

# Density compensation, species composition, and richness of ants on a neotropical elevational gradient

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**Abstract.** The distribution of species on elevational gradients challenges our understanding of ecological processes, particularly in the context of biotic responses to climate change. We report here the distribution of leaf-litter ants on the Barva Transect, a continuous gradient of wet forest on Costa Rica's Atlantic slope. Seven sites were sampled, distributed from 50 to 2000 m. Worker density and microsite occupancy were high and relatively constant from 50 m to 1500 m and then abruptly dropped to near zero at 2000 m. Species density at the 1 m<sup>2</sup> scale was high and constant to 1070 m and then declined at higher elevations. Species richness of assemblages at the 1 km<sup>2</sup> scale was constant or rose slightly from 50 m to 500 m and then steeply declined. Because assemblage richness and species density declined more rapidly than worker density, density compensation with elevation is suggested and supported by a measure of mean population density. Statistically, temperature was the best predictor of both species richness and worker density. Relative humidity, soil nutrients, elevation-specific regional area, and the mid-domain effect were poor predictors of richness. Sites from 50 m to 500 m were similar in species composition. In contrast, assemblages at 1070 m, 1500 m, and 2000 m were highly differentiated. Thus elevational ranges were narrow for species at mid to upper elevations and broad for those at the lowest elevations.

Density compensation at higher elevation suggests that if temperature or productivity are influencing the decline in diversity it must be indirectly through speciation and extinction processes, rather than by greater numbers of individuals. The broad ranges of lowland species may be a response to as yet unmeasured environmental factors (e.g., NPP) or to climate changes associated with the current interglacial period. Interglacial warming may have driven species to higher elevations, but the lack of competitors at the lower range margins may have allowed the lowest-elevation species to move upslope without a concomitant contraction of the lower range boundary. Global warming threatens a loss of narrowly-distributed montane species, but lowland biotic attrition may be ameliorated by range expansion among lowland species.

**Key words:** Barva transect; biotic attrition; climate change; Costa Rica; density compensation; elevational gradient; Formicidae; Hymenoptera; range shifts; species density; species richness.

**Received** 20 December 2010; **accepted** 9 February 2011; **published** 10 March 2011. Corresponding Editor: D. Holway.

**Citation:** Longino, J. T., and R. K. Colwell. 2011. Density compensation, species composition, and richness of ants on a neotropical elevational gradient. *Ecosphere* 2(3):art29. doi:10.1890/ES10-00200.1

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## INTRODUCTION

As sites of strong ecological pattern, elevational gradients can provide insights into the historical and contemporary forces that shape life on the planet (Lomolino 2001, Rahbek 2005, McCain 2009, Colwell and Rangel 2010). Elevational

gradients are of small enough spatial scale that all species in the regional species pool potentially have access to all parts of the gradient, minimizing effects of behavioral dispersal limitation. Increasingly, elevational gradients are viewed not only as testing grounds for ecological theory but also as important arenas for

observing responses to climate change (Colwell et al. 2008, Deutsch et al. 2008, Chen et al. 2009). We present here an analysis of leaf litter ant abundance (worker density), richness, and species turnover along a continuously forested tropical elevational gradient, for a very large (more than 12100 individuals of 400 species) quantitative dataset gathered with uniform methods.

Ants are a dominant element of tropical ecosystems (Folgarait 1998, Wilson and Holldobler 2005), yet no thorough descriptive dataset for ant abundance and diversity along a full, continuous tropical elevational gradient has previously been available. Such a dataset is important for two reasons: (1) it allows testing of macroecological hypotheses; and (2) it provides baseline data for monitoring biotic response to climate change (Parmesan 2006, Chen et al. 2009).

Typically, studies of assemblage (alpha) diversity along elevational gradients quantify or estimate species richness of assemblages as a function of elevation, then seek environmental or historical variables that best explain those patterns statistically (McCoy 1990, Samson et al. 1997, Pyrcz and Wojtusiak 2002, Sanders 2002, Sanders et al. 2003, 2007, McCain 2005, 2007a, 2007b, Herzog et al. 2005, Oommen and Shanker 2005, Cardelús et al. 2006, Grytnes and Beaman 2006, Kluge et al. 2006, Watkins et al. 2006, Brehm et al. 2007, Beck and Chey 2008, Kumar et al. 2009). Between sea level and mountain-tops, richness may show a monotonic decline, a mid-elevation peak, or less often a more complex pattern (Rahbek 1995, 2005, McCain 2009). These patterns, which are more sensitive to whether or not the complete gradient is adequately sampled than to the spatial resolution of sampling (Rahbek 2005, Noguez-Bravo et al. 2008), have been linked to energy theory, interactions of rainfall and temperature, regional source pools at particular elevations (usually with area as the proxy), and geometric constraints on ranges (mid-domain effect).

Studies of beta diversity or species turnover along elevational gradients have also informed ecological theory. Ideas about the degree of integration of biotic communities were tested along elevational gradients in pioneering work by Whittaker (1960), who argued for a lack of

zonation, with species having ranges that are distributed more or less independently of each other along the gradient (e.g., Lieberman et al. 1996). Others have shown significantly elevated rates of species turnover at particular elevations (e.g., Kluge et al. 2008).

In this paper we examine the following questions related to alpha and beta diversity of ants on a tropical mountainside:

- How do ant density and diversity (at 1 m<sup>2</sup> and 1 km<sup>2</sup> spatial scales) vary with elevation?
- Can the patterns be related to temperature, rainfall, soil characteristics, area, and/or geometric constraints?
- Do species ranges show non-random associations, producing zones of elevated species turnover? If so, how do zones of species turnover relate to species richness patterns and environmental factors?

We will argue that a combination of environmental factors, biotic interactions, and historical effects jointly drive ant diversity patterns. We develop the hypotheses that (1) probably as a result of interspecific competition at their low-elevation bounds, elevational ranges are narrower than the likely thermal tolerances of species would predict (Price and Kirkpatrick 2009, Jankowski et al. 2010; Sunday et al., *in press*), (2) the warming of the current interglacial has shifted ranges upward, and (3) the species in the lowest elevational band have lacked competitors at their lower range boundaries. The result is that the lowlands have a single assemblage that spans a relatively broad range of environmental conditions, while upland species occupy narrower climatic zones and show more rapid spatial species turnover with elevation. This pattern also suggests that potential lowland biotic attrition caused by contemporary global warming (Colwell et al. 2008) may be ameliorated by expanded ranges of lowland species (Feeley and Silman 2010).

## METHODS

### *Study site*

Field sampling was carried out from 2001 to 2007 on the Atlantic slope of Costa Rica, along a continuously forested elevational gradient known as the La Selva–Volcán Barva gradient

(Lieberman et al. 1996) or the Barva Transect (Cardelús et al. 2006) (Appendix A). It climbs the northern slope of the inactive Volcán Barva, in the Cordillera Volcánica Central. The transect is anchored by La Selva Biological Station (McDade et al. 1993), at 50 m elevation, situated at the base of the mountain. Although the elevation of the highest peak is 2900 m, our highest sampling point was at 2000 m. Less than 2% of the regional area occurs above 2000 m, on a few steep summits (Gilman 2007). The entire transect is forested, protected within Braulio Carrillo National Park since 1985, although parts of it are a mosaic of old growth and regenerating second growth forest. The vegetation is evergreen wet forest. Rainfall is high and seasonality weak. Published estimates of environmental variables along the gradient appear in Cardelús et al. (2006), Watkins et al. (2006), Kluge et al. (2006), Brehm et al. (2007), and Kluge et al. (2008).

#### Sampling methods

The sampling unit was a “miniWinkler” sample of arthropods extracted from a 1 m<sup>2</sup> forest floor plot, following the methods of Fisher (1999a) (hereafter simply referred to as *Winkler samples*). At seven elevations (*sites*) along the Barva Transect (at 50 m, 150 m, 300 m, 500 m, 1070 m, 1500 m, and 2000 m elevation), Winkler samples were taken along approximately equal-elevation transects, with 5 m or 10 m spacing between samples. Total sample size was 2022 Winkler samples; within-site sample size varied from 150 to 599 samples. The total number of workers was recorded for each sample, as a measure of overall ant density, and all ant workers were identified to species. A sample-by-species incidence (presence-absence) matrix was produced for each of the seven sites, based on workers only. See Appendix A for further details. Voucher specimens are currently deposited at the Instituto Nacional de Biodiversidad, Costa Rica, or in the Longino research collection at The Evergreen State College, Olympia, WA.

