# Range size and ant communities across elevations

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**Abstract:** Understanding the patterns of species ranges, community structure, and species richness is a key step in uncovering the underlying ecological and evolutionary processes. Here, I explore patterns of ant communities along elevational gradients across the globe. With 20 robust ant elevational datasets, 16 of which include species-level elevational distribution data, I investigate elevational range sizes, community variation and structure, and richness at the species, genus, and subfamily levels. With these datasets, I show that ant elevational range sizes are smaller in the tropics and increase with latitude. Gradient-wide beta diversity and turnover correspondingly increase with latitude. These patterns dissolve at higher taxonomic levels where ant communities are highly nested. Ant elevational range size does not increase consistently with elevation. Unlike beta diversity, elevational patterns of richness do not show a latitudinal trend. Richness is typically highest at intermediate elevations and patterns are qualitatively similar across taxonomic levels. The richness pattern along an elevational gradient is not driven by a single genus or subfamily, but rather emerges from the roughly congruent patterns of each subtaxon. Despite incredible biological variability, the species richness of many ant genera and subfamilies appear to be driven by similar processes.

**Keywords:** Formicidae, richness, taxonomic level, altitude, range size, beta diversity

# Introduction

Patterns of species richness and community composition are directly determined by the overlap and delineation of species ranges. Ants are no exception. Discovering the patterns of overlapping ranges, the dynamics of range boundaries, and the underlying determinants is a key step in understanding the macro-scale distribution of ant diversity. In this review and meta-analysis, I use elevational gradients as a tool for comprehending patterns of ant community structure, community variation, and species richness.

Elevational gradients provide a rich system for studies of community patterns (McCain 2009a, 2010). Mountains act as compact, globally replicated systems, occurring on every continent and varying in many characteristics that may affect richness, including climate, history, and geography (Rahbek 1995; Lomolino 2001; McCain and Grytnes 2010). Detailing how ant communities change along elevational gradients may yield insight into processes affecting ant species diversity across spatiotemporal scales. Due to their immense diversity, community studies of ants can be conducted at different trophic and taxonomic levels.

Despite comprising the majority of animal species, insects have received relatively little focus in macroecological studies (Diniz-Filho et al. 2010; Beck et al. 2012). Given the astonishing array of insect diversity, a complete picture of biodiversity requires their inclusion. Ants have a number of advantages for global studies of diversity. As predators, competitors, scavengers, and dispersers, they have major ecological impacts in nearly all terrestrial ecosystems (Hölldobler and Wilson 1990). In contrast to many insect taxa, the individuals used for identification are wingless. Consequently, their movement is restricted, reducing the impact of windblown accidentals captured at elevations at which they cannot long survive. Additionally, because of historic interest, ant taxonomy is relatively well known when compared to other insect taxa.

Ants are an incredibly diverse taxon by nearly any ecological metric. Dietary breadth ranges from the specialist predators in the subfamily Amblyoponinae to the generalist omnivores in the subfamilies Myrmicinae and Formicinae. Nesting habits and structures are highly varied, with differences in site preferences among genera, among species, and even variability within species (Hölldobler and Wilson 1990; Anderson and McShea 2001). Ant species vary dramatically in worker body size (Cushman et al. 1993), from monomorphic to highly polymorphic (Wilson 1953), in colony size (Kaspari and Vargo 1995), in expression of caste ratios (McGlynn et al. 2012), in level of ecological aggression and dominance (Andersen 1997; Cerdá et al. 2013), and in number of queens (Hölldobler and Wilson 1977).

In addition to this tremendous range of biological characteristics, the many subfamilies and genera contain hugely disparate numbers of species. In such a diverse and numerically heterogeneous taxon as ants, it seems reasonable to expect that the factors shaping the distribution of ant species might vary among subfamilies or genera. Given the uneven richnesses of ant subtaxa, it is possible that patterns of ant species richness and compositional change may be driven primarily by the most speciose subfamily or genus, rather than reflecting the combined tendencies of each subtaxon.

Here, I review the work to date on ant communities across elevations, investigating patterns and evaluating latitudinal trends at the species, genus, and subfamily level. Understanding the distribution of biodiversity necessitates a comprehensive, global perspective. Using elevational data from studies with strong designs and ample sample sizes, I explore (1) the variation in elevational range size among and along gradients, (2) the variation in the ant community composition across elevations, (3) the elevational patterns of species richness, and (4) the congruency of the most speciose subtaxon on each elevational gradient with the remaining subtaxa.

# Datasets

To identify ant elevational distribution datasets at local spatial scales, I performed Web of Knowledge and Google Scholar literature searches using all combinations of the keywords 'ant', 'elevation\*' or 'altitud\*', 'gradient', 'diversity', and 'insect'. These searches primarily returned studies with discrete sampling sites interspersed along single elevational gradients. To identify ant elevational distribution datasets at regional spatial scales, I searched for publications with 'ants of' in the title. This search typically returned guides to the ant fauna of specific geopolitical regions. Such guides often compile museum records and many years of collections across a region, detailing the recorded occurrences of each ant species. Elevational ranges were interpolated by assuming each species was present between its lowest and highest recorded occurrence within a dataset.

