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Changes in Species Richness, Abundance, and Composition of Arboreal Twig-nesting Ants Along an Elevational Gradient in Coffee Landscapes

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ABSTRACT

The distribution, diversity, and assembly of tropical insects have 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. Ant diversity and abundance may shift along elevation gradients, but no studies have examined if the proportion of occupied twigs or richness of arboreal twig-nesting ants vary with elevation. In coffee agroecosystems, there are over 40 species of arboreal twig-nesting ants. We examined communities of twig-nesting ants in coffee plants along an elevational gradient to answer the following questions: (1) Do species richness and colony abundance decline with elevation or show a mid-elevation peak? (2) Does community composition change with elevation? (3) Is elevation an important predictor of change in ant abundance, richness, and relative abundance of common species? We surveyed 42 10 × 10 m plots in 2013 from 450 to1550 m elevation across a coffee landscape in Chiapas, Mexico. We sampled a total of 2211 hollow coffee twigs, 77.1 percent of which were occupied by one of 28 species of ants. *Pseudomyrmex simplex* was more abundant in lower elevations, whereas *Pseudomyrmex ejectus* dominated in high elevations. Species richness and the percent of occupied hollow twigs both peaked at mid-elevations (800–1050 m). In sum, we found that species richness, abundance, and composition of arboreal twig-nesting ants shift with elevation. These findings may provide important insights for understanding ant communities in coffee agroecosystems.

Abstract in Spanish is available with online material.

Key words: agroforestry; biodiversity conservation; Chiapas; coffee agroecosystems; Formicidae; Mexico.

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 has contributed to 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). It is important to study patterns of species richness and composition along elevational gradients 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 (ants – Longino *et al.* 2014, animals – Gaston 2000, plants – Kessler *et al.* 2001), or display a mid-elevation peak with elevation change (Olson 1994, Sanders 2002, Bachman *et al.* 2004, McCain 2004). These patterns have led to two main hypotheses relating to biodiversity change along eleva-

tional gradients. First, some hypothesize there is a greater species richness and diversity at lower elevations, as 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).

Insects, and in particular, ants display large variation in their responses to elevation gradients. Insect species richness can increase with elevation, decrease with elevation, peak at middle elevations, or may not vary with elevation change at all (Hodkinson 2005). Several studies examining changes in ant communities 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) found mid-elevation peaks in ant species richness, and much of the variation in ant richness could be explained by area and geometric constraints. In contrast, species richness of ants in arid ecosystems tends to be greater at high elevations because lower

temperatures and higher precipitation support more primary production, which provides an environment with lower levels of physiological stress (Sanders *et al.* 2003). It is important to note that the diversity–elevation relationship can be affected by the extent of the gradient sampled (Rahbek 2005). For instance, 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 along shorter elevational gradients of ~500–1500 m, 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 around 600–800 m.

Although many studies examine changes in species richness and community composition of ants along elevation gradients in natural systems, few have examined elevational gradients in agricultural systems, despite their prevalence in tropical landscapes. Coffee agroecosystems, in particular, represent one habitat type that grows across a wide range of elevations in the tropics. These multistrata agroforestry systems 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). In Mexico, coffee grows best between 600 and 1400 m (Moguel & Toledo 1999). Traditionally, coffee-growing techniques were compatible with sustaining biodiversity and the traditional mosaic structure of coffee landscapes maintains and even improves biodiversity (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 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, and has negative impacts on the provisioning of other ecosystem services such as pollination, nutrient cycling, and predation provided by organisms such as ants (Jha *et al.* 2014). Ants reduce herbivory (Rocha & Bergallo 1992, Vandermeer *et al.* 2002) 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 are 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 the number and the diversity of available twigs in coffee habitats (Armbrecht *et al.* 2004, Philpott & Foster 2005). Boring beetles (Curculionidae: Scolytinae) might help create these nest sites as they hollow out dead twigs (Ward 1991, Kirkendall 1993, Hulcr *et al.* 2007). In the case where ants occupy hollow twigs while they are still on the coffee plants, they may be providing important biological control services. Twig-nesting ants are associated with reductions in attacks by 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).

We examined twig-nesting ant communities along an elevational gradient to examine whether ant species richness, abundance, and community composition shift with elevation. In contrast to other studies examining changes in ant species richness and community composition along elevation gradients where not only the focus organism but also the habitat types demonstrated marked turnover along the elevation gradient, we studied a single host plant (coffee) and a single habitat type (coffee agroecosystems). We specifically sought to answer the following questions: (1) Do species richness and colony abundance decline with elevation or show a mid-elevation peak? (2) Does community composition change with elevation? (3) Is elevation an important predictor of change in ant abundance, richness, and relative abundance of common species?

