. 2014). Fungi, such as the coffee rust (*Hemileia vastatrix*) have a historical reputation of causing widespread collapses in coffee production. Despite these perceptions, years of ecological research have revealed that the control of this fungal disease as well as pest outbreaks is highly complex and not often linearly related to shade in coffee farms (Vandermeer et al. 2010, Jha et al. 2014).

Some of the observed changes in vegetation also correlated with changes in ant communities. For example, vegetation complexity had a significant positive correlation with the relative abundance of *P. filiformis* and was included in the best model for predicting overall nest occupation, species richness, and relative abundance of *N. echinatinodis*. *P. filiformis* is distributed between S. Mexico and Paraguay, and most reported sightings have been in forested habitats (AntWeb 2013), making more frequent encounters in coffee with more complex vegetation consistent with previously recorded information. Observed changes in ant community features with changes in vegetation complexity support other studies that have long demonstrated effects of coffee shade management on biodiversity and communities of ants in coffee agroecosystems (Perfecto et al. 1996, Perfecto et al. 1997, Perfecto et al. 2003, Philpott et al. 2008a).

I also found that twig-nesting ants were influenced by the number of hollow twigs in a plot. The proportion of occupied twigs and species richness both increased linearly with number of hollow twigs, relative abundance of *P. ejectus* increased with the number of hollow twigs, and relative abundance of *P. hylaeus* decreased with increases in the number of hollow twigs. Nest availability may be an extremely important determinant of community composition for twig-nesting ants. Ants compete for nesting resources, and nest-site limitation can be indicated by occupation of a large fraction of the available resources, takeovers of nests by different colonies or species, and occupation of artificial nests (Philpott & Foster 2005). Coffee agroforests that differ in availability of nest sites have been used to demonstrate the importance of nest-site limitation for ants, and that nest-site limitation can contribute to a loss of ant diversity (Philpott & Foster 2005). In my observations, I documented that both nest occupation and ant species richness increases as the number of available nests increase – showing that low nest availability, and low numbers or a low diversity of available nests may indeed be an important limiting factor in ant communities (Armbrecht et al. 2004, Philpott & Foster 2005).

Interactions between elevation and land management

One question of interest is whether or not elevational impacts on ecological communities may shift depending on habitat or land management. In this study, I examined a range of coffee agroecosystems, but I did not specifically aim to examine whether elevational gradients observed for the ant community changed with coffee farms of different management types, or how these changes compared to natural areas nearby. I did find, however, that nest occupation, species richness, and abundance of the five most common ant species were all affected by elevation, but only one of the factors varied significantly with changes in vegetation. Few others have explicitly addressed whether elevational impacts differ depending on disturbance levels, land use, or management change. Axmacher et al. (2004) compared alpha diversity along an elevational gradient on Mount

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Kilimanjaro, and the gradient included agricultural area, agroforestry area, and forest. They concluded that diversity patterns of geometrid moths differ along the elevational gradients with and without managed land. In Karnataka, India, Gadagkar et al. (1990, 1993) studied insect and ant diversity in 36 1-hectare plots from 12 habitat types, in sites representing elevations from sea level to 600 m, with different levels of disturbance (relatively undisturbed reserve forests, relatively disturbed forests, and monoculture plantations). They found that insect diversity was highest with intermediate levels of canopy cover, disturbed sites had lower richness and diversity in their ant fauna, and ant diversity was positively correlated with plant species diversity. Although the literature suggests a reduction in ant diversity due to increasing disturbance levels (Gadagkar et al. 1990, Mackay et al. 1991, Gadagkar et al. 1993, Perfecto & Vandermeer 2002), Gadagkar et al. (1990) also concluded from results, in addition to diversity reduction with increasing disturbance, altitudinal variation may override even extreme differences in levels of disturbance.

History and influence of Coffee systems in Chiapas

Coffee production in Chiapas affects much more than vegetation complexity and arboreal twig-nesting ant colonies. It affects biodiversity (Philpott & Bichier 2012) and complex food webs in coffee agroecosystems (Vandermeer et al. 2010), but also strongly affects the livelihoods of Mexican citizens (Nestel 1995) and indigenous people of Chiapas (García 1996, Pérez-Grovas et al. 2001). In this section, I discuss how the history of coffee production in the Soconusco region of Chiapas, and political economic realities of coffee production may interface with elevation and habitat drivers of ant communities in order to affect twig-nesting ants, and provisioning of ecosystem services.