To restrict the analysis to robust, well-sampled datasets, I required that a dataset provide ant elevational data within a mountainous region or along a gradient and meet five *a priori* criteria: (1) even sampling effort with standardized methods across the gradient; (2) sampling sites interspersed along at least 70% of the gradient; (3) sampling within the lowest 400m of the gradient; (4) no elevational sampling gaps greater than 500m; and (5) relatively little anthropogenic disturbance. These criteria, adapted from previous studies (McCain 2009a, 2010), are required to ensure the accurate description of the naturally occurring pattern (McCoy 2002; McCain 2005; Rahbek 2005; Nogués-Bravo et al. 2008). The common richness patterns, however, differ primarily across the lower portion of the elevational gradient (Nogués-Bravo et al. 2008). Consequently, violations of the second criterion were allowed when the majority of the unsampled region was at high elevations where declining richness had been demonstrated.

A total of 68 candidate datasets were identified (Appendix). A number of publications used non-independent datasets or sampled geographically disparate sites, leaving 47 independent datasets that detailed ant distributions or richness within a single region or along a gradient. There were 20 that met all five *a priori* sampling criteria, with 16 of those providing species-level elevational range data (Table 1). Thus, the majority of published studies describing ant richness across elevations did not employ sampling regimes sufficient to confidently capture the underlying richness pattern. Nevertheless, the robust datasets included local and regional scales, tropical and temperate zones, mainland and island gradients, and wet and arid climates.

### Elevational richness patterns

Using definitions from the literature (McCain 2009a, 2010), I classified the ant elevational richness pattern along each gradient into one of six categories: (1) *decreasing* (D), with richness highest at the mountain base, declining steadily with increasing elevation; (2) *low plateau* (LP), with richness consistently high across at least the lowest 300m before declining; (3) *mid-peak* (MP), with a richness peak >300m from the mountain base and with >25% greater richness than at the base; (4) *low plateau with a mid-peak* (LPMP), with a richness peak >300m from the base, but also high across the lowest 300m; (5) *increasing* (I), with richness increasing with elevation; and (6) *no pattern*, with richness not showing a consistent pattern across elevations.

# Elevational range size

Tropical species are predicted to have smaller elevational ranges on average than temperate species (Janzen 1967; Ghalambor et al. 2006; McCain 2009b). This is because seasonal temperature variation is more dramatic in temperate locations than in tropical locations. Tropical organisms experience a narrower range of temperatures annually and are consequently expected to have narrower thermal tolerances (Janzen 1967). Latitudinal trends in thermal tolerances and elevational range sizes exist in both vertebrate and invertebrate taxa (McCain 2009b; Sunday et al. 2011; Sheldon and Tewksbury 2014; Sheldon et al. 2015). While ants have not been evaluated comprehensively, small elevational range sizes have been noted along several tropical mountains, with many species detected at only one sampled elevation (Olson 1994; Samson et al. 1997; Fisher 1998; Brühl et al. 1999; Longino and Colwell 2011).

To minimize the influence of mountain height on the average elevational range size when comparing elevational gradients across latitudes, I analyzed truncated gradients (McCain 2009b) in addition to complete gradients (*n*=16). For each of three truncation heights (1600m: *n*=13; 1800m: *n*=12; 2000m: *n*=10), I excluded gradients shorter than the threshold. The remaining datasets were truncated at the threshold such that only the lowest 1600m, 1800m, or 2000m were included. The mean elevational range was then calculated for each truncated gradient.

At the species level, mean elevational range significantly increases with latitude in all four sets of gradients (Fig. 1; all: *n*=16, *P*=0.009, *R2*=0.353; 1600m subset: *n*=13, *P*=0.021, *R2*=0.344; 1800m subset: *n*=12, *P*=0.012, *R2*=0.437; 2000m subset: *n*=10, *P*=0.033, *R2*=0.384). These data show that ant species elevational ranges are smaller in the tropics, consistent with other taxa (McCain 2009b; Sheldon and Tewksbury 2014; Sheldon et al. 2015) and with the seasonality hypothesis (Janzen 1967). Interestingly, this latitudinal trend in elevational range size does not hold at higher taxonomic levels in ants. Neither the mean genus elevational range size nor the mean subfamily elevational range size changes across latitudes (genus: *n*=16, *P*=0.22; subfamily: *n*=16; *P*=0.40). This suggests that, though individual species may be constrained by thermal tolerance, the variability in thermal tolerance among congeners encompasses the increased annual variation at high latitudes.

