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The truncated bell: an enigmatic but pervasive elevational diversity pattern in Middle American ants

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Studies on elevation gradients in Panama and Costa Rica have shown that leaf-litter ants exhibit a mid-elevation peak in diversity. This diversity pattern has been observed in other groups and regions, but uncertainty remains as to just how pervasive it is and what might explain it. Here we examine the robustness of the mid-elevation peak in ant diversity across the entire Middle American corridor, from Veracruz, Mexico, to Costa Rica. We sampled 56 sites distributed throughout Middle America. All were in closed-canopy evergreen wet forest, spanning 11° latitude, from near sea level to 2600 m elevation. Ants were extracted from 100 litter samples from each site and identified to genus or species. Model selection was performed on richness and diversity variables to test if ant diversity best fits a linear model or one allowing for a mid-elevation peak. Linear models were also used to examine the relationships among diversity measures and temperature, precipitation, and seasonality. Species richness measures and diversity indices that incorporate relative abundance show a similar relationship to elevation throughout the region: a truncated bell curve with a mode near 400 m. A cubic relationship is statistically favored over quadratic or linear. Temperature is a significant correlate with diversity, but does not predict a bell-curve. Precipitation and precipitation seasonality fail to explain much of the variability, and no combination of environmental variables predicts a bell curve. Potential causes of the truncated bell curve include lowland biotic attrition, mid-point attractors, and ecotonal transitions from lowland to montane communities. Analysis of 17 subclades within ants mostly showed the same truncated curve but six clades were anomalous. Distinctive behavioral or historical features potentially explain their patterns.

Keywords: Formicidae, elevational gradient, macroecology

Introduction

Terrestrial life is distributed in predictable ways across latitudinal and elevational gradients. Documenting those patterns has been a scientific goal for centuries and is particularly important in the current era of large-scale human disturbance and rapid habitat conversion. Accompanying documentation are efforts to explain patterns by proposing specific mechanistic hypotheses that can be tested (Sundqvist et al. 2013,

Graham et al. 2014). Elevational gradients are of particular interest because they provide replicated examples of how animals and plants distribute themselves with respect to a few key environmental variables that can change rapidly over short spatial scales (Rahbek 1995, Lomolino 2001). Several taxa or functional groups have emerged as frequent subjects of diversity studies. Among insects, ants are commonly studied because they are a dominant component of ecosystems, they are diverse, and species-level identification is increasingly possible (Wilson and Hölldobler 2005, Szewczyk and McCain 2016, Tiede et al. 2017). Here we report diversity patterns of leaf-litter ants in wet forests of the Middle American corridor.

The mountainous terrain of Middle America is a natural laboratory for gradient studies in the tropics. Tropical mountains lack strong annual variation in temperature, removing a major variable that influences the biota in the temperate zone (Janzen 1967, Colwell et al. 2008). Incident solar energy is more evenly distributed with respect to aspect, such that north and south-facing slopes have similar temperature profiles. Precipitation varies greatly throughout the corridor, but sites can be selected that have abundant moisture throughout the year, reducing the impact of precipitation as a controlling variable. Also, there is a conservation imperative to focus on tropical mountains because they are expected to experience the earliest effects of anthropogenic climate change (Wright et al. 2009, Laurance et al. 2011, Mora et al. 2013) and some effects are already occurring (Pounds et al. 1999).

Multiple processes have been proposed to explain the elevational distribution of diversity, including ecological and historical factors (Lomolino 2001). Macroecology has often focused on contemporary environmental factors that vary with elevation and may determine local diversity. Theory associated with metabolism and productivity predict temperature and precipitation as major factors (Kaspari et al. 2000, Brown et al. 2004, Kaspari 2004, McCain 2007a, Sanders et al. 2007, Malsch et al. 2008). Spatial hypotheses include area and mid-domain effects (Rosenzweig 1995, Colwell and Lees 2000, McCain 2007b, Colwell et al. 2016). Historical factors, such as phylogeny, niche conservatism, and time may also influence diversity patterns (Ricklefs and Schluter 1993, Wiens and Donoghue 2004, Wiens and Graham 2005, Machac et al. 2011, Smith et al. 2014, Weiser et al. 2018). Niche conservatism and habitat filtering can limit access to different portions of an elevational gradient, favoring some clades over others. Ants originated in the widespread warm tropical conditions of the late Cretaceous to Eocene (Moreau and Bell 2013), and lineages adapted to cold conditions may be younger and with less time to diversify. Lowland biotic attrition (Colwell et al. 2008) has been proposed as a historical mechanism that decreases diversity at the lowest elevations, as rapid climate change shifts climate zones upslope and no species are available to disperse into the novel warm conditions at the bottom of the gradient. To examine the influence of niche conservatism and time, diversity patterns in a large clade can be dissected into contributions from multiple subclades (Weiser et al. 2018).

Studies of ant distributions on mountains have revealed a variety of patterns. A general approach has been to apply linear models, with richness as the response variable, and multiple predictor variables (temperature, precipitation, area, mid-domain effect). Szewczyk and McCain (2016) reviewed 20 studies of ant diversity on elevational gradients. The most common pattern was an asymmetrical mid-elevation peak in diversity, with the peak below the midpoint of the gradient. The results were idiosyncratic, with different models being favored in different studies. On mountains with arid bases, a combination of temperature and precipitation provided the best model. On wet mountains, temperature or area alone was often the best model, but the fit was not very good and the mid-elevation peak was not explained. In the absence of precipitation effects at low elevations, the low-elevation decline in ant diversity may be attributed to greater human disturbance at low elevations (Nogues-Bravo et al. 2008, Forister et al. 2010).

Two studies in wet forests of the Middle American corridor (Olson 1994, Longino and Colwell 2011) showed a diversity peak around 500 m elevation. These were in very wet areas of primary forest, where moisture or human disturbance could not be limiting factors. The study of Smith et al. (2014) also showed a mid-elevation peak, but the lowest portion of the gradient was in tropical dry forest, where moisture limitation could be a factor. In the study of the Barva Transect in Costa Rica (Longino and Colwell 2011), ant communities were measured by taking samples of forest floor leaf litter from each of seven sites distributed along the elevational gradient. Here we replicate that sampling protocol in 49 additional wet forest sites throughout the Middle American corridor, across 11° of latitude and 2600 m of elevational range, for a total sample of 56 sites. A previous publication addressed ant abundance across most of those sites (Longino et al. 2014). Here we examine diversity, assessing the presence of patterns across a large spatial extent.