METHODS

SITE DESCRIPTION.—We conducted 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 northeast of the nearest city, Tapachula. The annual rainfall in this area is ~4500 mm on average (Philpott *et al.* 2008b). Approximately 93.7 percent of the study area is coffee, and the remaining 6.3 percent is small forest fragments (Philpott *et al.* 2008b). Of the coffee production, about 50 percent can be classified as shaded monoculture—or farms with few shade trees dominated by a single species or genus, which in our case is *Inga* spp. (Moguel & Toledo 1999). Other farms in the study region have more diverse and dense tree cover, and there is just one sun coffee farm. Landholdings in the Soconusco are mostly large-scale coffee farms (200–300 ha).

We established 42 study plots between 450 and 1550 m (Fig. S1). This elevational range covers the extent over which *Coffea arabica* is cultivated in the study area. Plots were selected haphazardly along the elevation gradient, but some plots occurred in each of the management systems described (*e.g.,* with diverse and dense tree cover, shaded monoculture, and sun coffee systems). Plots occurred on several different large, estate coffee farms (Fincas Brazil, Argovia, Genova, Santa Anita, Maravillas, Irlanda, Hamburgo, and San Francisco) and on nearby smallholder farms (*e.g.,* Ejido Sinai). Plots were 10 × 10 m in size, and relatively evenly spaced across the elevation gradient. We established plots haphazardly in areas not occupied by *Azteca sericeasur* ants, as these ants are known to have aggressive interactions with twig-nesting ants (Philpott 2010). Each plot was located at least 400 m from other plots to ensure independence of the ant colonies in each plot.

VEGETATION SAMPLING.—Because twig-nesting ants can be strongly affected by coffee management (Philpott & Foster 2005), and because coffee vegetation management can sometimes co-vary with elevation, we sampled vegetation characteristics for

each study plot. We used a convex spherical densiometer to measure the canopy cover, and took five measurements in each plot (one in the center and to 5 m to the N, S, E, and W of the center). We took the mean value of the five measurements for each plot. We also surveyed trees and recorded the species, height, and circumference at 1.35 m aboveground for each tree. We recorded the number of coffee plants and the average height of coffee plants in each plot. Thus, our vegetation data included number of trees, number of tree species, mean tree height, mean tree circumference, average coffee height, and canopy cover. Because many vegetation characteristics are frequently correlated with one another, we calculated a vegetation complexity index (VCI) to generate a single vegetation value to describe the plots (see Philpott *et al.* 2008a, De la Mora *et al.* 2013). To calculate the VCI, we divided values for each variable (number of trees, number of 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 correlates with vegetation complexity, we transformed values from 0 to 1, then subtracted from 1. We summed the transformed values of each variable for each plot, and divided by 7 to obtain the VCI value.

ANT SURVEYS.—We surveyed ants nesting in hollow twigs of *C. arabica* plants. We sampled 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, we broke off all dead twigs and snapped them open to search for ants. For each coffee plant, we recorded data on: (1) number of hollow twigs; (2) number of occupied hollow twigs; and (3) identity of each ant species found occupying the twigs. We collected voucher specimens of all ant species, placed them in ethanol (70%), and identified them later in the lab according to several resources (*e.g.,* Bolton 1994, 2012, AntWeb 2013, Longino 2013). Voucher specimens are held in S.M.P.'s ant collection at the University of California Santa Cruz. We surveyed all ants in plots during June–July 2013.

DATA ANALYSIS.—We used generalized linear models (GLMs) with the glm function in R (R Development Core Team 2014) to examine relationships between elevation and: (1) proportion of occupied hollow twigs; (2) the number of ant species observed; (3) the Chao2 estimator of ant species richness; and (4) the proportion of occupied twigs occupied by each of five common ant species found (as five separate dependent variables). We defined common species as those that occupied >50 twigs, and used the proportion of occupied twigs occupied by each species as a measure of relative abundance. To calculate the Chao2 values, we used EstimateS v. 9.0 (Colwell 2013), and included individual coffee plants in each study plot as the samples. For the GLMs, we tested four different models for each of the eight dependent variables: (1) elevation; (2) elevation + VCI; (3) elevation + number of hollow twigs; and (4) elevation + VCI + number of hollow twigs. We explicitly added VCI and the number of hollow twigs into the models to test whether the changes in vegetation com-