Coffee is an extremely important crop in Mexico for many reasons. First, many coffee-growing areas in southern Mexico have been designated by CONABIO (a government agency responsible for the conservation of biodiversity) as priority areas for conservation due to high numbers of species and of endemic species (Moguel and Toledo 1999, Perfecto et al. 2003). For this

reason, conservation groups and scientists have lauded coffee agroecosystems as productive systems in which we can combine biodiversity conservation and economic development (Perfecto et al. 2003). However, the Instituto Mexicano del Café (INMECAFE) encouraged high productivity by intensification during the 1980's and 1990's, and assisted farmers with technical assistance advising removal or reduction of shade trees, and increased use of agrochemicals (Nestel 1995, Renard 2010). These approaches may be detrimental to sustainability of the land, as well as to ecosystem services provided on farms (Jha et al. 2014). Second, coffee production has played a significant role in the national economy of Mexico by contributing to export trade (Nestel 1995). But from the perspective of the small producer in Mexico, coffee is a crop with many contradictions – it is simultaneously a source of wealth and misery (Echevería & Gordillo 2008). Like the majority of food and products in U.S. free trade, most of the retail cost of coffee is distributed to intermediaries, and the producers are left with little profit. Still, more and more land is developed for agricultural export.

The agricultural development of the Soconusco region in Chiapas began with the arrival of German coffee farmers in 1850, which led to the first capitalist agricultural organizations in Mexico, and the Soconusco became a land of enormous natural and cultural wealth (Echevería & Gordillo 2008). In the first decades of the 20th century, an average coffee farm was 230 ha (range between 20-1500 ha), and German farmers were those primarily involved in industrializing and exporting coffee (Echevería & Gordillo 2008). Small and indigenous producers struggled. Small farmers did not have the means to initially build or acquire the facilities and machinery to compete in the coffee market and make profit. Thus, many small producers became subsidiaries of the large producers who had such infrastructure (Echevería & Gordillo 2008).

Although there are many benefits to the coffee production in Chiapas, issues of food and social justice are prevalent. The typical layout of coffee farms in the Soconusco region reflects the hierarchy in the system. The farm owner's home, big and luxurious, overlooks the land, production facility, and the cluster of small living spaces where workers live with their families. Education is

unreliable, inconsistent and underdeveloped. Policy tries to hold farm owners responsible for providing good education to working families, but enforcement is often not enough to establish and provide the education needed (Lewis 2010). Finally, pesticides and agrochemicals have long-term health effects on people regularly exposed to them (Maroni & Fait 1993). The health risks, low wages and a poor education-system for coffee laborers exacerbate social injustice, and because these issues are unseen to consumers, they often persist (Vickers 2002, Opotow 2011).

As the generations of family owned farmland increase, farm owners seem to become more disconnected to the land they manage. By the 3rd generation of Soconusco farm owners, it became a custom to have a house in the city as well as at the farm (Echevería & Gordillo 2008). Disconnect to the land is a common issue of the 21st century, where the authenticity of nature for many people has become an abstraction to watch, consume, wear or ignore (Louv 2008). Environmentally degrading practices such as agricultural intensification and industrialization often follow the ignorance of generations to whom the beauty and delicate complexity of the natural world is unknown. I argue that this disconnect to the environment has enforced other degrading issues such as disrespect and greed, creating the positive feedback loops that have generated – and continue to generate – the "threat of mass extinction" (Tilman et al. 2002 in Philpott & Armbrecht 2006).

Research strives to provide convincing arguments as to why and how to implement sustainable practices, but information is not readily accessible to the majority of people. Thus, environmental education and the sharing of information are increasingly important to the survival of ecosystems and of life in general. We will protect and sacrifice for what we love or what is important to us. This suggests that if the majority of human beings learn to love all life forms, perhaps by realizing that "we are literally kin to other organisms" (Wilson 1984), then biodiversity may be preserved. However, considering the first law of human altruism (Hardin 1977), the only means of grounding Aldo Leopold's conservation ethic may have to be by selfish reasoning – to rely on the

principle that people would conserve land and biodiversity if it resulted with material gain for themselves or their family.