We address the following questions:
1) How robust is the mid-elevation peak in diversity? Does it persist when measured across 56 widely-distributed sites? Or does the pattern become blurred when the sites are not replicates within individual elevation gradients?
2) Do species richness and diversity indices differ in elevational patterns? With richness measures, it does not matter if species are common or rare. A 500 m elevation diversity peak could potentially be caused by mass effects (Shmida and Wilson 1985, Pulliam 1988). Ant communities around 500 m elevation may be supplemented by rare immigrants from nearby upslope cloud forest communities, creating the diversity peak. In contrast to richness measures, diversity indices are strongly influenced by the relative abundances of the most common species and less affected by rare species. Diversity indices should thus be less affected by mass effects.

3) To what extent do environmental variables predict diversity? Will temperature continue to be the sole, albeit inadequate, correlate of diversity because of the parallel decline above 500 m elevation? Although moisture and seasonality are presumed to be non-limiting in the subjectively chosen sites, there is greater variability across all 56 sites than in the 7-site study of Longino and Colwell (2011). With the larger geographic scope, will precipitation and seasonality emerge as significant predictors?

4) How do diversity patterns for sub-clades compare with the pattern for ants as a whole?

Methods

Sites and sampling methodology

A total of 56 sites were quantitatively sampled for ants over the span of 15 yr, with sites distributed from southern Costa Rica to the state of Veracruz, Mexico, an extent of 11° latitude and 30–2600 m elevation (Fig. 1, Supplementary material Appendix 1 Table A1). The results reported here are from multiple projects, from 2001 to 2016, but all follow a similar sampling protocol. Sites include 7 from the Barva Transect in Costa Rica (Projects ALAS and TEAM, Longino and Colwell 2011); 1 from the Osa Peninsula, Costa Rica (carried out by an undergraduate field course); 34 from Nicaragua to Chiapas, Mexico (Project LLAMA, Longino et al. 2014); and most recently 8 from additional sites in Costa Rica and 6 in the states of Oaxaca and Veracruz, Mexico (Project ADMAC). Sites were subjectively chosen to be closed-canopy evergreen forest in areas with abundant rainfall. Sites varied in land-use history, ranging from decades-old regenerating forest to mature old-growth forest, and from sites deep within large reserves to small islands of forest in agricultural landscapes. In Costa Rica, lowland wet forest habitats are continuous with cloud forest habitats. From Nicaragua northward, wet forests in the Caribbean lowlands are often separated from island-like mesophyl cloud forests by a matrix of pine forest or more xeric habitats.

The sampling unit was a 'miniWinkler' sample of arthropods extracted from a 1 m^2 forest floor quadrat, following the methods of Fisher (1999a). Litter in a quadrat (including any vegetation and suspended organic matter immediately above the quadrat) was chopped 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. For three ALAS sites on the Barva Transect, the 34 LLAMA sites, and the 14 ADMAC sites, miniWinkler samples were distributed in two haphazardly-placed transects of 50 samples, with 5 m spacing between samples. For four TEAM sites on the Barva Transect, samples were distributed in 10 transects of 10 samples each, with 10 m spacing between samples, and transects distributed in a 1 km^2 area. For the Osa Peninsula site, samples were in a grid of 10 transects of 10 samples each, with 5 m spacing between samples and approximately 50 m spacing between transects. Total sample size was 5599 miniWinkler samples (one sample was lost). Latitude and longitude of each sample are in Supplementary material Appendix 1 Table A2.
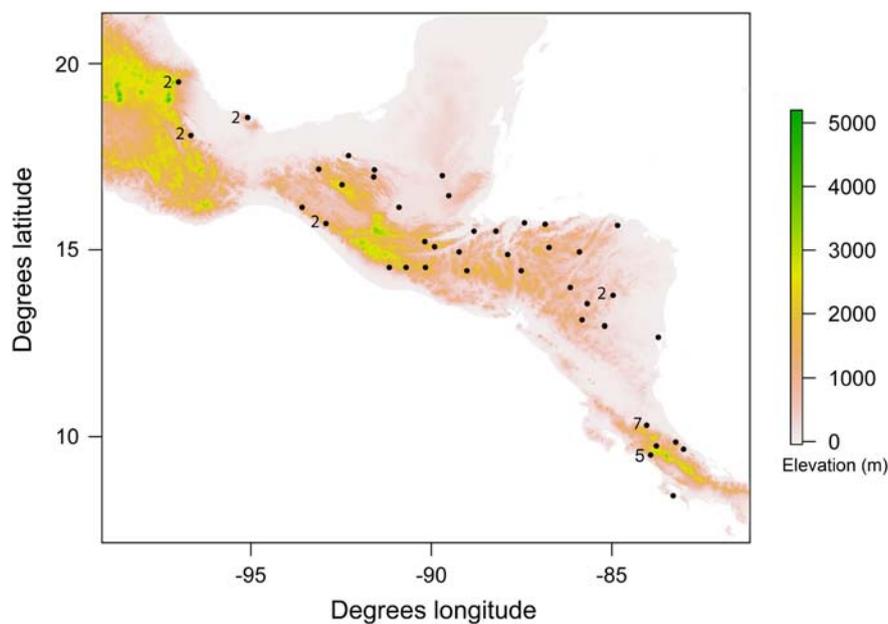
Figure 1. Map of 56 sample sites. Numbers next to sites indicate multiple sites in close proximity. See Supplementary material Appendix 1 Table A1 for details.

Ant workers were removed from each sample and identified, with identifications being to species for most groups, but to genus for certain groups that are difficult to sort to species. Taxon sufficiency studies suggest that ecological conclusions are robust to such approaches (Groc et al. 2010). Arboreal species that occasionally occur in miniWinkler samples were excluded, as were pest ants that were likely contaminants. Details of taxa and taxon selection are in Supplementary material Appendix 1. Incidence data (presence–absence) were recorded, resulting in a frequency (out of 100 samples) for each taxon at each site (Supplementary material Appendix 1 Table A3).