plexity or the number of hollow twigs along the elevation gradient mediated patterns of elevation change. We ran two versions of each of these models with elevation as either a linear (elevation +) or quadratic predictor (elevation + elevation^2 +) of the dependent variables. We compared AIC values to select the best-fit model for each of the dependent variables tested (Table S1). For number of ant species, lnChao2, and proportion of occupied twigs with *Pseudomyrmex simplex* we used GLM with the Gaussian family. For proportion of occupied twigs, proportion of twigs with *Pseudomyrmex ejectus*, proportion of twigs with *Nesomyrmex echinatinodis*, proportion of twigs with *Procryptocerus scabriusculus*, and proportion of twigs with *Pseudomyrmex filiformis*, we used the 'cbind' function and a GLM with binomial error and the logistic link function. The 'cbind' function allows the inclusion of two columns of variables (in our case number of occupied twigs and number of not occupied twigs) to create the dependent variable used in the analysis. For all binomial models where overdispersion was detected (*i.e.,* where residual deviance >> degrees of freedom for the residual deviance) we re-ran models with the 'dispmod' package in R. Overdispersed models were detected for proportion of twigs with *N. echinatinodis*, *P. scabriusculus*, and *P. filiformis*. For all models with VCI, we used natural log transformed VCI values. To determine the goodness-of-fit of the best models identified with AIC, we calculated a pseudo-R^2 value as [(null deviance - residual deviance)/null deviance] following Dobson (2002). All residuals from the best models conformed to the conditions of normality as checked with QQ-Plots and Shapiro tests.

We repeated analyses for proportion of hollow twigs occupied by ants and for the number of twig-nesting ant species eliminating plots without ants (at 649 m, 1299 m, 1445 m, 1514 m, and 1519 m) to ensure that the one low elevation and three high elevation plots without ants were not skewing the results. The qualitative results of this analysis were identical to those reported here.

To examine the differences in species composition of twig-nesting ants along the elevation gradient, we first grouped the plots into 200 m elevation bands, and graphed the relative abundance of all species within each band.

RESULTS

VEGETATION SURVEYS.—Several of the vegetation factors including variation in tree species richness, the number of trees per plot, and mean tree height and circumference were not correlated with changes in elevation (Table 1). Although 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 elevation. Canopy cover significantly declined with increasing elevation ($y = -0.0005x + 1.0336$, Table 1), as did vegetation complexity (VCI) ($y = -0.0003x - 0.5023$, Table 1).

ANT SURVEYS.—Within the 42 plots, we surveyed a total of 1572 coffee plants on which we found 2211 dry, hollow twigs. On average, we found 1.41 ($\pm$ 0.06 SE) hollow twigs per plant, and

TABLE 1. *Range (min. to max.) of vegetation variables and vegetation complexity index values measured in study plots in coffee agroecosystems in the Soconusco region of Chiapas, Mexico. Statistical results are from simple linear regression between elevation and the vegetation factor.*

Factor measured	Range of values	t-stat	Correlation coefficient	R^2	P
Canopy cover (%)	6.7–98.0	−5.26	−0.639	0.409	<0.001
No. of trees	1–11	0.426	0.067	0.005	0.673
No. of tree species	1–7	−0.529	−0.083	0.007	0.600
Tree height (m)	3.14–15	−1.46	−0.225	0.051	0.152
Tree circumference (cm)	19.64–149.17	−0.506	−0.08	0.006	0.615
No. of coffee plants	17–71	2.731	0.396	0.157	0.009
Coffee height (m)	1.3–4.5	0.359	0.057	0.003	0.721
Vegetation Complexity (VCI)*	0.262–0.816	−3.12	−0.442	0.196	0.003

*Regressions test elevation versus lnVCI.

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 percent of the hollow twigs were occupied by one of the 28 arboreal twig-nesting ant species collected (Fig. 1). The most common species encountered (and the percentage of nests they occupied) were *Pseudomyrmex simplex* (37.6%), *Pseudomyrmex ejectus*

(16.9%), *Procryptocerus scabriusculus* (10.6%), *Pseudomyrmex filiformis* (8.7%), and *Nesomyrmex echinatinodis* (6.0%).