#### Analysis

Geographical patterns at the 1 m<sup>2</sup> scale were examined for ant worker density (mean number of individual workers per sample), species-specific occupancy (the proportion of samples within a site in which each species occurred), and

species density (mean number of species per sample). Because these measures are not biased by sampling intensity, we based them on the full set of samples at each elevation. Since worker density was strongly right-skewed at most sites, it was transformed as  $\log(n + 1)$ . Patterns at a scale of approximately 1 km<sup>2</sup> (the assemblage or community) were examined with richness measures and diversity indices using all samples at a site (Gotelli and Colwell 2011).

Because the number of samples varied widely among sites, measures known to be biased by sampling intensity were examined after sample-based rarefaction (Colwell et al. 2004) to a common number of species occurrences (Gotelli and Colwell 2001, 2011). After rarefaction, assemblage species richness was measured as the observed number of species, and minimum asymptotic richness was estimated with the Chao incidence-based coverage estimator (ICE) (Lee and Chao 1994). Three diversity indices were examined: Fisher’s Alpha, (exponential) Shannon, and (reciprocal) Simpson. The ratio of mean ant worker density (the mean of the log-transformed raw densities) to rarefied species richness was computed as a measure of mean population density per species. Samples from the 2000 m site, where ants were extremely rare, yielded only 271 species occurrences. These richness and diversity measures were not rarefied for this site nor for the 1500 m site, where 1170 occurrences were recorded, the second-highest number. Measures for all remaining sites were based on samples rarefied to 1170 species occurrences. Linear interpolation between the number of occurrences in accumulated samples was used, as necessary, to obtain rarefied richness and diversity estimates for 1170 species occurrences. Richness estimators and diversity indices were computed for rarefied samples using EstimateS 8.2 (Colwell 2009).

Although rarely examined, the location of a species’ maximum abundance (maximum occupancy in this case) on an elevational gradient can be regarded as an indicator of optimal conditions within its range (Shoo et al. 2005). To examine the distribution of maximum occupancies along the transect (i.e., the number of species that have maximum occupancies at a particular site), sites should be evenly spaced with respect to elevation. Thus, for our analysis of maximum occu-

pancy, we restricted the analysis to the sites at 50 m, 500 m, 1070 m, 1500 m, and 2000 m, resulting in five sites separated by intervals of approximately 500 m elevation. Since a larger sample size allows detection of a greater number of rare species, a site with larger sample size could spuriously appear to have more species reaching maximum occupancy there because of the greater occurrence of rare species unique to that site. To reduce this effect we restricted the analysis of maximum occupancy to species that occurred in 1% or more of the samples in at least one of the five sites.

To assess the potential role of environmental variables in driving the elevational distribution of ant density and diversity, we considered temperature (daily minimum, mean, and maximum), rainfall, relative humidity, and soil nutrients (N and P) (rainfall data from Kluge et al. 2006; all other variables from Gilman 2007). To examine the influence of source-pool area, we considered elevation-specific regional area, estimated from a digital elevation model as the proportional area in each 100 m elevation band on the Atlantic slope of Costa Rica (Gilman 2007).

In addition to these variables, we evaluated the potential role of geometric constraints on ranges (the mid-domain effect) by modeling the expected pattern of richness over the gradient under random placement of estimated ant elevational ranges, using RangeModel software (Colwell 2008). After data rarefaction (as detailed earlier), each observed range was interpolated between observed elevational limits. Following Cardelús et al. (2006) and Brehm et al. (2007), each range was also extrapolated, by extending the observed range limit by half the distance between the two closest sampling points, to ensure that species observed at only a single site would be included in the model. Alternative MDE models were constructed for the full domain of the transect (0–2900 m) and for the observed limits of estimated ant ranges (0–2050 m).

The explanatory potential of these environmental and spatial variables for ant density and diversity measures was evaluated with SAM software (Rangel et al. 2010). After reducing both explanatory and response variable sets to representative subsets to avoid multicollinearity, we used multiple linear regression with AIC-based

model selection (Burnham and Anderson 2002), taking spatial autocorrelation into account.

Spatial patterns of species co-occurrence were examined first with non-metric multidimensional scaling (NMS; Kruskal 1964, Mather 1976), a technique shown to perform well in other studies of tropical insect diversity (Brehm and Fiedler 2004). The “slow and thorough” Autopilot mode of PC-ORD 4.34 (McCune and Grace 2002) used the best of 40 runs with the real data along with 50 runs with randomized data for a Monte Carlo test of significance. Community dissimilarities for the NMS were expressed as Sørensen distances. All species for which maximum occupancy was <1% at all sites, 37% of the total species pool, were omitted from the ordination. Data were relativized to summed occupancy for each site.

As a graphical approach to examining turnover in assemblage composition along the transect, we calculated the Chao-Sørensen similarity estimator, based on the incidence matrices for replicates within sites (Chao et al. 2005), for each pair of sites. Because it includes all species, this approach makes full use of the dataset, including rare species (unlike the NMS analysis), and readily allows visualization of the elevational decay of similarity from each site to each other site.

## RESULTS

In all, 121133 worker ants (19251 species occurrences) representing 400 species were collected and identified (Appendix B, Supplement). Mean density of workers/m<sup>2</sup> was constant or slightly declining from 50–1500 m, then abruptly declined to a low level at 2000 m (Fig. 1A, Supplement). Occupancy rates (the proportion of 1 m<sup>2</sup> plots occupied) showed an even more dramatic discontinuity above 1500 m: occupancy was 100% at all sites up to 1500 m and then dropped to 75% at the 2000 m site (Fig. 1B, closed circles). Occupancy by the single most abundant species at each site, a measure of numerical dominance, gradually increased from 50 m to 1500 m and then abruptly dropped at 2000 m (Fig. 1B, open circles). Species density (mean species/m<sup>2</sup>) remained high up to 1070 m and then declined precipitously to a low value at 2000 m (Fig. 1C).