Climatic variables

Four climatic variables were obtained for each site, using 1 × 1 km resolution values from the WorldClim database (Hijmans et al. 2005): annual mean temperature (hereafter 'temperature'), minimum temperature of the coldest month, annual precipitation ('precipitation'), and precipitation seasonality ('seasonality') (Supplementary material Appendix 1 Table A1). Pearson correlation coefficients between environmental variables are in Supplementary material Appendix 1 Table A4 and bivariate scatterplots are in Supplementary material Appendix 1 Fig. A1. Temperature and minimum temperature of the coldest month were strongly co-linear and the latter is not considered further. Elevation was strongly co-linear with temperature, weakly negatively correlated with precipitation, and weakly positively correlated with seasonality. Temperature varies little over the latitudinal range of the study sites. Costa Rican sites have higher precipitation and lower seasonality than sites further north.

Diversity indices

Three richness measures and four diversity indices were examined. The richness measures were observed richness in the 100 samples ('richness'), the incidence-based coverage estimator ('ICE', Lee and Chao 1994), and richness rarefied to a common coverage value ('rarefied richness'). Coverage is the proportion of individuals in a community that are in the sampled species; it can be estimated as a function of the total sample size, the number of singletons, and the number of doubletons (Chao and Jost 2012). Coverage rises rapidly early in a sampling program, because most individuals are in the most common species. Chao and Jost recommend comparing diversity by rarefying to a common coverage value rather than a common sample size (samples or individuals). Coverage in this study was based on incidence data, using total number of species occurrences, number of uniques, and number of duplicates. For the full dataset of all ants, coverage based on 100 samples was above 0.93 at all sites and above 0.98 for over half of them. Sample-based diversity curves and richness estimators were calculated with EstimateS (Colwell 2016). Coverage and rarefied richness were calculated using EstimateS output.

The four diversity indices used were Fishers Alpha, Exponential Shannon (Jost 2006), Inverse Simpsons, and Inverse Berger–Parker. The first three were calculated using EstimateS. Berger–Parker is the proportion of individuals in a sample represented by the single most common species. Inverse Berger–Parker is the reciprocal, so that communities with lower dominance have higher values. Inverse Berger–Parker was calculated directly from the data set. These diversity indices tend to stabilize early in a sampling program, and just the observed values for the full 100 samples were used (i.e. without rarefaction).

Statistics

To test whether richness and diversity variables showed mid-elevation peaks, they were modeled as linear, quadratic, and cubic functions of elevation. Richness and diversity variables were also modeled as linear functions of temperature, precipitation, and seasonality. Interactions were not included. Model performance was evaluated by comparing Akaike information criterion (AICc) values, using R ver. 3.4.3, and the package AICcmodavg (R Core Team).

Taxon subsets

In addition to the full, all-ants dataset, elevational patterns of species richness were examined for 17 subclades. The subclades were genera, genus groups, or subfamilies, all known to be monophyletic. The clades were somewhat subjectively chosen to be mutually exclusive and to each contain at least 10 species in the study. Further details of subclade selection are in Supplementary material Appendix 1.

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.fr48qn7> (Longino and Branstetter 2018).

Results

Full dataset

All measures of richness and diversity except Inverse Berger–Parker were highly co-linear, with correlation coefficients above 0.9 and most above 0.98 (Supplementary material Appendix 1 Table A5, Fig. A2). For all richness and diversity measures except Inverse Berger–Parker, the relationship to elevation was best modeled with a cubic function (Table 1). The maximum predicted value was always substantially above the value at the intercept (i.e. sea level) and occurred between 339–525 m. For Inverse Berger–Parker, a quadratic model was supported. The relationship of richness and diversity to elevation is a truncated bell curve with a mode around 400 m (Fig. 2; Supplementary material Appendix 1 Fig. A3).

Table 1. Regression models of species richness and diversity variables as a function of elevation for Formicidae. Linear, quadratic, and cubic models are compared. Models are ranked by ΔAICc values, comparing the best model (lowest AICc) to the other models. Low values indicate higher support and models with ΔAICc < 4 are equally well supported. Maximum value is the predicted maximum value of the variable within the elevational domain of the study. n = 56 sites. ***, p < 0.001; **, p < 0.01; *, p < 0.05.

Variable	Model	ΔAICc	Intercept	Coefficient linear	Coefficient quadratic	Coefficient cubic	r^2	Maximum value	Elev. of maximum
Richness	cubic	0.00	97.93 ***	9.676e-02 ***	–1.368e-04 ***	3.353e-08 ***	0.88	117	418
	quadratic	24.13	119.50 ***	–3.148e-02 *	–8.033e-06		0.81		
	linear	24.62	125.69 ***	–0.050 ***			0.80		
ICE	cubic	0.00	114.70 ***	0.143 ***	–1.889e-04 ***	4.629e-08 ***	0.84	145	453
	quadratic	23.19	144.50 ***	–0.034 *	–1.108e-05		0.75		
	linear	23.59	153.02 ***	–0.060 ***			0.75		
Rarefied richness	cubic	0.00	76.24 ***	0.081 ***	–1.172e-04 ***	2.944e-08 ***	0.85	92	410
	quadratic	21.52	95.17 ***	–3.137e-02 **	–4.073e-06		0.77		
	linear	22.93	98.31 ***	–0.041 ***			0.77		
Fishers alpha	cubic	0.00	26.40 ***	0.028 ***	–4.070e-05 ***	1.021e-08 ***	0.84	31.74	339
	quadratic	20.33	32.97 ***	–0.011 **	–1.465e-06		0.76		
	linear	21.71	34.10 ***	–0.014 ***			0.76		
Exponential Shannon	cubic	0.00	44.70 ***	0.050 ***	–6.748e-05 ***	1.645e-08 ***	0.84	55	440
	quadratic	21.05	55.28 ***	–0.013 *	–4.280e-06		0.77		
	linear	21.72	58.58 ***	–0.023 ***			0.76		
Inverse Simpsons	cubic	0.00	28.95 ***	0.031 **	–4.061e-05 ***	9.654e-09 ***	0.79	35.5	454
	quadratic	13.36	35.16 ***	–6.048e-03	–3.525e-06 *		0.73		
	linear	15.23	37.87 ***	–0.014 ***			0.71		
Inverse Berger–Parker	cubic	0.00	11.20 ***	0.010 *	–1.193e-05 **	2.494e-09 *	0.64	13.76	525
	quadratic	2.69	12.81 ***	9.261e-04	–2.346e-06 **		0.61		
	linear	9.77	14.62 ***	–0.005 ***			0.54		