The proportion of hollow twigs occupied by ants, the species richness of ants occupying hollow twigs, and the estimated (Chao2) richness of ants occupying twigs were correlated with changes in elevation as well as plot characteristics. The GLM model that best predicted hollow twig occupation (for all ants) included elevation, the number of hollow twigs, and VCI (pseudo-r^2 = 0.254). The proportion of occupied hollow twigs was significantly higher at middle elevations (Fig. 2A; Table 2). Although VCI was retained in the model with lowest AIC value, it was not a significant predictor of the proportion of occupied nests. However, the proportion of occupied hollow twigs did increase linearly with the number of available hollow twigs (Fig. 2B; Table 2). Likewise, the best model for twig-nesting ant species richness included elevation, the number of hollow twigs, and VCI (pseudo-r^2 = 0.715). Ant species richness was highest at mid-elevations, resulting in a significant quadratic response to elevation (Fig. 2C; Table 2). Ant species richness increased linearly with the number of available hollow twigs (Fig. 2D; Table 2). Likewise, the best model for estimated (Chao2) twig-nesting ant species richness included elevation, the number of hollow twigs, and VCI (pseudo-r^2 = 0.557). Estimated species richness of ants was highest at mid-elevations, resulting in a significant quadratic response to elevation (Fig. 2E; Table 2). Ant species richness increased linearly with the number of available hollow twigs (Fig. 2F; Table 2).
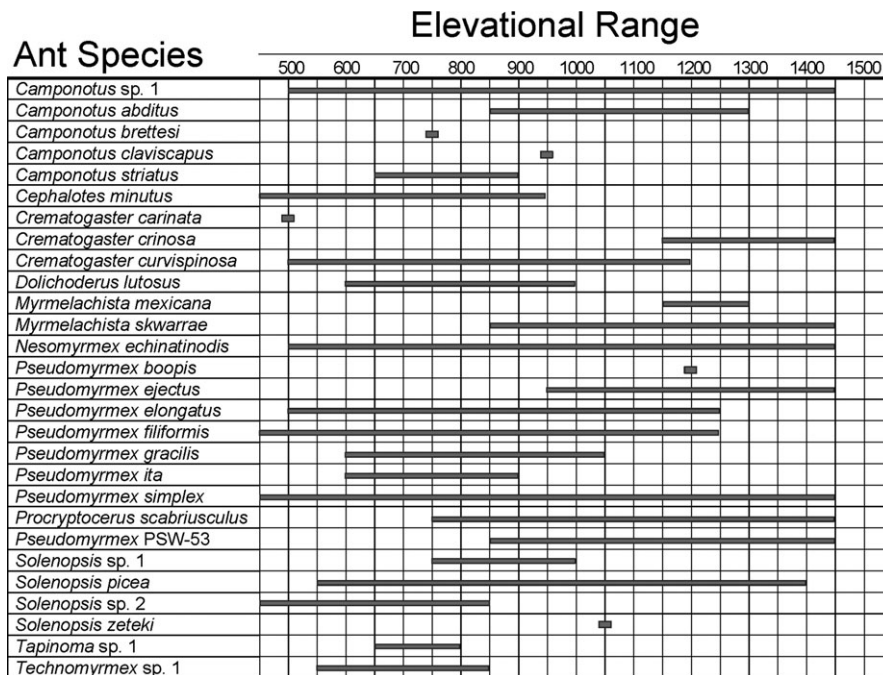

FIGURE 1. Elevational ranges of the twig-nesting ant species collected from coffee plants during field research in the Soconusco region of Chiapas, Mexico. Bars show the span of the elevational range, not that ants were present at each elevation between the highest and lowest elevations selected. Small boxes indicate that the species was only found in one plot at one elevation.
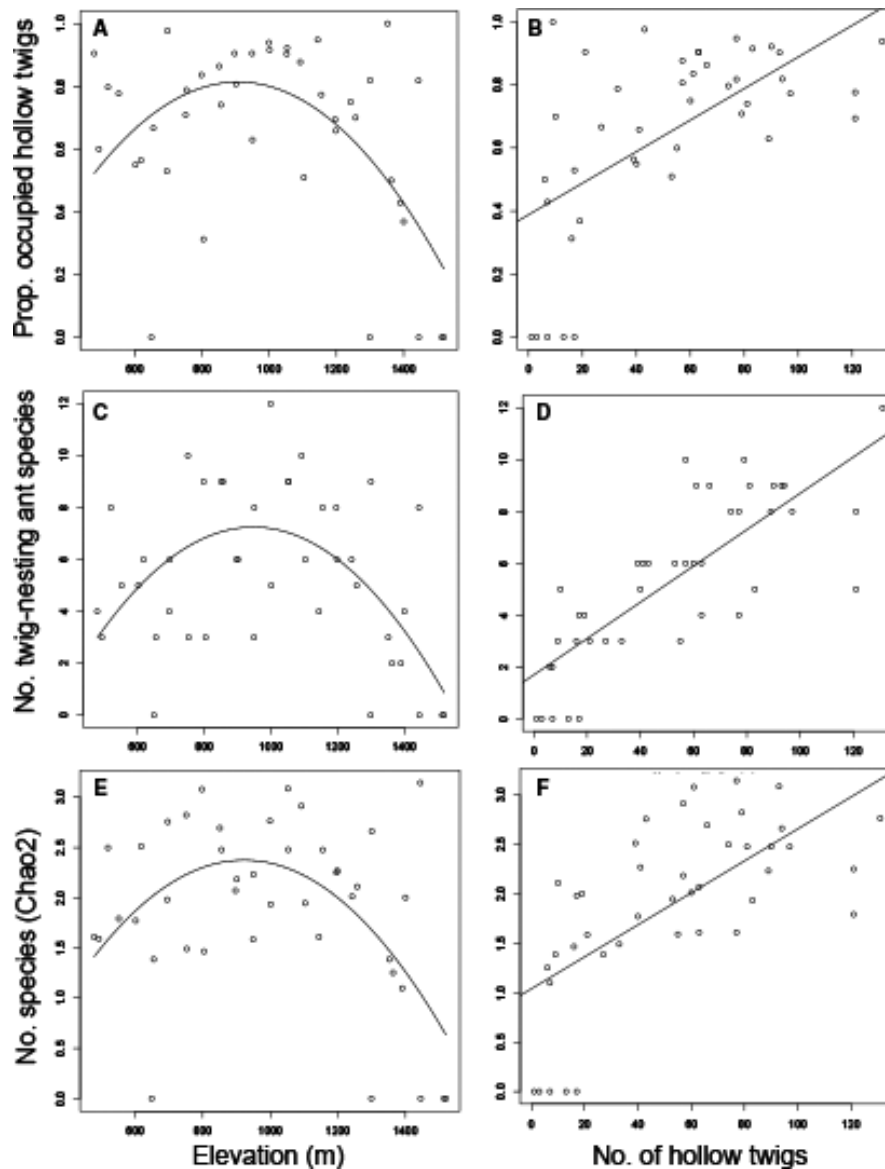
FIGURE 2. Relationships between the elevation and number of hollow coffee twigs and (A, B) proportion of hollow coffee twigs occupied by twig-nesting ants, (C, D) the number of ant species occupying twigs, and (E, F) estimated ant species richness in coffee agroecosystems in Chiapas, Mexico. Lines show best-fit lines for quadratic (A, C, E) or linear (B, D, E) relationships between variables. All relationships are significant ($P < 0.007$).