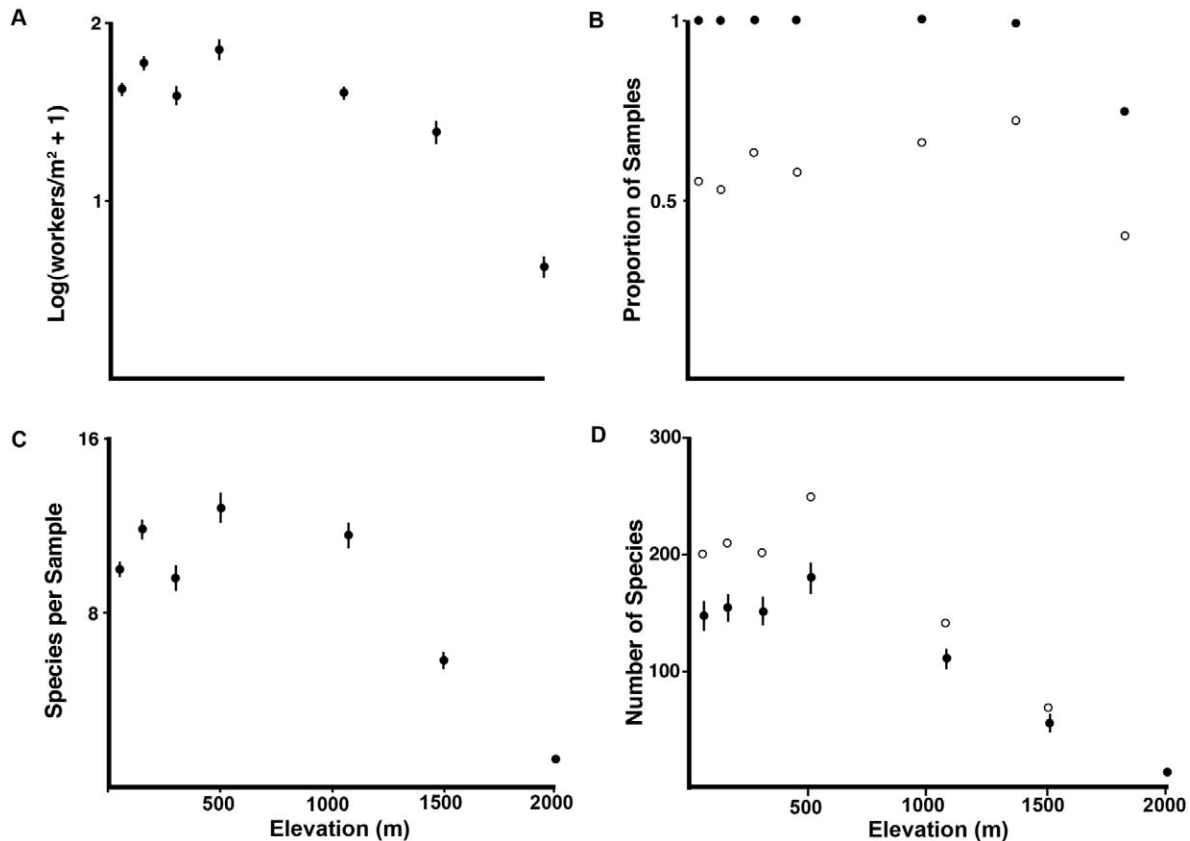


Fig. 1. Ants on the Barva Transect: A, log transformed worker density; B, proportion of samples with ants (filled circles) and with the single most abundant species at each site (open circles); C, species density (species/m<sup>2</sup>); D, species richness, rarefied to 1170 species occurrences (closed circles), and Chao's Incidence-based Coverage Estimator (ICE) (open circles). Error bars are 95% confidence intervals; sample sizes ranged from 150 to 599. See Methods for further explanation.

Measures of assemblage species richness (rarefied richness and ICE richness estimates) were roughly congruent, showing a high lowland richness, increasing slightly to 500 m, beginning to decrease by 1070 m, and then dropping sharply to 2000 m (Fig. 1D). Diversity indices rose slightly from 50 m to 500 m, then dropped precipitously to 2000 m (Fig. 2A). The number of species reaching maximum occupancy showed a distinct peak at 500 m (Fig. 2B). Because each species is plotted only once in Fig. 2B, each site clearly had a distinct set of species with maximum occupancy at that elevation. The ratio of mean (log transformed) ant worker density to rarefied species richness, a measure of mean population density per species, proved to be virtually constant up to 500 m, then began to

accelerate sharply beginning at 1100 m (Fig. 2C). The ratio of geometric mean worker density to rarefied species richness shows a similar pattern.

Rank-occupancy plots (the incidence equivalent of traditional rank-abundance plots) also reflect the trends in diversity decline with elevation (Fig. 3). All sites from 50 to 1070 m form a cluster of higher diversity curves. The curves for the 1500 m and 2000 m sites are steeper and more linear.

A comparison of occupancy, worker density, species density, and rarefied richness reveals discordant responses to elevation above 500 m (Fig. 4A). All values are high below 500 m, and all values are low at 2000 m, but at mid-elevations, on a relative basis (using sample  $z$ -scores; see caption to Fig. 4), occupancy >

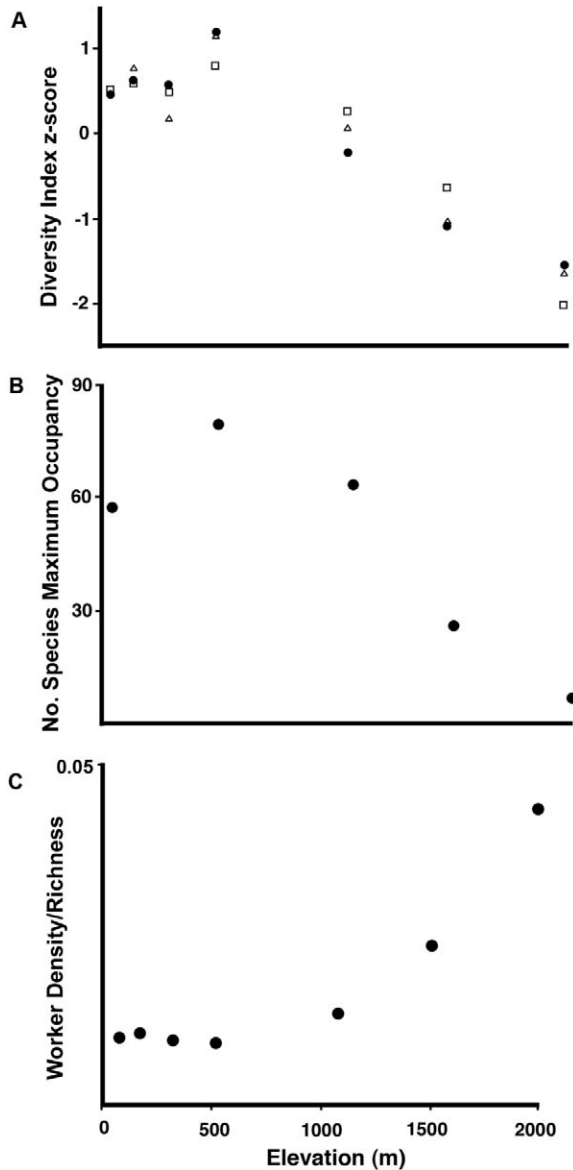


Fig. 2. Ants on the Barva Transect: A, Fisher's alpha (filled circles), Shannon index (open squares), Simpson index (open triangles) (to facilitate comparison, index values were converted to sample z-scores for each index); B, number of species that reach maximum occupancy at a given site; C, density compensation: the ratio of mean worker density (Fig. 1A) to rarefied species richness (Fig. 1D).

worker density > species density > assemblage richness, indicating that occupancy and worker density decreased more slowly with increasing elevation than species density and richness, suggesting density compensation. The elevation-

al pattern for the ratio of worker density to rarefied species richness affirms this suggestion (Fig. 2C).

Regression analysis was carried out with all available candidate explanatory variables (Fig. 4B, Supplement). Multiple regression with a sample size of  $n = 7$  elevations, at least as many candidate explanatory variables, and several related response variables must be approached with extreme caution. We began by examining collinearity among the candidate explanatory variables. Because mean, minimum, and maximum annual temperature were highly collinear (multiple  $r^2 = 0.99$ ), we selected mean annual temperature to represent this key variable. Because soil nitrogen and soil phosphorus were closely correlated ( $r^2 = 0.93$ ), we reduced these related but distinct variables to the first principal component (principal axis) between them. With regard to response variables, rarefied species richness, estimated asymptotic species richness, and the three diversity indices (exponential Shannon, Simpson, and Fisher's alpha) were highly intercorrelated (multiple  $r^2 = 0.98$ ). As the simplest among these, we selected rarefied richness to represent this response group. We chose to examine mean worker density (workers/ $m^2$ , transformed as  $\log[n + 1]$ ) as a second response variable because of its importance in interpreting results of the study, and because it was relatively independent of richness and diversity variables ( $r^2 = 0.83$  with rarefied richness). Because species density was closely related to worker density ( $r^2 = 0.93$ ), we did not examine it separately in the regression analysis.

All possible multiple linear regressions with one, two, and three explanatory variables were considered as candidate models, with rarefied richness and worker density as response variables, using AIC as a model selection tool (Burnham and Anderson 2002). A simple model with mean annual temperature as the sole explanatory variable emerged as the best explanation (minimum AIC) for rarefied species richness ( $r^2 = 0.89$ ,  $P = 0.003$ ). AIC was substantially lower ( $\min\Delta AIC > 7$ ) for this model than for any other single-variable model or for any combinations of rainfall, relative humidity, area, soil nutrients, and both MDE variants (full elevational domain and a domain matching the extent of occurrence of ants).