In linear models of richness and diversity as a function of temperature, precipitation, and seasonality, temperature emerged as the dominant factor (Table 2). For richness, exponential Shannon, inverse Simpson, and inverse Berger–Parker, models with temperature alone were not significantly improved by adding precipitation and seasonality. For ICE, rarefied richness, and Fisher's Alpha, models were significantly improved by adding precipitation and seasonality, but with modest improvements in r^2. When significant, coefficients for precipitation were positive and for seasonality were negative. However, all favored models predicted monotonic declines of values with increasing elevation (e.g. richness, Fig. 2). None of the models predicted a mid-elevation peak.

Taxon subsets

Patterns of observed species richness and elevation varied among subclades (Table 3, Fig. 3; other richness and diversity measures were highly correlated with observed species richness and are not reported). Within the large subfamily Myrmicinae, all the larger subclades (*Pheidole*, *Strumigenys*, *Atta* genus group) and one smaller one (*Carebara*) showed significant evidence of a mid-elevation peak, paralleling the results for ants as a whole. Other smaller myrmicine clades (*Basiceros* genus group, *Crematogaster*, *Megalomyrmex*, *Rogeria*) ranked a cubic model first and were qualitatively similar to patterns for all ants, but the more complex model was not strongly supported when compared to the simpler ones (ΔAICc < 4).

Within the Myrmicinae, two genera differed from the dominant pattern. *Adelomyrmex* showed a weak relationship to elevation. Model testing did not differentiate the three models, but a linear relationship was ranked first. Richness declined with elevation, but more gradually than most of the other subclades. In most subclades, the rightmost portion of the curve was concave up. In *Adelomyrmex*, it was concave down. Elevation explained relatively little of the variation (r^2 < 0.20). *Stenamma* showed a distinct mid-elevation peak, with a quadratic model favored, but the peak was shifted right (higher elevation) compared to other subclades, with a mode around 1000 m.

For ponerine ants, only one of the four examined clades showed evidence of a mid-elevation peak (*Rasopone ferruginea* group), and two clades, *Leptogenys* and Odontomachiti, exhibited clear monotonic declines. The subfamily Ectatomminae had a mid-elevation peak similar to ants as a whole. Dorylinae (army ants and relatives) and Proceratiinae were similar to *Adelomyrmex*, with no mid-elevation peak and gradually declining curves that were concave down.

Discussion

We documented ant diversity in wet forest habitats throughout Middle America, an important biodiversity hotspot (Myers et al. 2000), providing benchmarks for what are increasingly isolated and fragmented habitat remnants in a highly modified and intensively used landscape. These results
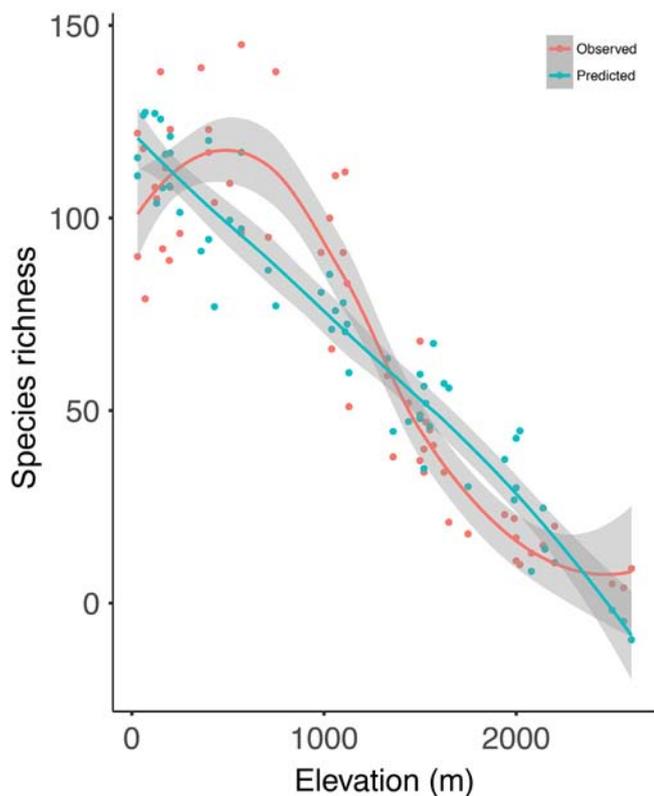
Figure 2. Ant species richness as a function of elevation at 56 sites in Middle America, from Veracruz, Mexico, to southern Costa Rica. Predicted values are based on a linear combination of temperature, precipitation, and seasonality (Table 2). Smoothed curves are LOESS fits (R, ggplot2).

expanded on a previous study of a single elevational transect (Longino and Colwell 2011). Here we focused on alpha diversity, both pure species richness measures and diversity measures that incorporate relative abundance. We discovered that the relationship between diversity and elevation is remarkably constant, from Veracruz, Mexico, to Costa Rica. Although not quantitatively assessed, the sites encompassed a broad range of disturbance histories and patch sizes, yet the pattern was clear. The relationship of ant diversity and elevation is a truncated bell curve, with a peak at ~400 m elevation.

The uniform presence of a similar mid-elevation peak in ant diversity throughout Middle America remains enigmatic. We would expect such a pattern if environmental factors were causing it, because environmental variables are relatively uniform across the study region (in the selected wet forest habitats). But no environmental variables emerged that would explain the decline in diversity at the lowest elevations. Beck et al. (2017), in a large study of the distribution of geometrid moth diversity across many distinct elevational gradients, found that a mid-elevation diversity peak was most common, and yet they too found no clear explanation, other than a slight influence of area-integrated productivity.