One small way in which coffee producers may benefit from the environment (and conserving biodiversity) is through the provisioning of ecosystem services. Ecosystem services are an essential part of our food system (Farber et al. 2002, Worm et al. 2006, Swinton et al. 2007, Fisher & Turner 2008) and may contribute to poverty alleviation in agricultural landscapes (Smukler et al. 2012). As a consequence of destructive agricultural practices, nearly 40% of the world's agricultural land has been seriously degraded (Rivera 2000 in Donohoe 2003). To preserve the land that sustains us, food production by agriculture can no longer move forward without considering the important ecosystem functions that ensure sustainability (i.e. ecosystem health and long-term production) of the earth's terrestrial environments. Although we know nature provides services that are essential to sustaining life on our planet (Daily 1997), the economic valuation of ecosystem services is complicated (Farber et al. 2002), which is why Heal (2000) suggests that, regarding economics, the provision of incentives for conserving ecosystem services is key. Ants serve as important indicator species (Hoffmann and Anderson 2003), and more specifically, arboreal twig-nesting ants in coffee agroecosystems play an important role in pest control (De La Mora et al. 2008, Larsen & Philpott 2010, Gonthier et al. 2013). Thus, the results demonstrating changes in relative abundance of certain ant species with changes in vegetation complexity, as well as changes in ant abundance, richness, and composition with elevation should be examined more carefully to understand implications for ecosystem service provision, and ultimately for producers.

Conclusions

In sum, elevation had a significant influence on hollow twig occupation by ants, ant species richness, relative abundance of common species, and community composition of arboreal twig-nesting ants in coffee agroecosystems across the Soconusco region of Chiapas. Species richness and colony abundance peaked at mid-elevations, supporting the MDE hypothesis. Some species were influenced by hollow twig availability or vegetation complexity or both, but elevation was an important factor for all ant-related variables examined. Individual species of ants interact differently in the complex food web, carrying out unique functions (Vandermeer et al. 2010). Some species of ants can coexist with each other while other species may decline in response to competition (Philpott 2010, Livingston & Philpott 2010). The change observed in community composition at different elevations is likely a reflection of complex ecological processes, and changes in complex interactions may result in disruptions to the ecological services provided by twig-nesting ants in coffee agroecosystems.

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Table 1: Range of vegetation variables and vegetation complexity index values measured in study plots in coffee agroecosystems in the Soconusco region of Chiapas, Mexico[§].

Factor measured	Range of values (min to max)	t-stat	R^2	P
Canopy cover (%)	6.7 - 98.0	-5.26	0.409	<0.001
No. of trees	1 to 11	0.426	0.005	0.673
No. of tree species	1 to 7	-0.529	0.007	0.600
Tree height (m)	3.14 - 15	-1.46	0.051	0.152
Tree circumference (cm)	19.64 - 149.17	-0.506	0.006	0.615
No. of coffee plants	17 - 71	2.731	0.157	0.009
Coffee height (m)	1.3 - 4.5	0.359	0.003	0.721
Vegetation Complexity (VCI)	0.262 - 0.816	-3.12	0.196	0.003

[§] Statistical results are from simple linear regression between elevation and the vegetation factor.

Table 2: GLM results for best-fit models of the proportion of hollow twigs occupied by ants,

number of ant species, and the relative abundance of common ant species.