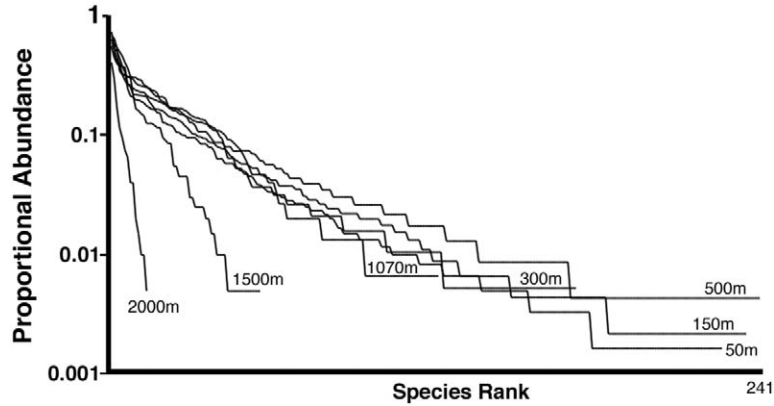


Fig. 3. Rank-occupancy plots for ants on the Barva Transect. Occupancy is the proportion of samples in which a species occurred.

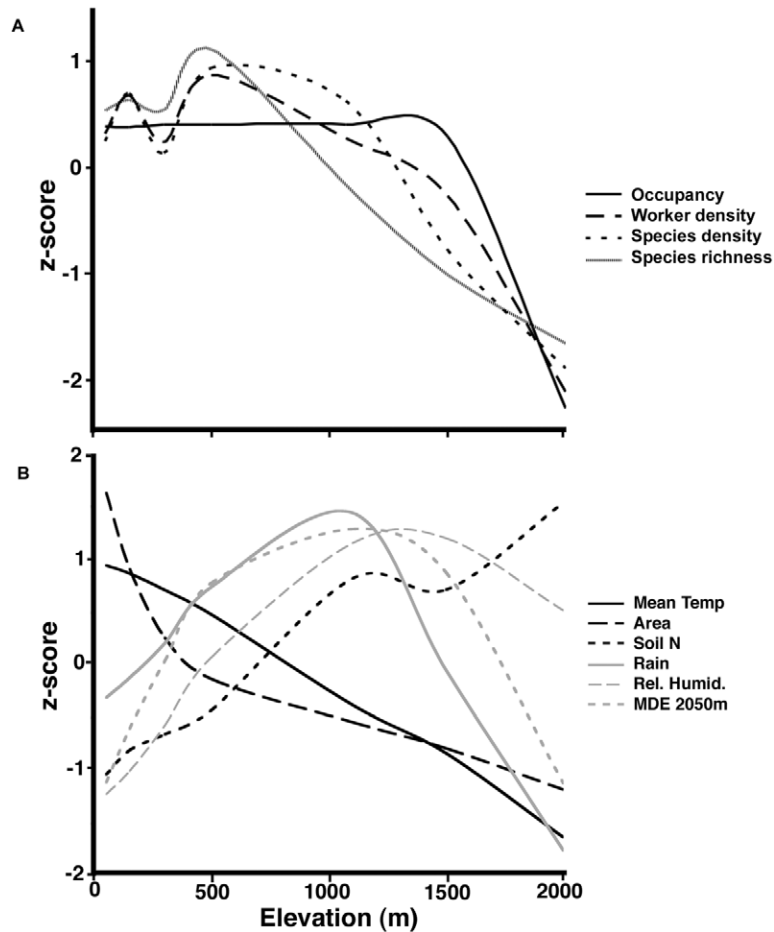


Fig. 4. Comparison of (A) ant occupancy, worker density, species density, and rarefied richness; and (B) principal candidate explanatory variables on the Barva Transect. To facilitate comparison, values are replaced by their sample z-scores:  $(\text{value} - \text{mean of seven values}) / (\text{standard deviation of seven values})$ .

Permutation tests of Moran's  $I$  for the regression residuals (Rangel et al. 2010) showed that the temperature model captured variation in rarefied species richness with no significant residual spatial autocorrelation.

The results for mean worker density were only slightly more complicated. Three models shared closely similar minimum AIC values ( $\text{min}\Delta \text{AIC} < 1.3$  between the lowest and highest among them). Of the three models, however, a single-variable model with mean annual temperature as the sole explanatory variable ( $r^2 = 0.72$ ,  $P = 0.023$ ) was the only one with non-significant residual spatial autocorrelation. The other two models were (1) temperature and relative humidity ( $r^2 = 0.96$ ,  $P = 0.012$ ) and (2) rainfall and soil nutrients ( $r^2 = 0.96$ ,  $P = 0.007$ ). In both, spatial autocorrelation was highly significant for the closest two distance classes (up to 10 km), weakening confidence in these models. Sample size ( $n = 7$ ) is insufficient to consider spatial regression techniques.

NMS Autopilot in PC-ORD chose a 1-dimensional representation as providing a statistically significant reduction in stress, as compared with randomized data. All four lowland sites clustered together, with the same NMS score, while the three upper elevation sites each had distinctive scores (Fig. 5). The Chao-Sørensen similarity analysis based on incidences showed a similar pattern, with uniformly high overlap among sites at 500 m and below, and low species overlap values among the higher elevation sites (Fig. 6).

Variation in species composition along the gradient was largely driven by shifts from one species to another within genera. The ant species represented 69 genera, 35 of which included both lowland and specialized montane species. These 35 contained all of the largest and most abundant genera: *Pheidole*, *Solenopsis*, *Pachycondyla*, *Nylanderia*, and *Pyramica*. The largest ant genus was *Pheidole*, with 82 species on the transect, and the patterns revealed by all ants were largely reflected in the patterns among the species of this genus alone. Most of the genera with lowland and highland species showed greater diversity in the lowlands. Only three genera—*Adelomyrmex*, *Simopelta*, and *Stenammas*—were more diverse in the highlands. Twenty-nine genera were entirely lowland (to 500 m) or lowland with some species whose ranges ex-

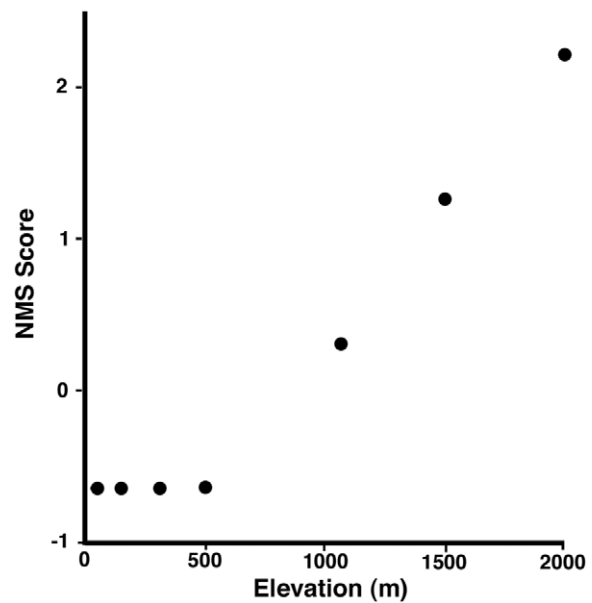


Fig. 5. Non-metric multidimensional scaling analysis of Barva Transect ants. All four lowland sites have identical scores, while each of the three upper elevation sites have distinct scores.

tended into the highlands. Only five genera were restricted to highland sites, and all of these were low diversity and low worker occupancy. There was no evidence of attenuation of trophic diversity with elevation. Generalized omnivores, specialized predators (army ants, Dacetini, Basicerotini), and herbivores/fungivores (Attini) occurred in similar proportions from sea level to the 1500 m site, and even the 2000 m site, with its greatly reduced ant fauna, nonetheless had army ants.