We did not explicitly test an area effect, but it is unlikely that area could explain the lowland diversity decline. Elsen and Tingley (2015) showed that mountain ranges vary in their area profile (hypsographic curve). The mountain ranges in our study region were mostly too small to appear in their review, but all should have a pyramid shape within the zone of ant occupancy, with the lowest elevations being in or adjacent to broad lowland coastal regions. Thus we doubt that area could explain the mid-elevation peak in Middle America.

If chance and purely historical factors were determining diversity, we would expect greater spatial variability in diversity patterns. There is species turnover across both elevational and latitudinal gradients, such that there is little species overlap between Veracruz and Costa Rica, yet the elevational diversity patterns are very similar. Colwell and Rangel (2010) modeled the evolution of communities on tropical mountains, incorporating stochastic speciation and extinction, temperature as the sole niche parameter, a degree of inherited niche (temperature) conservatism, late Quaternary glacial cycles that shifted the niche up and down-slope, and effects of area (smaller at higher elevation). They were able to produce model results that were similar to the observed ant diversity pattern, but one of their primary conclusions was that even with the same parameter settings, stochastic effects generated a wide variety of outcomes. The widespread occurrence of the same pattern, in spite of somewhat independent speciation histories in different regions, suggests there must be common processes constraining diversity patterns. Colwell et al. (2016) modeled richness as a combination of geometric constraints and environmental gradients, proposing 'midpoint attractors', an optimal position on a gradient to which stochastically placed species ranges were drawn. This model closely predicted the patterns of ant diversity seen here and elevational diversity gradients of other taxa.

Both the Colwell and Rangel community evolution model and the midpoint attractor model have species responding in a continuous way to the elevational temperature gradient. In these models there is no particular break point on the gradient, and a continuous curve with respect to elevation is generated. In contrast to these models, other studies emphasize abrupt ecotonal shifts. Shukor (2001) examined small mammals on Mount Kinabalu in Borneo and found a mid-elevation diversity peak caused by distinct lowland and upland assemblages that overlapped at the ecotone. Ferro (2013) found discrete lowland, mid-elevation, and upland communities of mammals in the Argentinian Andes. Multiple studies of ant richness and composition on elevation gradients have emphasized abrupt transitions between lowland and cloud forest habitats (Samson et al. 1997, Fisher 1998, 1999b, Brühl et al. 1999, Burwell and Nakamura 2011, Nowrouzi et al. 2016). Likewise in Middle America there is an ecotonal shift from lowland rainforest to cloud forest, but somewhat higher, around 1000 m elevation. There can often be a relatively abrupt physiognomic change between these two forest types (Grubb 1977, Bruijnzeel and Veneklaas 1998). Lowland forests are characterized by thin leaf litter

Table 2. Regression models of species richness and diversity variables as a function of temperature (T), precipitation (P), and seasonality (S) for Formicidae. Models are ranked by ΔAICc values, with low values indicating higher support. Models with ΔAICc < 4 are equally well supported. n = 56 sites. Significance values of model coefficients: ***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$.

Variable	Model	ΔAICc	Intercept	T	p	S	r²
Richness	T+S	0.00	−79.69 ***	8.346 ***		−0.406 *	0.76
	T+P+S	0.85	−90.56 ***	8.059 ***	4.673e-03	−0.327	0.76
	T+P	1.44	−123.10 ***	8.455 ***	6.864e-03		0.75
	T	2.67	−118.10 ***	9.087 ***			0.74
	P+S	58.18	78.06 *		0.01582 *	−0.8809 **	0.31
	S	62.33	140.48 ***			−1.246 ***	0.24
	P	63.71	6.74		0.02387 ***		0.22
ICE	T+S	0.00	−80.54 *	9.771 ***		−0.626 *	0.72
	T+P+S	0.05	−98.34 **	9.302 ***	0.008	−0.497	0.72
	T+P	1.55	−147.83 ***	9.903 ***	0.011 *		0.71
	T	4.24	−139.83 ***	10.916 ***			0.69
	P+S	47.60	96.28 **		0.021 **	−1.137 **	0.34
	S	52.57	177.23 ***			−1.610 ***	0.26
	P	54.03	4.26		0.031 ***		0.24
Rarefied richness	T+P+S	0.00	−78.14 ***	6.255 ***	0.007 *	−0.297	0.77
	T+P	1.42	107.80 ***	6.615 ***	9.031e-03 **		0.76
	T+S	2.92	−61.77 ***	6.687 ***		−0.416 **	0.75
	T	8.04	−101.17 ***	7.448 ***			0.72
	P+S	54.85	52.74 *		0.016 **	−0.728 **	0.38
	P	61.14	−6.17		0.022 ***		0.29
	S	62.51	114.64 ***			−1.089 ***	0.27
Fishers alpha	T+P+S	0.00	−25.14 ***	2.133 ***	0.002 *	−0.120 *	0.77
	T+S	2.57	−19.62 **	2.279 ***		−0.160 **	0.75
	T+P	2.67	−37.09 ***	2.279 ***	0.003 **		0.75
	T	9.24	−34.78 ***	2.571 ***			0.72
	P+S	53.26	19.50 *		0.005 **	−0.267 **	0.39
	P	60.64	−2.10		0.008 ***		0.29
	S	60.67	40.49 ***			−0.389 ***	0.29
Exponential Shannon	T+S	0.00	−36.51 **	3.856 ***		−0.182	0.72
	T+P+S	1.55	−40.60 **	3.748 ***	0.002	−0.152	0.72
	T	1.63	−53.71 ***	4.188 ***			0.70
	T+P	1.66	−55.73 ***	3.932 ***	0.003		0.71
	P+S	52.48	37.82 *		0.007 *	−0.410 **	0.28
	S	55.60	65.21 ***			−0.570 ***	0.22
	P	57.54	4.65		0.011 ***		0.20
Inverse Simpson	T	0.00	−31.32 ***	2.579 ***			0.65
	T+S	0.59	−23.38 **	2.425 ***		-0.084	0.66
	T+P	2.13	−30.17 ***	2.527 ***	5.542e-04		0.65
	T+P+S	3.00	23.36 *	2.426 ***	−9.009e-06	−8.400e-02	0.65
	P+S	47.89	27.40 **		0.003	−0.251 *	0.21
	S	48.44	40.60 ***			−0.328 ***	0.18
	P	51.77	7.09		0.006 **		0.13
Inverse Berger–Parker	T	0.0	−7.17 **	0.809 ***			0.49
	T+P	1.06	−6.71 **	0.867 ***	−0.001		0.49
	T+S	2.30	−6.78	0.802 ***		−0.004	0.48
	T+P+S	3.16	−5.053	0.847 ***	7.425e-04	−0.017	0.48
	S	32.52	14.37 ***			−0.085 *	0.08
	P+S	34.53	12.67 **		4.296e-04	−0.075	0.07
	P	35.88	6.61 **		0.001		0.03