Factor	Deviance	Residual DF	Residual Deviance	P
Proportion of hollow twigs occupied by ants				
lnVCI	1.598	40	355.33	0.206
No. hollow twigs	68.278	39	287.05	<0.001
Elevation (linear)	0.901	38	286.15	0.342
Elevation (quadratic)	19.954	37	266.2	<0.001
No. ant species				
lnVCI	9.972	40	401.93	0.076
No. hollow twigs	251.91	39	150.02	<0.001
Elevation (linear)	1.017	38	149.01	0.571
Elevation (quadratic)	31.807	37	117.2	0.001
Proportion of twigs occupied by Pseudomyrmex simplex				
Elevation (linear)	1.3516	35	1.6533	<0.001
Proportion of twigs occupied by Pseudomyrmex ejectus				
No. hollow twigs	0.16392	35	1.51498	0.004
Elevation (linear)	0.84201	34	0.67297	<0.001
Proportion of twigs occupied by Procryptocerus hylaeus				
No. hollow twigs	0.094	35	166.45	0.759
Elevation (linear)	17.243	34	149.21	<0.001
Elevation (quadratic)	44.176	33	105.03	<0.001
Proportion of twigs occupied by Pseudomyrmex filiformis				
lnVCI	49.905	35	652.81	<0.001
Elevation (linear)	52.643	34	600.17	<0.001
Proportion of twigs occupied by Nesomyrmex echinatinodis				
lnVCI	0.005	35	207.79	0.941
Elevation (linear)	3.953	34	203.84	0.047
Elevation (quadratic)	40.067	33	163.77	<0.001

Figure 1: Map of the 42 coffee agroecosystem study plots along the elevational gradient between 450 – 1550 m in the Soconusco, Chiapas, Mexico. Plots occurred on several different large, estate coffee farms (Brazil, Argovia, Genova, Santa Anita, Maravillas, Irlanda, Hamburgo, and San Francisco) and nearby smallholder plots (e.g. Ejido Sinai).

Figure 2: Elevational ranges of the twig nesting ant species collected from coffee plants during my field research in the Soconusco region of Chiapas, Mexico; small boxes indicate that the species was only found in one plot at one elevation.
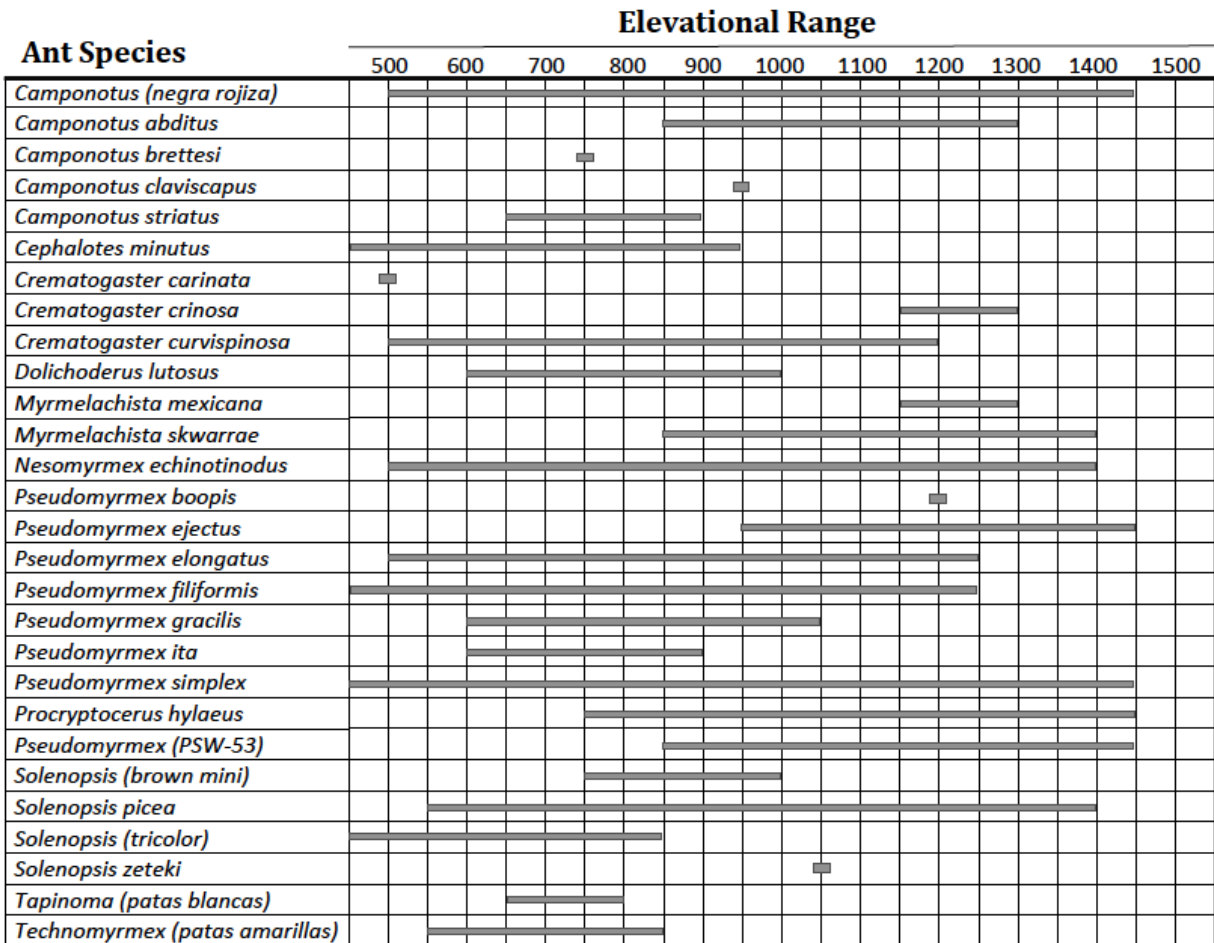