In summary, a continuously-forested elevational transect on the Atlantic slope of Costa Rica hosted a diverse ant community in the forest floor litter layer, with at least 400 species. Ant worker density per square meter varied little from near sea level to 1500 m but was abruptly lower at 2000 m. Number of species per square meter (species density) also remained high and relatively constant but began to decline by 1500 m, slightly below where worker density declined. Assemblage richness and diversity (approximately at the square kilometer scale) increased slightly from near sea level to 500 m then dropped steeply to near zero at 2000 m. Because richness declined at a lower elevation than worker



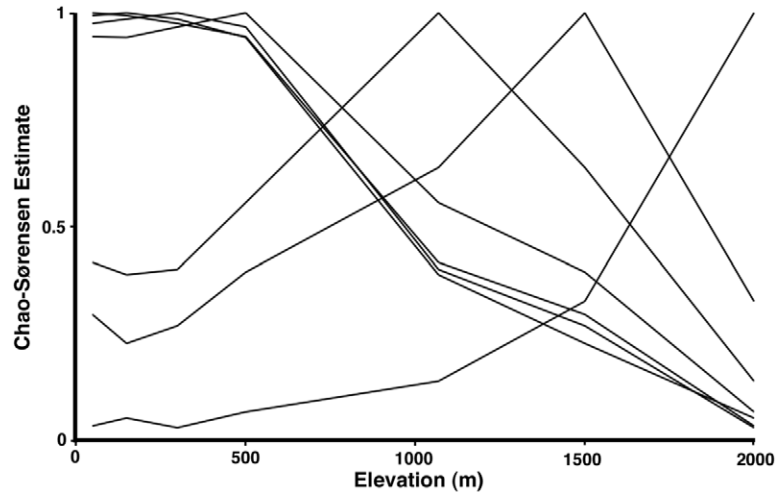


Fig. 6. Chao-Sørensen Estimate, using incidence data, plotted on a “faunal congruity curve,” a graphical representation of species overlap data (Terborgh 1971). In faunal congruity plots, the x-axis is the gradient of interest (elevation in this case), and the y-axis is the species overlap value. Each site has a separate curve on the plot. At the focal site’s location on the gradient, a maximum overlap is plotted (1 for Chao-Sørensen Estimate). At progressively more distant sites on the gradient, the overlap with these more distant sites is plotted. Typically, a site’s curve appears as a peak, sloping in both directions. The steepness and shape of a peak reflect the nature of species turnover with distance from the focal site. When multiple sites are plotted in the same graph, they appear as a series of peaks spread horizontally across the gradient. Areas of rapid turnover are revealed as areas where curves are steep, and areas of little species turnover have shallow curves or peaks with broad shoulders. The Barva Transect ants show almost no faunal turnover from 50–500 m and large faunal turnover among sites above that elevation.

density, a measure of mean population density rose sharply above 1100 m, suggesting density compensation. Declining temperature with increasing elevation bore a strong statistical relation to both assemblage richness and worker density, whereas other environmental and spatial variables did not prove explanatory. Species composition was relatively uniform among the sites at 500 m and below, whereas the 1070 m, 1500 m, and 2000 m sites each revealed a distinctive fauna. Even though the lowland fauna was relatively uniform, the location where each species reached its maximum occupancy was skewed toward the upper end of the range, with more species reaching maximum occupancy around 500 m than near sea level.

## DISCUSSION

### *Relationship of richness to elevation and environmental variables*

The litter ants show a diversity peak around 500 m, asymmetrical in both location and rate of

change above and below the peak, with respect to the full elevational transect (Fig. 4A). Given the coarseness of our sampling we cannot precisely locate the diversity peak: it could occur from slightly below 500 m to somewhere between 500 and 1000 m. However, a centrally-located peak would be at 1000 m or above (depending on how one defines the upper boundary of the transect), so the asymmetry is not in question. The rate of upslope decline in diversity is much greater than the rate of downslope decline. Relatively few analyses of tropical diversity gradients are able to reveal a pattern such as this because the lower portions of elevational gradients are often deforested (Nogues-Bravo et al. 2008). However, very similar patterns have been shown for litter ants in Panama (Olson 1994) and Madagascar (Fisher 1996, 1998, 1999b). The Madagascar study showed a more symmetrical upslope and downslope decline, with distinctly lower diversity in the lowlands, but this pattern may have been caused or at least exacerbated by habitat distur-

bance at low elevations (Fisher 1998).

These patterns do not closely match any of the common single-factor environmental effects hypothesized to affect elevational patterns of diversity (Kluge et al. 2006) (Fig. 4). Temperature and area of elevational bands show a monotonic decline. Rainfall and predictions of geometric constraints are unimodal with a centrally located mode (around 1000 m). Relative humidity rises to a plateau at about 1000 m and remains high above that elevation. Nevertheless, on a statistical basis, temperature, alone, emerged as the single most explanatory model, with the low-elevation richness hump simply adding variance in an overall pattern of declining richness with elevation, and thus, with temperature.

Temperature also proved to be the most explanatory environmental variable in relation to ant worker density, but the relationship was weaker than for richness. Although richness and worker density were correlated ( $r^2 = 0.84$ ), the spatial pattern of ant worker density with elevation was distinctly different than for richness (Fig. 4A). Our finding that ant worker density and small scale (1 m<sup>2</sup>) species density remained constant and high from 50 m to 1500 m was surprising. Ants maintained a nearly constant ecological presence, even as larger-scale assemblage diversity was dropping. Not only did overall ant density remain high, but the dominant ants in the highlands achieved higher occupancy than their counterparts in the lowlands (Fig. 1B). These results strongly suggest density compensation, traditionally viewed as evidence that interspecific competition limits population densities (MacArthur et al. 1972). The steep rise of the ratio of worker density to species richness (a measure of mean population density) above 1100 m (Fig. 2C) offers strong evidence for density compensation. Fisher (1999a, Table 1) reported worker abundance data for an elevational gradient study in Madagascar. Unlike our study, abundance appears to show a monotonic decline with elevation.

Energy has often been viewed as a strong predictor of diversity patterns at large spatial scales (Kaspari et al. 2004, Hawkins et al. 2003, Currie et al. 2004). Although we were unable to test for correlation with productivity directly, our results were incompatible with a simple productivity-related explanation for species richness

based on contemporary interactions, in which higher productivity supports higher density, which in turn allows higher richness (Kaspari et al. 2000, Currie et al. 2004). In this case one would not expect to find density compensation. Kaspari et al. (2004) favored a hypothesis of an energy effect on speciation rates in ants. The lower diversity of ants at higher elevations on the Barva Transect, in this view, would thus be due to lower speciation rates over the long-term, a process compatible with density compensation. Perhaps a speciation-extinction equilibrium, mediated by temperature, as Kaspari proposed, has shaped a regional diversity-elevation relationship at the higher elevations.

We found a discontinuity between 1500 m and 2000 m, where not only assemblage diversity and species density, but also worker density and occupancy dramatically declined (Fig. 4A). At the 2000 m site, many patches occur where ants are completely absent, unlike any lower site. Perhaps this difference reflects a threshold beyond which temperature and resource effects begin to limit ant abundance in the tropics, as suggested by Brown (1973), Olson (1994), and Brühl et al. (1999). But mechanistic explanations for this rather abrupt transition remain unexplained and unexplored. The lowland discontinuity, in which diversity stabilizes or slightly declines below 500 m, also demands explanation. Temperature declines linearly with elevation, so the temperature-speciation model would predict the highest diversity at the lowest elevation.

#### *Relationship of community composition to elevation*

Most studies of insects on elevational gradients find montane specialists (e.g., Fisher 1998, 1999b for ants, Pycrz and Wojtusiak 2002 for butterflies), and this study is no exception. However, the degree of elevational zonation found on the Barva Transect is especially striking. We found evidence for at least four episodes of species replacement along the 2000 m gradient, with distinctive faunas from sea level to 500 m, 1070 m, 1500 m, and 2000 m (Fig. 6). However, the community at the lowest elevation occurs across an anomalously broad elevational range. Above 500 m, elevational increments of 500 m result in almost complete species turnover. In contrast, the communities at 50 m and 500 m are nearly identical.