The elevational ranges for species of twig-nesting ants varied (Fig. 1) and changes in elevation correlated with the proportion of occupied twigs occupied by each of the most common species (Fig. 3; Table 2). *P. simplex* was highly abundant at lower elevations accounting for 79.5 percent 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 (pseudo-$r^2 = 0.450$) (Fig. 3A; Table 2). Similarly, *P. filiformis* occupied a wide range of elevations, but occupied a higher proportion of nests at lower elevations, accounting for >20 percent of occupied nests below

1050 m. Relative abundance of *P. filiformis* dropped with elevation increase (Fig. 3B), but did not significantly vary with either elevation or changes in VCI in the model that corrected for significant overdispersion (Table 2) (pseudo-$r^2 = 0.175$). In contrast, *P. ejectus* was most abundant at higher elevations, inhabiting 56.9 percent of occupied nests above 1100 m. The relative abundance of *P. ejectus* increased linearly with elevation (Fig. 3C) and with the number of hollow twigs (Table 2) (pseudo-$r^2 = 0.599$). Relative abundance of *P. scabriusculus* was highest at mid-elevations, and relative abundance of this species decreased with an increasing number of hollow twigs in a plot (pseudo-$r^2 = 0.5$) (Fig. 3D;

TABLE 2. *Generalized linear model (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
No. estimated ant species (lnChao2)				
lnVCI	0.661	40	30.93	0.184
No. hollow twigs	13.361	39	17.569	<0.001
Elevation (linear)	0.876	38	16.693	0.128
Elevation (quadratic)	2.704	37	13.989	0.007
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 scabriusculus*[*]				
No. hollow twigs	0.5739	35	49.079	0.449
Elevation (linear)	9.4588	34	39.620	0.002
Elevation (quadratic)	6.5188	33	33.102	0.011
Proportion of twigs occupied by *Pseudomyrmex filiformis*[*]				
lnVCI	1.9141	35	23.003	0.1665
Elevation (linear)	1.7993	34	21.203	0.1798
Proportion of twigs occupied by *Nesomyrmex echinatinodis*[*]				
lnVCI	0.0681	35	43.782	0.794
Elevation (linear)	0.1584	34	43.623	0.690
Elevation (quadratic)	10.3764	33	33.247	0.001

[*]Results for 'dispmod' models to correct overdispersion.

Table 2). Finally, the relative abundance of *N. echinatinodis* was highest at mid-elevations, and declined where vegetation complexity (VCI) was higher (pseudo-r^2 = 0.319) (Fig. 3E; Table 2).

Community composition of twig-nesting ant species changed with elevation. We did not perform statistical tests to examine the changes in composition, but visual representations show dramatic changes in the relative abundance of common species within different elevational bands studied (Fig. 4).