Ant Species	500	600	700	800	900	1000	1100	1200	1300	1400	1500

Figure 3: Relationships between the proportion of hollow coffee twigs occupied by twig-nesting ants and (a) elevation (P<0.001) and (b) the number of available hollow twigs (P<0.001) and between the number of ant species occupying twigs and (c) elevation (P=0.001) and (d) the number of hollow twigs (P<0.001) in coffee agroecosystems in the Soconusco region of Chiapas, Mexico.
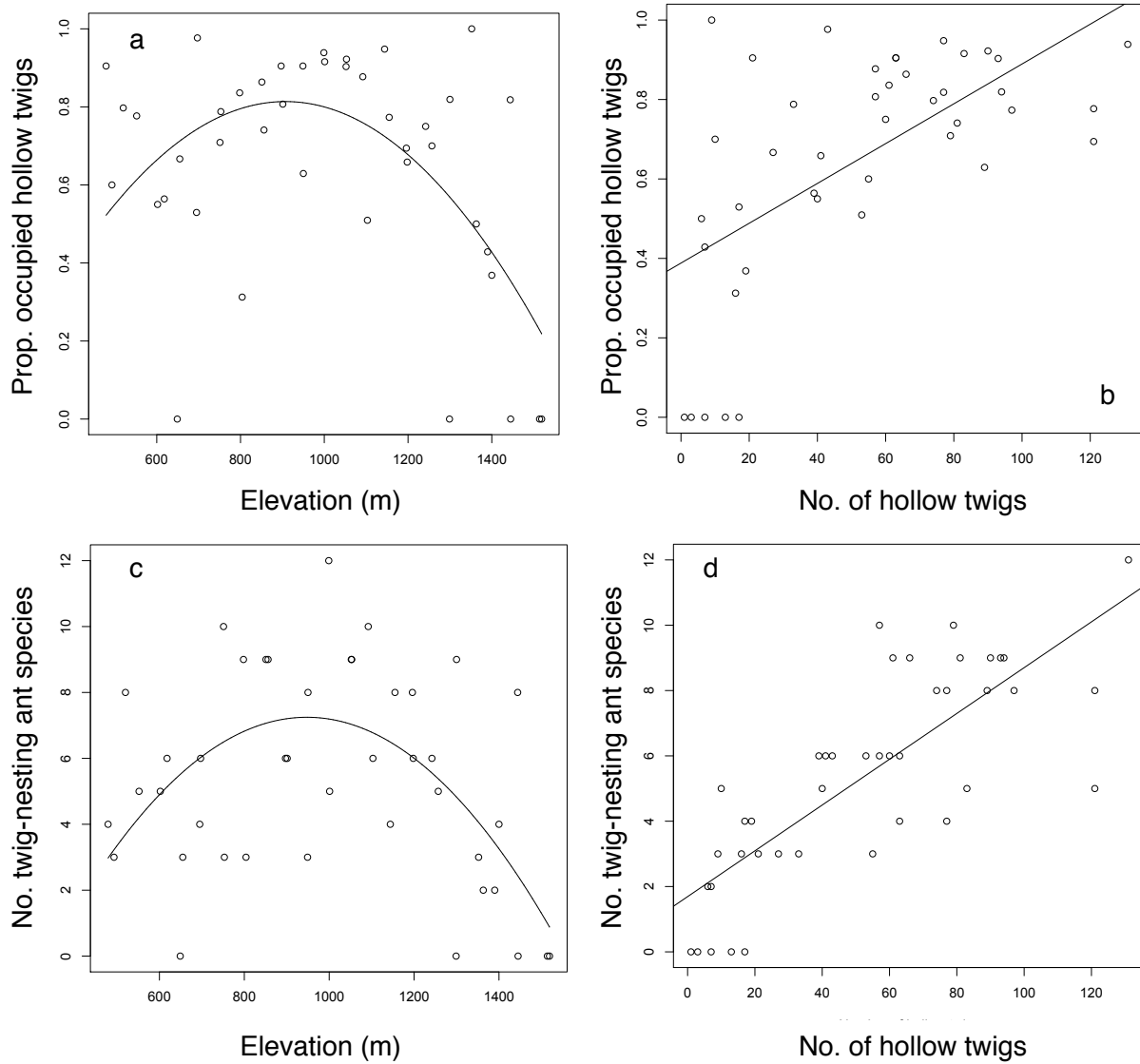
Figure 4: Proportion of occupied coffee twigs occupied by common ant species ((a) *Pseudomyrmex simplex,* (b) *P. filiformis*, (c) *P. ejectus,* (d) *Procryptocerus hylaeus*, and (e) *Nesomyrmex echinotinodus*) along an elevational gradient from 450 to 1550 m in coffee agroecosystems in the Soconusco region of Chiapas, Mexico. All relationships are significant (P<0.001).
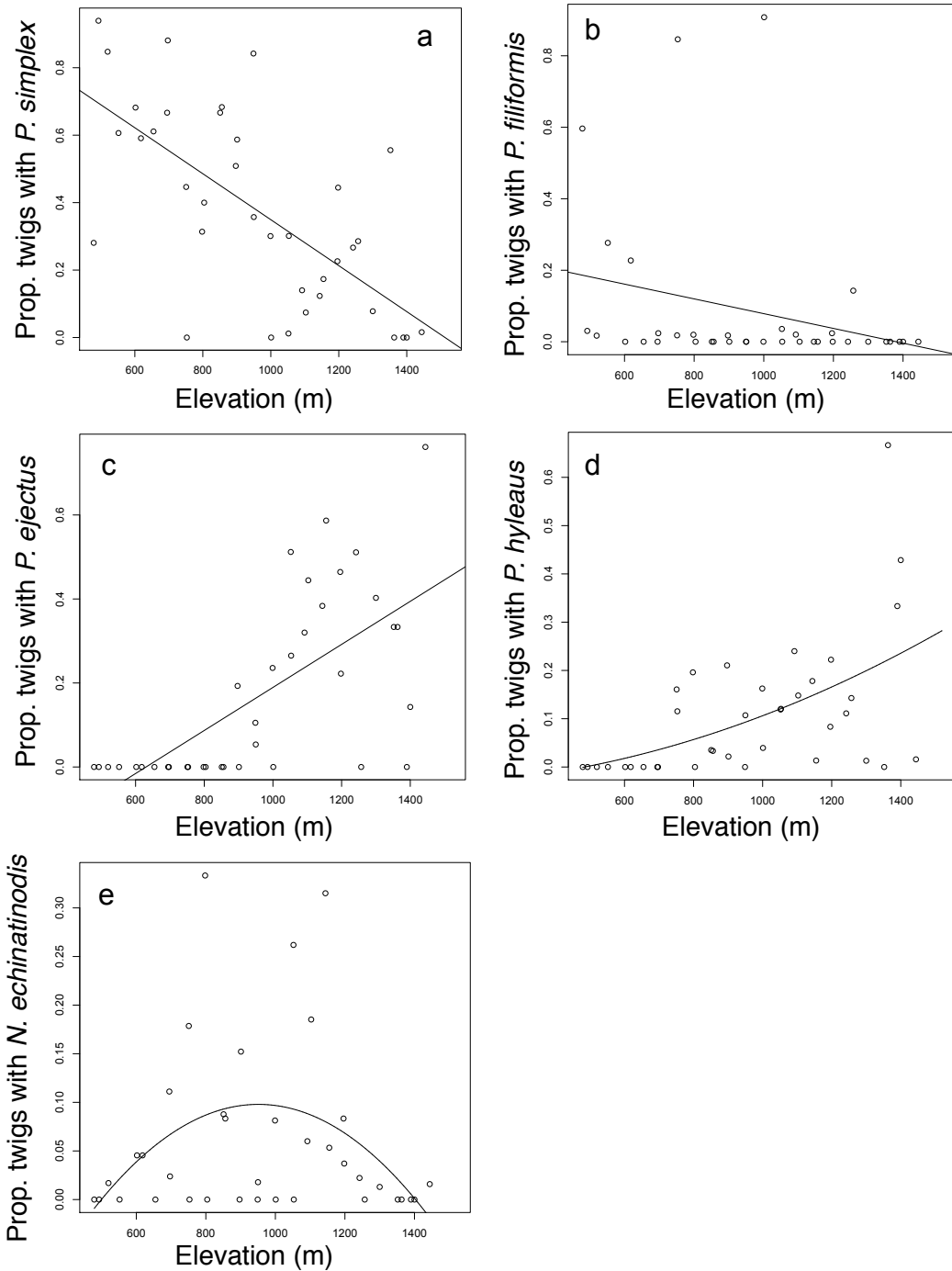