### *Explaining species elevational ranges*

Diversity patterns along an elevational gradient are ultimately determined by the ranges of individual species. Thus a consideration of the determinants of species ranges may contribute to an understanding of diversity patterns. Along a local (30 km ground distance) elevational gradient like the Barva Transect, every species has the potential to be everywhere on the gradient over short periods of ecological time. Even a low-vagility litter ant species could be expected to walk the full distance in a few thousand generations. Thus contemporary forces must maintain range boundaries. Price and Kirkpatrick (2009) examined the paradox that range limits can be stable with respect to climate, even when selection is strong for adaptation to the prevailing climate at cooler and warmer range limits. They showed, on theoretical grounds, that interspecific competition can result in stabilizing selection at range edges, resulting in stable range limits with respect to climate, even when gene flow from the center of the range is insufficient to prevent adaptation at the edge (Kirkpatrick and Barton 1997). They predict that, with climate change, if species are constrained by interspecific competition, they will tend to follow their historical climate envelope, rather than adapt to changed conditions. The Price and Kirkpatrick model suggests that a species' thermal tolerance range may be greater than that of their realized range.

Sunday et al. (*in press*), in a meta-analysis of extensive published data on thermal tolerances of insects (and other terrestrial ectotherms) at all latitudes, showed unequivocally that, with increasing latitude, upper thermal limits decline only slightly, whereas lower thermal limits decline steadily. This pattern clearly indicates that upper thermal tolerance limits do not generally set the equatorward range limits of insects. Although Sunday et al. did not analyze elevational patterns, their Supplemental Data show that the very same pattern arises for ectotherms as a function of increasing elevation for the 27 tropical species for which elevations are reported (sea level to 3300 m): upper thermal tolerance does not decline with elevation, whereas lower thermal limits decline. Unfortunately, only one of the species is an insect (a beetle); the rest are reptiles and amphibians. However,

Gaston and Chown (1999) showed the same pattern for dung beetles on an elevational gradient (albeit not a tropical one): critical thermal minima strongly decline with elevation whereas critical thermal maxima decline only weakly. If the same pattern holds for tropical ants on the Barva Transect, then upland species can tolerate much higher temperatures than they actually experience, whereas the upper range limits of lowland species may be limited by tolerance to cold, further supporting the idea that competition may set the lower range boundaries of montane ant species.

In fact, the upper elevational range limits of tropical insects and other ectotherm species, in general, may more likely be set by thermal tolerance at the upper boundary, while biotic interactions may have a greater influence on the lower boundary. This idea has had an intuitive appeal since the time of Darwin (1859), who wrote "When we travel southward and see a species decreasing in numbers, we may feel sure that the cause lies quite as much in other species being favoured, as in this one being hurt. So it is when we travel northward, but in a somewhat lesser degree, for the number of species of all kinds, and therefore of competitors, decreases northward; hence in going northward, or in ascending a mountain, we far oftener meet with stunted forms, due to the *directly* injurious action of climate, than we do in proceeding southward or in descending a mountain." In a recent example of a lower elevational range limit being determined by interspecific competition, Jankowski et al. (2010) showed for a neotropical bird community that competitively dominant lowland species limited the lower range boundary of upland species.

These considerations suggest that interspecific competition at range boundaries may explain why the ants at the lowest elevation of the Barva Transect have the broadest elevational range. Colwell et al. (2008) and Colwell and Rangel (2009) proposed lowland biotic attrition as a possible consequence of global warming, with lowland species shifting their ranges upward, there being no species adapted to even higher temperatures to fill in behind them. Holloway et al. (1990) proposed that lowland attrition had already occurred as a result of lowland range contractions during full glacial periods, explain-

ing declines in moth diversity at the lowest elevations. In the case of ants on the Barva Transect, the broader range of lowland ants may be the result of recent interglacial warming combined with a lack of competition at the lower range boundary (sea level). Thus there is a weak rather than strong drop in richness from 500 m to 50 m, and many species that occur at both the 50 m and 500 m sites have their highest occupancy at the 500 m site. The current climate at 500 m may represent the ancestral optimal climate for ants that were restricted to near sea level for long periods during repeated Quaternary glacial maxima. If so, ant species may have oscillated up and down the slope throughout the Pleistocene. In this scenario, the exception would be species at the lowest elevations, whose ranges would be "elastic", with the lower limit remaining pegged to sea level (Colwell and Rangel 2009, Feeley and Silman 2010). In the same way, lowland biotic attrition driven by contemporary global warming (Colwell et al. 2008) may be ameliorated by further expansion of the ranges of lowland species.

In summary, two competing hypotheses predict the observed pattern among low-elevation ants. On the one hand, ant diversity may reflect NPP levels. Ant communities may be adapted to particular ranges of NPP, and NPP may show relatively little change over a broad elevational range from sea level to somewhere between 500–1000 m. Alternatively, the broad ranges of lowland ants may be due to climate change over the last 15,000 years, associated with the current interglacial period. The lowest elevational band may be a relatively unusual temperature regime (interglacial temperature maxima have been brief) for which there are no specialized occupants that could out-compete higher elevation ants, and ants from the previous lower limit of the transect have simply expanded their range into this novel habitat. Disentangling these hypotheses will require measurements of NPP along the transect and direct assessment of the thermal tolerances of the ant species. Field studies of competitive relationships are desirable but logistically challenging.

#### ACKNOWLEDGMENTS

We thank the ALAS staff Danilo Brenes, Flor

Cascante, Maylin Paniagua, and Ronald Vargas, and TEAM staff Joel Alvarado, Deimer Alvarez, Felix Corrales, Humberto Garcia, Gilbert Hurtado, Johanna Hurtado, Marcos Molina, and Karol Mora. Karol Mora deserves special thanks for her exceptional work preparing and identifying the TEAM ants. Michael Kaspari and two anonymous reviewers provided constructive comments on the manuscript. Project ALAS was supported by National Science Foundation grant DEB-0072702 and National Geographic Society grants 7331-02 and 7751-04. TEAM was supported by Conservation International. During the writing of this paper, JTL was supported by NSF grant DEB-0640015 (Project LLAMA) and RKC by NSF grants DEB 0639979 and DBI-0851245.

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## APPENDIX A

### Additional information on study sites and methods

The sampling unit was a “miniWinkler” sample, following the methods of Fisher (1999a) (hereafter simply referred to as Winkler samples). Litter within a 1 m<sup>2</sup> forest floor plot (including any vegetation and suspended organic matter immediately above the plot) was minced with a machete, gathered into a sifter, and shaken vigorously. Sifting continued until all litter in the plot was sifted or a maximum of 6 L of siftate was obtained (in the latter case material from different parts of the plot was subsampled). Siftate was transferred to cloth sacks and moved to a laboratory or shelter, where each sample was suspended in an individual Winkler extractor for three days. Falling arthropods were collected into 95% ethanol.

Winkler samples were collected at seven sites along the transect (Fig. A1), under the auspices of two different projects: Project ALAS (<http://purl.oclc.org/ALAS>) and Conservation International’s TEAM project (<http://www.teamnetwork.org/en/>). ALAS samples were acquired as transects of 50 samples, with 5 m spacing between samples, three to five transects per site, taken over a single 10-week period. TEAM samples were acquired as transects of 10 samples, with 10 m spacing, four transects per sampling period, four sampling periods per year, with at least one year of sampling for each site. Total sample size was 2022 Winkler samples; within-site sample size

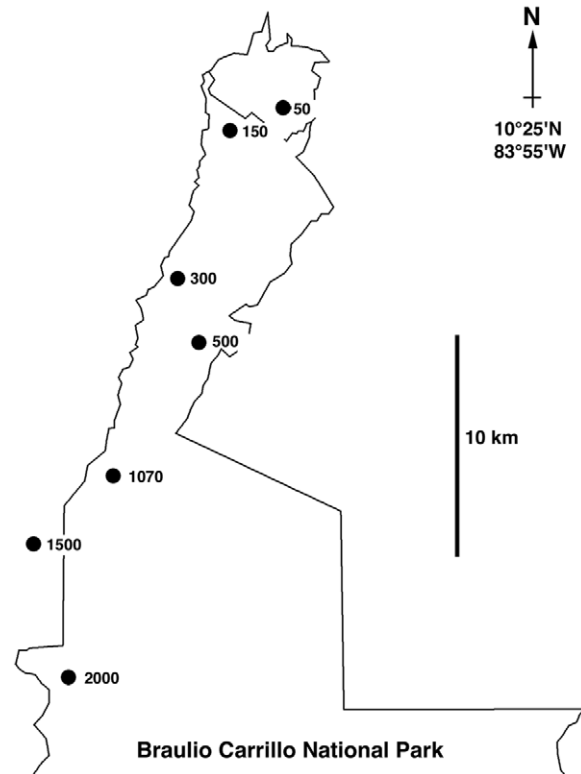


Fig. A1. Spatial and elevational distribution of sample sites on the Barva Transect. Sites are labeled by elevation in meters.