DISCUSSION

Our results indicate that for arboreal twig-nesting ants in coffee agroecosystems, species richness, abundance, and communities shift with changes in elevation. We documented that the propor-

tion of hollow twigs occupied, the species richness of coffee-dwelling twig-nesting ants, and the estimated (Chao2) richness of ants was highest at the middle elevations sampled. Second, we demonstrated that relative abundance of individual ant species shifts along the elevation gradient (Figs. 3 and 4)—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 resulted in shifts in community composition with changes in elevation. Finally, we documented that elevation was a consistent predictor of changes in ant communities, and that other management factors (*e.g.*, vegetation complexity) also influenced ant communities along this gradient.

ANTS AND ELEVATION.—When studying the richness and abundance of species in natural ecosystems, mid-elevation peaks in richness and abundance are common (~50% of studies) (Rahbek 2005). In our study, both twig-nesting ant species richness and the proportion of hollow twigs occupied peaked at mid-elevations. According to pseudo-r^2 values, elevation, VCI, and the number of hollow twigs explained a large amount of the variation in observed and estimated species richness, but did not predict as well the proportion of occupied twigs. These results were not initially expected as productivity tends to be higher in lower elevations, and many have documented declines in richness with increasing elevation (MacArthur 1972, Brown 1988, Stevens 1992, Rahbek 1995, Longino *et al.* 2014). In many recent studies, including those on ants, elevational gradients are potentially explained by the mid-domain effect (MDE), which comes about with an increase in species' range overlap toward the center of the domain as species ranges are bounded by the elevation extremes (Colwell & Lees 2000, Sanders 2002). Although we did sample the complete elevational gradient of cultivation of *Coffee arabica*, the ants that inhabit these coffee plants may occur in higher and lower elevations. Thus, we did not explicitly test for geographic constraints in our data. However, the fact that we only sampled ants in one specific plant species and one agroecosystem type along this entire gradient is a unique and novel contribution of this study, because most examinations of change in ant communities along elevation gradients sample these ants with a marked turnover in habitat type along that same gradient. Nevertheless, hump-shaped richness patterns may be related to a number of factors including habitat disturbance, overlapping ecotones, climatic severity, temperature, resource availability, predation, and competition (Rahbek 2005) so even in our system, there are multiple mechanisms that may contribute to the pattern we observed. Many elevation studies looking at ants have found mid-elevation peaks in richness, abundance or diversity (Samson *et al.* 1997, Fisher 1998, Sanders 2002, Sabu *et al.* 2008, Bishop *et al.* 2014, Smith *et al.* 2014). Our results are consistent with these studies as we found higher species richness and abundance of ants at mid-elevations.

Mid-elevation peaks in richness may be natural, or may be influenced by human disturbance at the landscape scale. In human-modified landscapes, where forest fragments are often more prevalent at higher elevations, mid-elevation peaks in rich-
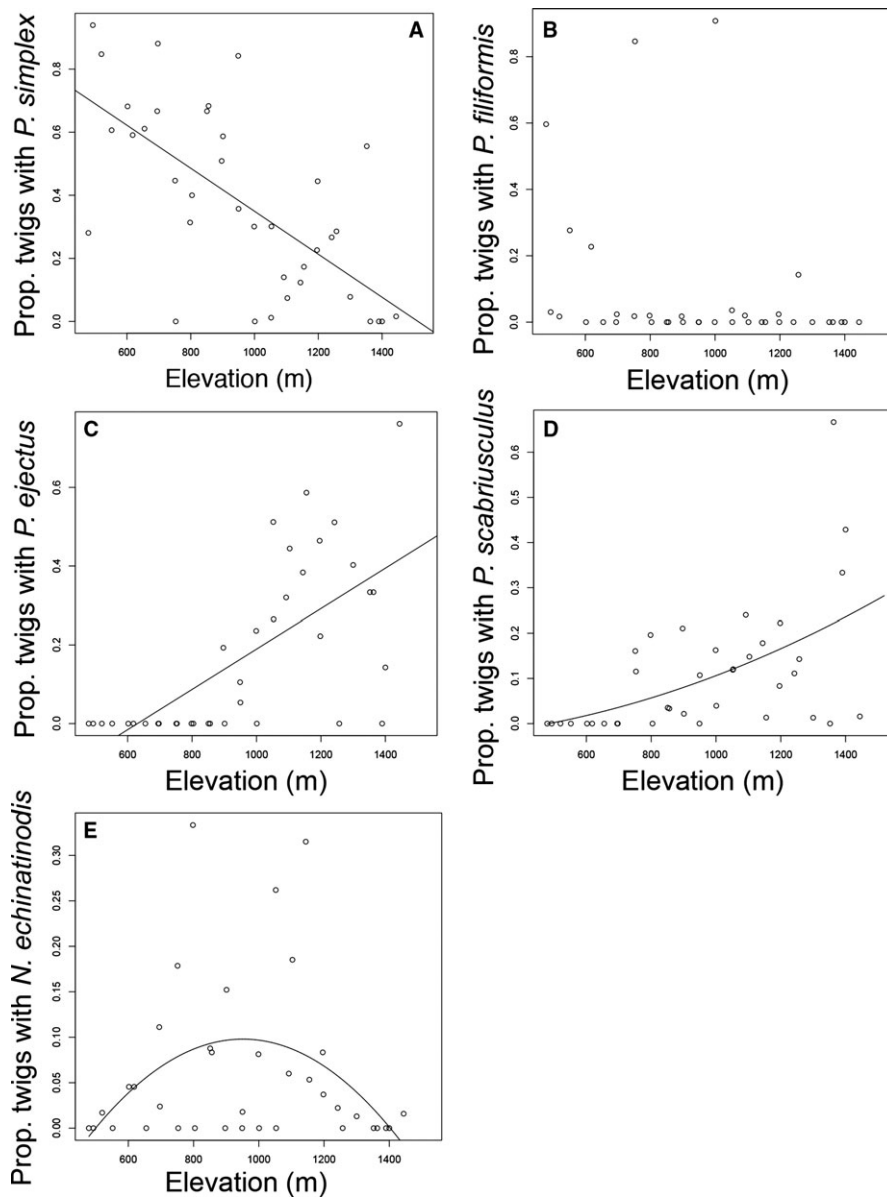
FIGURE 3. Generalized linear model (GLM) predicted values for proportion of occupied coffee twigs occupied by common ant species [(A) *Pseudomyrmex simplex,* (B) *P. filiformis,* (C) *P. ejectus,* (D) *Procryptocerus scabriusculus,* and (E) *Nesomyrmex echinatinodis*] along an elevational gradient from 450 to 1550 m in coffee agroecosystems in Chiapas, Mexico. Lines show best-fit lines for quadratic (D, E) or linear (A, B, C) relationships between variables. All relationships with fitted lines are significant ($P < 0.001$).