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Figure 5: Non-metric multidimensional scaling showing composition of arboreal, twig-nesting ant species in coffee agroecosystems in Chiapas, Mexico within three different elevation groups. Red boxes show low elevation (450-850 m) plots, black circles show mid elevation (850-1150 m) plots, and green triangles show high elevation (1150-1550 m) plots. See text for information on statistical differences between groups.
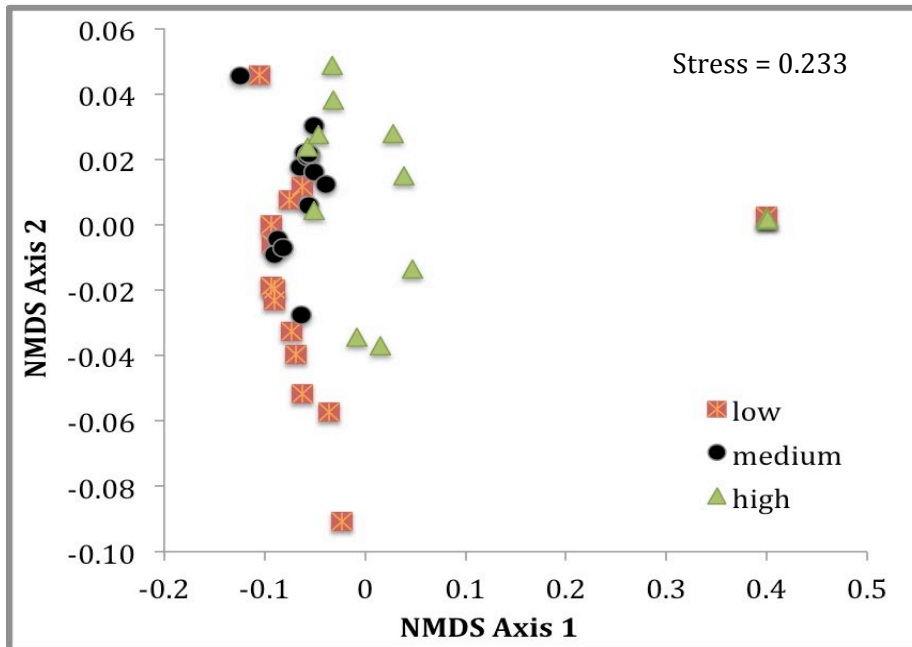
Figure 6: Visual representations of changes in twig nesting ant species-richness (bars) and species composition (pie charts) along an elevational gradient in coffee farms of the Soconusco, Chiapas. Numbers above the bars show the total number of species in each elevation band.