Table A1. Sample sizes (number of Winkler samples), sampling dates, latitude, longitude, and extent at each site on the Barva Transect. Extent is the radius of a circle around the latitude and longitude point within which all sampling occurred.

Elevation	N	Dates of Sampling	Lat	Lon	Extent (m)
50	599	Jan 2004–Sep 2007	10.417	–84.020	800
150	453	Sep 2004–Jul 2007	10.404	–84.039	750
300	190	Mar 2006–Jun 2007	10.345	–84.058	750
500	230	Oct 2005–Apr 2007	10.317	–84.049	750
1070	150	Feb–Mar 2001	10.268	–84.084	500
1500	200	Feb–Apr 2005	10.236	–84.118	700
2000	200	Feb–Apr 2002	10.176	–84.111	500

varied from 150 to 599 samples (Table A1).

An ALAS or TEAM technician examined arthropod samples and removed all worker ants. Within each sample, ants were sorted to morphospecies, and one or more workers of each morphospecies were dry-mounted. All voucher specimens were later identified to species under a common taxonomy by J. Longino. Misidentification of workers in the within-

sample morphospecies sort was a potential source of error, if a morphospecies was, in fact, a mix of two or more species. The single mounted voucher specimen would then not represent the group, and some species would be overlooked in the sample. This source of error was spot checked by Longino and found to be negligible.

## APPENDIX B

### Ant species list from the Barva Transect

#### AGROECOMYRMECINAE

*Tatuidris* JTL001

*Tatuidris tatusia*

#### AMBLYOPONINAE

*Amblyopone degenerata*

*Amblyopone orizabana*

*Prionopelta amabilis*

*Prionopelta modesta*

#### CERAPACHYINAE

*Cerapachys* JTL001

*Cerapachys* JTL002

*Cerapachys* JTL003

*Cerapachys* JTL004

*Cerapachys* JTL006

*Cerapachys* JTL007

#### DOLICHODERINAE

*Azteca tonduzi*

*Linepithema piliferum*

*Tapinoma ramulorum inrectum*

*Tapinoma ramulorum*

#### ECITONINAE

*Eciton burchellii foreli*

*Eciton vagans angustatum*

*Labidus coecus*

*Neivamyrmex adnepos*

*Neivamyrmex compressinodis*

*Neivamyrmex* CR001

*Neivamyrmex iridescens*

*Neivamyrmex* JTL002

*Neivamyrmex macrodentatus*

*Neivamyrmex pilosus mexicanus*

*Neivamyrmex punctaticeps*

*Nomamyrmex hartigii*

#### ECTATOMMINAE

*Ectatomma gibbum*

*Ectatomma ruidum*

*Ectatomma tuberculatum*

*Gnamptogenys annulata*

*Gnamptogenys banksi*

*Gnamptogenys bisulca*

*Gnamptogenys interrupta*

*Gnamptogenys* JTL002

*Gnamptogenys* JTL006

*Gnamptogenys mecotyle*

*Gnamptogenys minuta*

*Gnamptogenys mordax*

*Gnamptogenys porcata*

*Gnamptogenys regularis*

*Gnamptogenys simulans*

*Gnamptogenys strigata*

*Gnamptogenys tornata*

*Gnamptogenys volcano*

*Typhlomyrmex pusillus*

*Typhlomyrmex rogenhoferi*

#### FORMICINAE

*Acropyga exsanguis*

*Acropyga fuhrmanni*

*Acropyga goeldii*

*Acropyga keira*

*Acropyga panamensis*

*Acropyga smithii*

*Brachymyrmex cavernicola*

*Brachymyrmex* JTL002

*Brachymyrmex* JTL003

*Brachymyrmex* JTL004

*Brachymyrmex* JTL005

*Brachymyrmex* JTL007

*Brachymyrmex* JTL010

*Brachymyrmex santschii*

*Camponotus chartifex*

*Camponotus integellus*

*Camponotus* JTL005

*Camponotus* JTL013

*Camponotus novogranadensis*



*Camponotus salvini*  
*Camponotus sanctaefidei*  
*Myrmelachista flavocotea*  
*Myrmelachista joycei*  
*Myrmelachista mexicana*  
*Nylanderia austroccidua*  
*Nylanderia caeciliae*  
*Nylanderia guatemalensis*  
*Nylanderia JTL001*  
*Nylanderia JTL006*  
*Nylanderia JTL010*  
*Nylanderia JTL013*  
*Nylanderia steinheili*  
*Paratrechina longicornis*  
**HETEROPONERINAE**  
*Acanthoponera minor*  
*Heteroponera microps*  
*Heteroponera panamensis*  
**MYRMICINAE**  
*Acanthognathus ocellatus*  
*Acanthognathus teledectus*  
*Acromyrmex volcanus*  
*Adelomyrmex brenesi*  
*Adelomyrmex brevispinosus*  
*Adelomyrmex foveolatus*  
*Adelomyrmex laevigatus*  
*Adelomyrmex longinoi*  
*Adelomyrmex microps*  
*Adelomyrmex myops*  
*Adelomyrmex silvestrii*  
*Adelomyrmex tristani*  
*Aphaenogaster araneoides*  
*Apterostigma auriculatum*  
*Apterostigma chocoense*  
*Apterostigma collare*  
*Apterostigma dentigerum*  
*Apterostigma goniodes*  
*Apterostigma JTL013*  
*Apterostigma pilosum*  
*Apterostigma robustum*  
*Atta cephalotes*  
*Basiceros manni*  
*Carebara brevipilosa*  
*Carebara inca*  
*Carebara JTL007*  
*Carebara reina*  
*Carebara urichi*  
*Carebarella bicolor*  
*Cephalotes cristatus*  
*Crematogaster brasiliensis*  
*Crematogaster bryophilia*  
*Crematogaster curvispinosa*  
*Crematogaster flavomicrops*  
*Crematogaster limata*  
*Crematogaster longispina*  
*Crematogaster nigropilosa*  
*Crematogaster raptor*  
*Crematogaster snellingi*  
*Crematogaster sotobosque*  
*Crematogaster wardi*  
*Cyphomyrmex cornutus*  
*Cyphomyrmex longiscapus\_cf*  
*Cyphomyrmex major*  
*Cyphomyrmex muelleri\_cf*  
*Cyphomyrmex rimosus\_sl*  
*Cyphomyrmex salvini*  
*Cyphomyrmex snellingi*  
*Eurhopalothrix gravis*  
*Eurhopalothrix JTL006*  
*Eurhopalothrix JTL008*  
*Eurhopalothrix JTL009*  
*Eurhopalothrix JTL010*  
*Eurhopalothrix schmidtii*  
*Hylomyrma dentiloba*  
*Hylomyrma JTL001*  
*Hylomyrma JTL002*  
*Lachnomyrmex haskinsi*  
*Lachnomyrmex laticeps*  
*Lachnomyrmex longinoi*  
*Lachnomyrmex scrobiculatus*  
*Lenomyrmex colwelli*  
*Megalomyrmex drifti*  
*Megalomyrmex JTL003*  
*Megalomyrmex modestus*  
*Megalomyrmex mondabora*  
*Megalomyrmex silvestrii*  
*Monomorium floricola*  
*Mycocepurus tardus*  
*Myrmicocrypta ednaella\_cf*  
*Nesomyrmex asper*  
*Nesomyrmex echinatinodis*  
*Octostruma iheringi*  
*Octostruma JTL001*  
*Octostruma JTL002*  
*Octostruma JTL005*  
*Octostruma JTL008*  
*Octostruma JTL010*  
*Pheidole alfaroi*  
*Pheidole anastasii*  
*Pheidole arachnion*  
*Pheidole belocephs*