and an epiphyte community dominated by vascular plants with drought adaptations (e.g. tank bromeliads, orchids with pseudobulbs, epiphytic cacti). Cloud forests suddenly change to deeper leaf litter and duff, and an epiphytic community with an abundance of drought-sensitive taxa, including dense layers of bryophytes and ferns. This change is not reflected in profiles of temperature or total precipitation. Rather it is an influence of where the cloud base contacts the mountains, resulting in a more constant bathing in mist and less direct insolation. An alternative hypothesis to species responding in a continuous and independent fashion to a uniform temperature gradient is that distinct communities evolve in discrete habitats (Bush 2002). There may be a lowland ant community that occurs widely from sea level to 1000 m, and

Table 3. Regression models of species richness as a function of elevation for multiple clades of Formicidae. Linear, quadratic, and cubic models are compared. Models are ranked by ΔAICc values, with low values indicating higher support. Models with ΔAICc < 4 are equally well supported. n = 56 sites. ***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$.

Clade	Model	ΔAICc	Intercept	Coefficient linear	Coefficient quadratic	Coefficient cubic	r^2
Myrmicinae							
Pheidole	cubic	0.00	20.45 ***	3.768e-02 ***	−4.660e-05 ***	1.135e-08 ***	0.80
	quadratic	22.84	27.75 ***	−5.734e-03	−3.005e-06		0.69
	linear	23.79	30.06 ***	−1.273e-02 ***			0.68
Strumigenys	cubic	0.00	13.14 ***	1.111e-02 *	−1.636e-05 ***	3.937e-09 ***	0.78
	quadratic	9.40	15.67 ***	−3.951e-03 *	−1.234e-06		0.74
	linear	9.50	16.62 ***	−6.824e-03 ***			0.73
Atta genus group	cubic	0.00	9.29 ***	1.227e-03	−7.473e-06 *	2.222e-09 **	0.79
	quadratic	5.71	10.72 ***	−7.272e-03 ***	1.062e-06		0.76
	linear	7.34	9.90 ***	−4.798e-03 ***			0.74
Rogeria	cubic	0.00	4.57 ***	2.534e-04	−3.292e-06	9.913e-10 *	0.68
	quadratic	1.83	5.21 ***	−3.538e-03 ***	5.160e-07		0.67
	linear	2.08	4.81 ***	−2.336e-03 ***			0.66
Crematogaster	cubic	0.00	2.12 ***	3.821e-03	−5.256e-06 *	1.364e-09 *	0.39
	linear	1.24	3.01 ***	−1.435e-03 ***			0.35
	quadratic	3.56	3.00 ***	−1.397e-03	−1.646e-08		0.34
Basiceros genus group	cubic	0.00	4.26 ***	4.576e-03	−5.729e-06 *	1.273e-09	0.53
	quadratic	1.42	5.08 ***	−2.920e-04	−8.401e-07		0.51
	linear	2.80	5.73 ***	−2.249e-03 ***			0.49
Carebara	cubic	0.00	1.51 ***	3.478e-03 **	−4.380e-06 ***	1.106e-09 ***	0.56
	linear	7.84	2.32 ***	−1.056e-03 ***			0.46
	quadratic	9.81	2.22 ***	−7.543e-04	−1.297e-07		0.46
Megalomyrmex	cubic	0.00	2.59 ***	−4.772e-04	−1.418e-06	4.846e-10 *	0.78
	quadratic	2.69	2.90 ***	−2.331e-03 ***	4.433e-07 **		0.76
	linear	9.30	2.56 ***	−1.298e-03 ***			0.72
Adelomyrmex	linear	0.00	3.21 ***	−7.480e-04 ***			0.18
	quadratic	0.42	2.89 ***	2.078e-04	−4.104e-07		0.19
	cubic	2.83	2.91 ***	1.103e-04	−3.125e-07	−2.548e-11	0.17
Stenamma	cubic	0.00	0.27	8.574e-03 ***	−5.546e-06 *	9.863e-10	0.36
	quadratic	0.71	0.91	4.801e-03 ***	−1.758e-06 ***		0.33
	linear	17.59	2.26 ***	7.076e-04 *			0.07
Ponerinae							
Odontomachiti	quadratic	0.00	4.43 ***	−3.322e-03 ***	5.806e-07 *		0.68
	cubic	0.43	4.08 ***	−1.186e-03	−1.564e-06	5.583e-10	0.69
	linear	2.46	3.99 ***	−1.970e-03 ***			0.66
Neoponera	linear	0.00	1.51 ***	−6.617e-04 ***			0.24
	quadratic	2.13	1.43 ***	−4.377e-04	−9.617e-08		0.23
	cubic	3.04	1.17 **	1.148e-03	−1.688e-06	4.145e-10	0.24
Rasopone (*ferruginea* group)	cubic	0.00	0.04	3.185e-03 **	−2.474e-06 *	4.802e-10 *	0.25
	quadratic	1.76	0.27	1.349e-03 **	−6.291e-07 ***		0.21
	linear	13.82	0.76 ***	−1.166e-04			0.00
Leptogenys	quadratic	0.00	2.09 ***	−1.789e-03 ***	3.688e-07		0.51
	cubic	1.56	1.93 ***	−8.100e-04	−6.145e-07	2.560e-10	0.50
	linear	1.73	1.81 ***	−9.302e-04 ***			0.48
Other subfamilies							
Ectatomminae	cubic	0.00	3.08 ***	9.164e-03 **	−9.687e-06 ***	2.202e-09 **	0.52
	quadratic	7.11	4.50 ***	7.423e-04	−1.230e-06 *		0.44
	linear	10.92	5.44 ***	−2.123e-03 ***			0.39
Dorylinae	linear	0.00	2.56 ***	−7.095e-04			0.19
	quadratic	1.92	2.43 ***	−3.006e-04	−1.756e-07		0.18
	cubic	4.29	2.37 ***	4.703e-05	−5.246e-07	9.087e-11	0.16
Proceratiinae	linear	0.00	2.75 ***	−7.850e-04 ***			0.21
	quadratic	0.06	2.43 ***	1.923e-04	−4.196e-07		0.23
	cubic	2.32	2.54 ***	−4.649e-04	2.404e-07	−1.718e-10	0.22