ness may result from stronger habitat modification at low elevations (Tejeda-Cruz & Sutherland 2004). For example, Fisher (1998) found a mid-elevation peak 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 disturbance associated with a city at the high elevations of the third transect was likely the contributor of diversity reduction and the mid-do-

main pattern. Thus, human disturbance has been invoked as a driver of mid-elevation peaks in richness in different ways. Because this study was conducted in managed coffee agricultural systems, that tend to be more homogeneous than natural tropical habitats, we thought that we might not see changes in ant communities with elevation. However, we found our results to be consistent with those of unmanaged systems and contrary to the findings of Sanders *et al.* (2003).

ANTS, VEGETATION, AND HOLLOW TWIGS.—The fact that elevational gradients are many times representative of other environmental
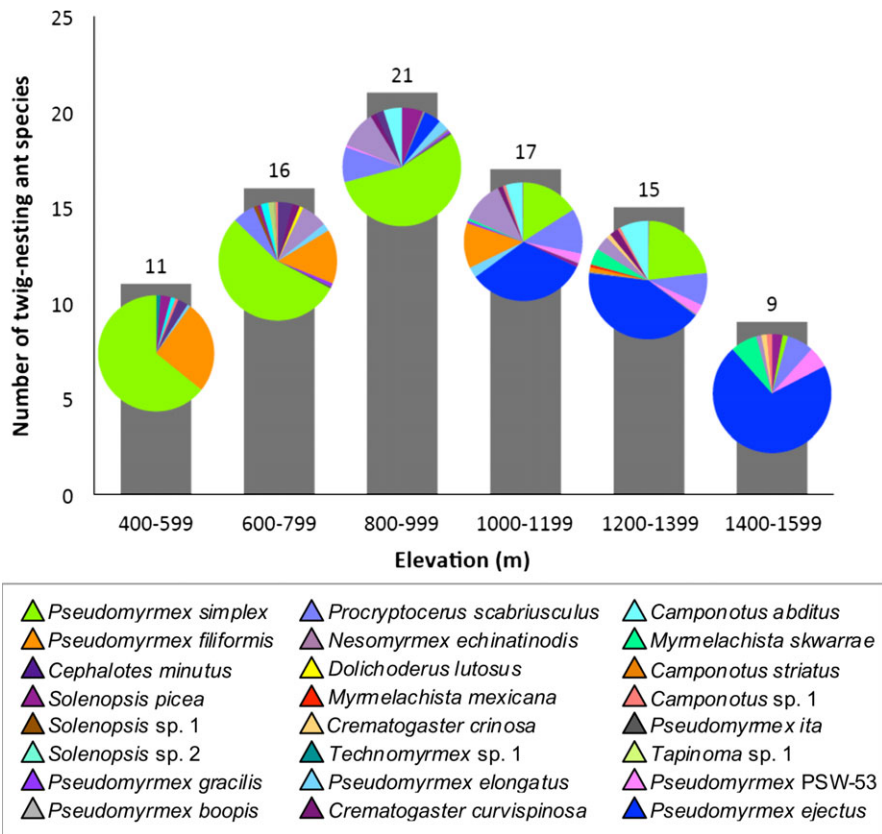
FIGURE 4. Visual representations of changes in twig-nesting ant species richness (bars) and species composition (pie charts) along an elevational gradient in coffee farms in Chiapas, Mexico. Numbers above the bars show the total number of ant species observed in each elevation band.