*Pheidole biconstricta*  
*Pheidole bicornis*  
*Pheidole boltoni*  
*Pheidole boruca*  
*Pheidole browni*  
*Pheidole carinata*  
*Pheidole cataphracta*  
*Pheidole celaena*  
*Pheidole cerina*  
*Pheidole chochoensis*  
*Pheidole citrina*  
*Pheidole colobopsis*  
*Pheidole cramptoni*  
*Pheidole debilis*  
*Pheidole diabolus*  
*Pheidole dossena*  
*Pheidole ectatommoides*  
*Pheidole eowilsoni*  
*Pheidole epiphyta*  
*Pheidole erratilis*  
*Pheidole fimbriata*  
*Pheidole fiorii*  
*Pheidole flavens*  
*Pheidole fossimandibula*  
*Pheidole gauthieri*  
*Pheidole gymnoceras*  
*Pheidole harrisonfordi*  
*Pheidole hasticeps*  
*Pheidole hazenae*  
*Pheidole hirsuta*  
*Pheidole indagatrix*  
*Pheidole JTL137*  
*Pheidole JTL138*  
*Pheidole JTL139*  
*Pheidole JTL144*  
*Pheidole JTL146*  
*Pheidole JTL147*  
*Pheidole karolmorae*  
*Pheidole karolsetosa*  
*Pheidole laselva*  
*Pheidole lucaris*  
*Pheidole mesomontana*  
*Pheidole monteverdensis*  
*Pheidole nasutoides*  
*Pheidole nebulosa*  
*Pheidole nigricula*  
*Pheidole nitella*  
*Pheidole olsoni*  
*Pheidole otisi*  
*Pheidole pararugiceps*  
*Pheidole perpusilla*  
*Pheidole picobarva*  
*Pheidole prattorum*  
*Pheidole prostrata*  
*Pheidole psilogaster*  
*Pheidole rectispina*  
*Pheidole rectitrudis*  
*Pheidole (rhinoceros or JTL-186)*  
*Pheidole rogeri*  
*Pheidole rugiceps*  
*Pheidole sagittaria*  
*Pheidole scalaris*  
*Pheidole scrobifera*  
*Pheidole sensitiva*  
*Pheidole simonsi*  
*Pheidole sparsisculpta*  
*Pheidole spathipilosa*  
*Pheidole specularis*  
*Pheidole subarmata*  
*Pheidole synarmata*  
*Pheidole tanyscapa*  
*Pheidole tennantae*  
*Pheidole tenuicephala*  
*Pheidole texticeps*  
*Pheidole ulothrix*  
*Pheidole vestita*  
*Pheidole vorax*  
*Pheidole walkeri*  
*Procryptocerus batesi*  
*Procryptocerus mayri*  
*Pyramica aethegenys*  
*Pyramica alberti*  
*Pyramica augustandrewi*  
*Pyramica brevicornis*  
*Pyramica cassicuspis*  
*Pyramica cremenata*  
*Pyramica dontopagis*  
*Pyramica erikae*  
*Pyramica excisa*  
*Pyramica fridericimuelleri*  
*Pyramica gundlachi*  
*Pyramica JTL012*  
*Pyramica lalassa*  
*Pyramica microthrix*  
*Pyramica myllorhapha*  
*Pyramica nigrescens*  
*Pyramica probatrix*  
*Pyramica rogata*  
*Pyramica schulzi*  
*Pyramica stauroma*  
*Pyramica subedentata*  
*Pyramica trieces*

*Pyramica wheeleri*  
*Rhopalothrix* JTL004  
*Rhopalothrix weberi*  
*Rogeria belti*  
*Rogeria cornuta*  
*Rogeria creightoni*  
*Rogeria cuneola*  
*Rogeria foreli*  
*Rogeria inermis*  
*Rogeria* JTL001  
*Rogeria* JTL004  
*Rogeria leptonana*  
*Rogeria tonduzi*  
*Sericomyrmex aztecus*  
*Solenopsis geminata*  
*Solenopsis* JTL001  
*Solenopsis* JTL002  
*Solenopsis* JTL003  
*Solenopsis* JTL005  
*Solenopsis* JTL007  
*Solenopsis* JTL008  
*Solenopsis* JTL009  
*Solenopsis* JTL014  
*Solenopsis* JTL015  
*Solenopsis* JTL021  
*Solenopsis* JTL025  
*Solenopsis* JTL027  
*Solenopsis* JTL028  
*Solenopsis* JTL029  
*Solenopsis* JTL030  
*Solenopsis* JTL031  
*Solenopsis picea*  
*Solenopsis subterranea*  
*Solenopsis terricola*  
*Solenopsis zeteki*  
*Stenamma expolitum*  
*Stenamma felixi*  
*Stenamma* JTL006  
*Stenamma* JTL010  
*Stenamma* JTL011  
*Stenamma* JTL012  
*Stenamma* JTL015  
*Stenamma* JTL017  
*Stenamma* JTL019  
*Stenamma schmidti*  
*Strumigenys biolleyi*  
*Strumigenys calamita*  
*Strumigenys consanii*  
*Strumigenys cordovensisi*  
*Strumigenys cosmostela*  
*Strumigenys elongata*  
*Strumigenys godmani*  
*Strumigenys ludia*  
*Strumigenys micretes*  
*Strumigenys nevermanni*  
*Strumigenys pariensis*  
*Strumigenys perdita*  
*Strumigenys platyscapa*  
*Strumigenys rogeri*  
*Strumigenys sevesta*  
*Trachymyrmex cornetzi*  
*Trachymyrmex isthmicus*  
*Trachymyrmex* JTL003  
*Trachymyrmex* JTL006  
*Trachymyrmex opulentus*  
*Trachymyrmex zeteki*  
*Tranopelta gilva*  
*Wasmannia auropunctata*  
*Wasmannia scrobifera*  
*Xenomyrmex panamanus*  
**PONERINAE**  
*Anochetus* JTL001  
*Anochetus* JTL002  
*Anochetus minans*  
*Anochetus orchidicola*  
*Belonopelta deletrix*  
*Cryptopone gilva*  
*Hypoponera distinguenda*  
*Hypoponera* JTL001  
*Hypoponera* JTL002  
*Hypoponera* JTL006  
*Hypoponera* JTL007  
*Hypoponera* JTL013  
*Hypoponera* JTL016  
*Hypoponera nitidula*  
*Hypoponera opacior*  
*Hypoponera parva*  
*Leptogenys josephi*  
*Leptogenys pubiceps complex*  
*Leptogenys punctaticeps*  
*Leptogenys pusilla*  
*Odontomachus erythrocephalus*  
*Odontomachus laticeps*  
*Odontomachus meinerti*  
*Pachycondyla aenescens*  
*Pachycondyla apicalis*  
*Pachycondyla arhuaca*  
*Pachycondyla cauta*  
*Pachycondyla cognata*  
*Pachycondyla constricta*  
*Pachycondyla guianensis*  
*Pachycondyla harpax*

*Pachycondyla impressa*  
*Pachycondyla* JTL015  
*Pachycondyla* JTL016  
*Pachycondyla* JTL017  
*Pachycondyla* JTL018  
*Pachycondyla pergandei*  
*Pachycondyla stigma*  
*Pachycondyla unidentata*  
*Pachycondyla verenae*  
*Pachycondyla villosa\_complex*  
*Platythyrea pilosula*  
*Platythyrea punctata*  
*Simopelta andersoni*  
*Simopelta* JTL005  
*Simopelta* JTL006  
*Simopelta paeminosa*  
*Simopelta pergandei*

*Thaumatomyrmex atrox*  
*Thaumatomyrmex ferox*  
 PROCERATIINAE  
*Discothyrea denticulata*  
*Discothyrea horni*  
*Discothyrea* JTL006  
*Discothyrea* JTL009  
*Discothyrea sexarticulata*  
*Proceratium convexiceps*  
*Proceratium goliath*  
*Proceratium micrommatum*  
*Proceratium panamense*  
 PSEUDOMYRMECINAE  
*Pseudomyrmex oculatus*  
*Pseudomyrmex simplex*  
*Pseudomyrmex tenuis*

#### SUPPLEMENT

Ant species occurrence data, ant worker density data, and environmental variables and response variables for regression analysis (*Ecological Archives* C002-003-S1).