a much less diverse cloud forest community that occurs at 1000 m and above. This may in part explain the trend for the right tail of the diversity curve to be concave up, combining the dropping out of the diverse lowland community and the appearance of a less diverse montane community that extends to higher elevations.
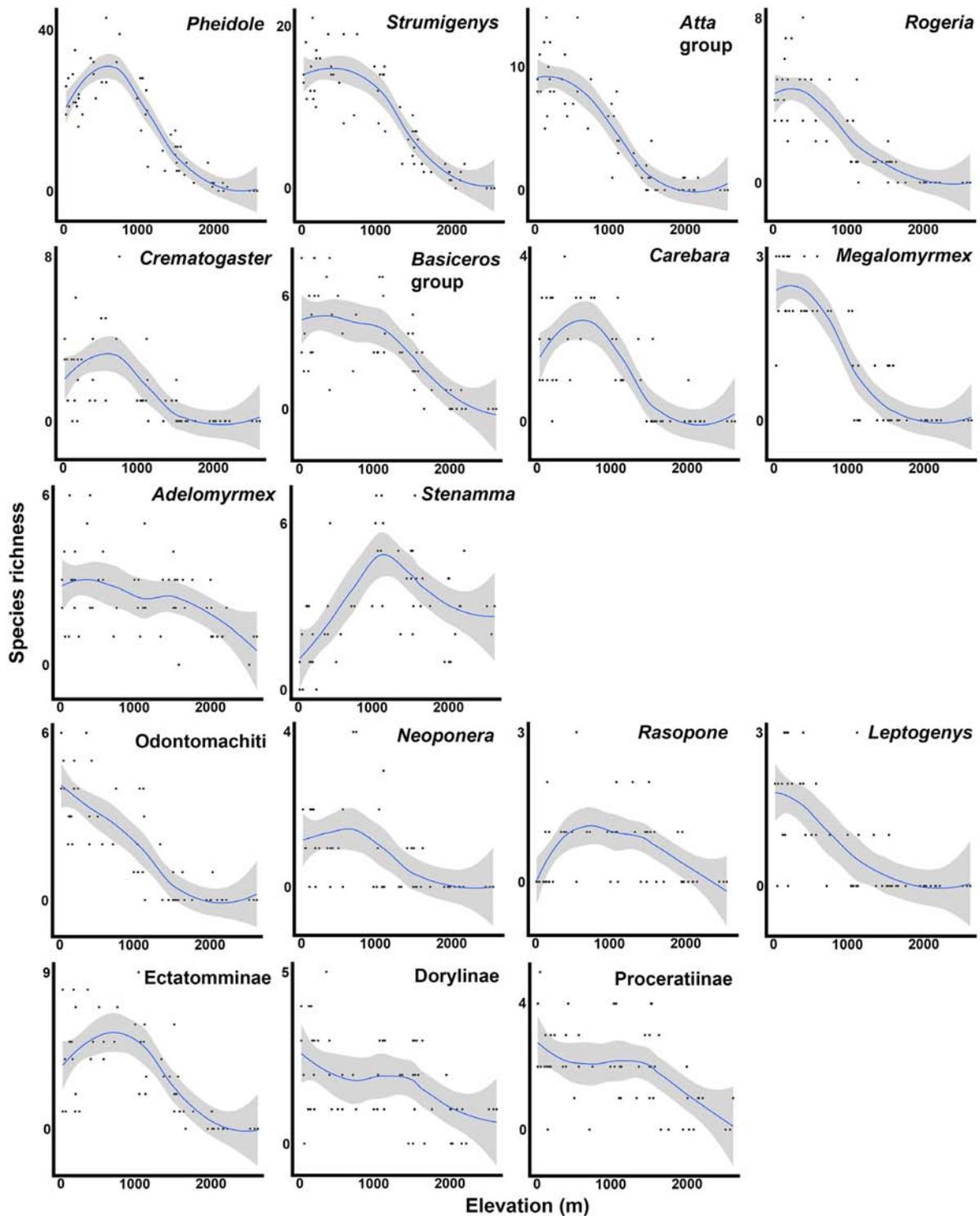
Figure 3. Species richness of ant subclades as a function of elevation at 56 sites in Middle America. Smoothed curves are LOESS fits (R, ggplot).

We know that certain species are montane specialists. Tropical montane specialization is scattered throughout ants, with many large clades having many lowland species and one or a few cloud-forest specialists. In Middle America this pattern is seen in the genera *Brachymyrmex*, *Hylomyrma*, *Hypoponera*, *Neivamyrmex*, *Neoponera*, *Pheidole*, *Solenopsis*, and *Strumigenys*. In fact, there is some evidence that ants exhibit multiple ecotonal shifts along elevational gradients in Middle America. The diverse mesophyl cloud forest between 1000–2000 m often gives way to oak-dominated forest above

2000 m. These very high elevation forests are home to a distinctive coterie of ant species: e.g. *Adelomyrmex anxiocalor*, *A. brenesi*, *A. micans*, *Perissomyrmex snyderi*, *Stenamma manni*, *S. megamanni*, *S. picopicucha*, and *Temnothorax striatus*. These species are restricted to these high montane forests and are not found in mesophyl cloud forest immediately below them.

How can a process involving stochastic evolution along a continuous thermal niche, as in the model of Colwell and Rangel, be differentiated from a model of discontinuous habitats arrayed along elevational gradients? The second model predicts a clustering of elevational range boundaries at the ecotones, and that independent clades will exhibit range boundary clustering at the same locations (within clades, range boundary clustering could occur due to niche conservation and be specific to the clade, not a general response to a common ecotone). However, two factors may blur that simple prediction. First, the sensitivity of range estimation to sampling effort makes precise measurements of range boundaries difficult. Secondly, and perhaps more importantly, clades may differ in the degree to which they exhibit the 'mass effect' of Shmida and Wilson (1985) and Pulliam (1988), in which range boundaries extend beyond the habitable space of a species because of a constant flow of immigrants from suitable to unsuitable areas.