gradients, and are 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. Some of the observed changes in vegetation correlated with changes in ant communities. For example, vegetation complexity was included in the best model for predicting overall nest occupation, species richness, and relative abundance of *N. echinatinodis* (but note that the best model explained relatively low proportion of the variance in the data for both *P. filiformis* and *N. echinatinodis*). Observed changes in ant community features with changes in vegetation complexity support other studies that have long demonstrated positive effects of coffee-shade management on biodiversity and communities of ants in coffee agroecosystems (Perfecto *et al.* 1996, 1997, Philpott *et al.* 2008a).

Although the number of hollow twigs in a plot did not correlate with changes in elevation, we did find that the number of hollow twigs was a highly important correlate of twig-nesting ant twig occupation and species richness. The proportion of occupied twigs, observed species richness, and estimated species richness all increased linearly with number of hollow twigs. Relative abundance of *P. ejectus* increased with the number of hollow twigs, and relative abundance of *P. scabriusculus* decreased with increases in the number of hollow twigs. Little information is available about the natural history of most of the species encountered in this study, but based on the observations of competition for artificial nest sites in the lab, *P. scabriusculus* is a poor competitor, losing ~60 percent of competitive encounters for access to nests (S. Philpott, unpubl. data). In sites with more hollow twigs, both number of twig-nesting ants and species richness increases, and *P. scabriusculus* may be eliminated from twigs by more aggressive ants in these sites. Nest availability and diversity may be an extremely important determinant of community composition for twig-nesting ants (Armbrecht *et al.* 2004, Powell 2009). 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 agroecosystems 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 our observations, we documented that both nest

occupation and ant species richness increased with nest availability—corroborating previous findings that low nest availability, and low numbers or a low diversity of available are an important limiting factor in ant communities (Armbrecht *et al.* 2004, Philpott & Foster 2005).

It is important to note that in our study, there were five plots in which we did not find ants perhaps due to twig characteristics, vegetation, or management of those particular plots. In the five plots with no ants, there were few hollow twigs per plot (average 8.2, range 1–17 hollow twigs) compared with the average number of hollow twigs found across all 42 study plots (52.62). Yet, there were seven other plots with fewer than 20 twigs, that had 3–9 occupied twigs and 2–5 ant species. Thus, twig availability is just one factor influencing the abundance and richness of ants. One of the plots (at 649 m elevation) was a plot with very high vegetation complexity. We suspect that in this plot that contained a large number of trees, tree species, and other shrubs, that overall twig availability (in addition to coffee twigs) is much higher, thus leading to lower coffee-twig occupation. Finally, one of the three highest elevation plots was located in a sun coffee farm, the only one in the region, that has heavily pruned, small coffee plants, and relatively heavy use of agrochemicals that both may also have limited ant occupation in that plot.

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, we examined a range of coffee agroecosystems, but we did not specifically aim to examine whether patterns in the ant community observed along elevational differed in coffee versus nearby natural habitats. We 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, land use, or management change. Axmacher *et al.* (2004) compared alpha diversity of moths along an elevational gradient on Mount Kilimanjaro, and the gradient included agricultural areas, agroforestry areas, 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 (Gadagkar *et al.* 1990, 1993, MacKay *et al.* 1991,

Perfecto & Vandermeer 2002), Gadagkar *et al.* (1990) also concluded that influence from elevational variation might trump even extreme differences in disturbance.

CONCLUSIONS

In sum, elevation was correlated with changes in hollow twig occupation by ants, ant species richness, estimated 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. Some species were influenced by hollow twig availability, 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). Ants serve as important indicator species (Hoffmann & Andersen 2003), and moreover, 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, and changes in ant abundance, richness, and composition with elevation should be examined more carefully to understand implications for ecosystem service provision, and ultimately for coffee farmers.

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SUPPORTING INFORMATION

Additional Supporting Information may be found with online material:

FIGURE S1. Map of the 42 coffee agroecosystem study plots along the elevational gradient 450–1550 m in the Soconusco region of Chiapas, Mexico.

TABLE S1. *Akaike information criterion values for eight GLM models examining the relationship between eight dependent variables related to arboreal twig-nesting ant communities and elevation, number of hollow coffee twigs, and the vegetation complexity index.*

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