The fact that multiple measures of diversity show a peak at 400 m elevation, including those dominated by relative abundance of common species, may indicate that ecotonal effects alone cannot explain all of the pattern. Lowland species, in the absence of montane specialists, may continue to exhibit a mid-elevation diversity peak. It may not be coincidental that the diversity peak at 400 m corresponds to the estimated upward shift in climate during the current interglacial, occurring somewhat abruptly a little over 10 000 yr ago (Bush 2002). The lowland diversity decline may be true lowland biotic attrition (Colwell et al. 2008) that has already occurred. The current climate at 400 m elevation may be the 'typical' climate that was broadly present at sea level throughout the lowland wet tropics, and to which the lowland ant fauna is adapted. Current temperatures below 400 m may be anomalously warm for the majority of lowland species, resulting in a slight decrease in diversity. The mid-point attractor model of Colwell et al. (2016) captures this effect, with the attractor for ants being around 400 m. Burwell and Nakamura (2016) showed mixed evidence for lowland attrition in ants of the Australian wet tropics. However, two of their gradients that did not show a lowland decline may have had access to species from more northern (and thus warmer) rainforest refuges, via dispersal. A third site did show a lowland decline, perhaps due to dispersal barriers preventing immigration from warmer sites.

Several subclades of ants failed to show the dominant pattern of a mid-elevation diversity peak centered near 400 m. Each has a distinctive biology or history that may explain their specific pattern. Two clades in the Myrmicinae have diverse radiations of montane forest specialists. *Adelomyrmex* shows relatively flat diversity throughout its elevational range, decreasing slightly toward the upper edge of the range.

There are similar numbers of lowland and montane specialists. Abundance, however, is much higher in cloud forest than in the lowlands (Longino et al. 2014; Supplementary material Appendix 1 Fig. A4). This pattern would be even more striking if biomass data were available. *Adelomyrmex* in the lowlands typically have smaller workers and presumably smaller colony sizes, because there are few workers per sample. In contrast, montane *Adelomyrmex* have larger workers and often occur with large numbers of workers per sample. The highlands of Guatemala and Chiapas have sites where *Adelomyrmex* are conspicuous and dominant elements of the leaf litter, and large colonies can be found nesting in rotten wood on the forest floor. The clade that contains *Adelomyrmex* and two other small genera is pantropical, with no temperate zone species, yet its greatest abundance is cloud forests of Middle America.

Stenamma shows a mid-elevation diversity peak, like ants as a whole, but the peak is shifted upward, to 1000 m. Most species are montane specialists, and relatively few species occur in the lowlands. Like *Adelomyrmex*, *Stenamma* abundance is the inverse of ants as a whole, rising from sea level to 1000 m, and then forming a plateau from there to the highest sampled sites (Longino et al. 2014, Supplementary material Appendix 1 Fig. A4). *Stenamma* is a holarctic genus, likely within a holarctic tribe (Branstetter et al. 2016), and it includes a major subclade in Middle America (Branstetter 2012, 2013). Thus, adaptation to cold may have been an early occurrence and the genus could be an initially montane lineage that is dispersing into the lowlands, rather than vice versa. Other small lineages appear to have north temperate origins and in Middle America are restricted to high montane sites: *Cryptopone*, *Perissomyrmex*, *Ponera*, and some groups of *Temnothorax* (Prebus 2017).

The subfamily Ectatomminae, part of a clade that is sister to the Myrmicinae, shows the dominant pattern, but other more distantly related subfamilies do not. The Ponerinae mostly show linear declines in diversity. Ponerine genera do have occasional montane specialists, but the great majority are lowland species and there is no suggestion of a mid-elevation peak. The Ponerinae are considered 'primitive', meaning they retain many plesiomorphic characters for ants as a whole. Ponerine niche conservatism may be strong and centered on the very warm conditions during early ant evolution. It is notable that ponerines are very poorly represented in the temperate zone, compared to Myrmicines. However, one small ponerine clade in our study, the *Rasopone ferruginea* group, did show a significant mid-elevation peak.

The pattern for Dorylinae may be due to their behavior. The larger and more diverse dorylines are the army ants. They have large nomadic colonies and species typically have very broad elevational ranges. *Labidus coecus*, a subterranean army ant, has one of the broadest elevational ranges of any known ant, from sea level to 3000 m. The group as a whole favors lowland habitats, with highest diversity near sea level. In our study area there is only one army ant species, *Neivamyrmex sumichrasti*, known to be a montane specialist, and only in the southern portion of its range. The cryptic non-army ant

dorylines (e.g. *Syscia*, identified only to genus in this study) are more poorly known, but show a greater degree of elevational specialization, and are potentially more myrmicine-like in their elevational distribution (unpubl.).

Finally, the Proceratiinae is a relatively small clade of poorly-known ants, mostly small and low density. They show lowland and montane specialization, but with similar diversity levels across the domain.

Conclusions

We show here that the relationship of multiple measures of ant diversity to elevation in the Middle American wet tropics is quite robust across multiple scattered sites. It does not depend on being part of individual continuous gradients. The pattern emerges from the combined effects of multiple ant clades, which show varying degrees of specialization for lowland or montane habitats. Even though the species are not the same from region to region, the various clades appear to maintain similar levels of montane specialization across regions, recapitulating the elevation–diversity relationship. The causes of the truncated bell curve remain elusive, but potentially involve lowland biotic attrition, niche conservatism with occasional ecotonal shifts, and younger ages of montane habitats.

Considering the future of biodiversity, it is a hopeful sign that similar diversity patterns are seen in small patches of remaining, or even regenerating, habitat, in places where the option of investigating a continuous elevational gradient has disappeared. This study emphasizes that even small habitat patches, surrounded by pastures or coffee farms, have significant biodiversity value. The quantitative results presented here will allow the assessment of biodiversity change over time in Middle America. Important questions remain about the sustainability of these habitats in the presence of continued fragmentation compounded by the impact of anthropogenic climate warming.

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