Mean elevational range size may increase with elevation along each gradient because high elevations, like high latitudes, also experience increased climatic variability (Stevens 1992). To avoid the disproportionate influence and non-independence of large-ranged species, I estimated mean range size at each elevation using two methods (Rohde et al. 1993; Gaston et al. 1998; McCain and Bracy Knight 2013). With the midpoint method, the mean range size at each elevation is estimated as the average range size of all species whose midpoints occur at that elevation. With the quartile method, only species with ranges < 1/4 of the gradient are used. In these datasets, there is little evidence that the mean ant species range size increases along elevational gradients using either method (Midpoint linear regressions: *b*>0 with *P*<0.05 in 2/16 gradients, *R2* mean: 0.15, median: 0.03; Quartile linear regressions: *b*>0 with *P*<0.05 in 3/16 gradients, *R2* mean: 0.20, median: 0.14).

In summary, though ant elevational range sizes do not show a consistent pattern along single elevational gradients, they do tend to increase with latitude. The thermal tolerances of tropical ant species may, in fact, be narrower than those of temperate species. Alternatively, smaller elevational ranges are also consistent with stronger interspecific competition in the tropics (Pianka 1966; Willig et al. 2003), though these hypotheses are not mutually exclusive. The smaller elevational ranges in the tropics should lead to more pronounced changes in the ant community composition along tropical elevational gradients.

# Species composition & beta diversity

In this section, I examine ant community variation across taxonomic levels at the scale of entire gradients () as well as between adjacent elevational bands. To investigate whether ant communities differ across elevations due to the replacement of taxa or to the addition and loss of taxa, I partition that variation into turnover and nestedness. I explore these patterns across latitudes and at the species, genus, and subfamily levels.

Beta diversity was originally defined as the ratio of regional diversity () to local diversity () where (Whittaker 1960). Over the ensuing decades, definitions and indices for estimating beta diversity have proliferated (Tuomisto 2010). In a broad sense, beta diversity quantifies the variation in the species composition across space or time (Anderson et al. 2011). That variation can occur either through the replacement of one species for another, called *turnover*, or through the loss or addition of species, called *nestedness* (Baselga 2010, 2012; Legendre 2014). Partitioning total beta diversity into turnover and nestedness reveals the proportion of compositional change resulting from the replacement or the addition of species (Baselga 2010). Different processes likely drive turnover and nestedness, and understanding their elevational patterns can clarify how ecological filtering, biotic interactions, and neutral processes structure ant communities (Svenning et al. 2011; Dapporto et al. 2014).

To summarize and compare the total variation in ant communities across entire elevational gradients, I calculated gradient-wide beta diversity as:

where is the total richness along the gradient and is the average richness of the sampled elevational bands (Tuomisto 2010). Because the number of sampled elevational bands affects this method, I standardized as:

where *N* is the number of elevational bands (Chao et al. 2012). To explore gradient-wide proportions of turnover and nestedness, I used the multi-site Sørensen-family metrics in the R package *betapart* (Baselga 2010, 2012; Baselga and Orme 2012). To estimate the change in ant communities between adjacent elevations along each gradient, I used the pairwise Sørensen-family metrics in the R package *betapart* to calculate beta diversity, turnover, and nestedness (Baselga 2010, 2012; Baselga and Orme 2012). The Sørensen-family indices allow for unbiased comparisons among communities of differing richness (Baselga 2012). I calculated each component using species, generic, and subfamily composition at each elevation.

### Species level

At the species level, gradient-wide beta diversity () decreases significantly with latitude (Fig. 2, black; *n*=20, *P*<0.001, *R2*=0.49). Consistent with the smaller elevational ranges at low latitudes, the ant species composition changes more rapidly across elevations at low latitudes.

The proportion of gradient-wide beta diversity due to turnover rather than nestedness does not vary significantly between tropical and temperate mountains (Fig. 3; Wilcoxon rank sum test: *W*=41, *P*=0.26). Turnover constitutes a greater proportion of gradient-wide beta diversity than does nestedness at the species level (Fig. 3; Paired t-test: *t15*=5.63, *P*<0.001). When all pairs of elevations are compared, communities at two different elevations each commonly have distinct species rather than one being a subset of the other.

At a narrower spatial resolution, this is not the case. Nestedness tends to be higher than turnover between adjacent elevations along most gradients. This seemingly contradictory pattern illustrates the importance of spatial scale to patterns of beta diversity. In comparisons of sites across the entire gradient, species gradually replace each other and high elevation communities are distinct from low elevation communities. Species are more often distributed individually with overlapping ranges rather than occurring as distinct abutting communities. A fascinating exception is that several tropical datasets have high turnover between adjacent elevations over a large portion of the gradient (Samson et al. 1997; Fisher 1998; Longino and Colwell 2011). This is consistent with strong abiotic constraints, competition, or a combination producing a high degree of elevational specialization in tropical species.

### Genus level

At the genus level, gradient-wide beta diversity () also declines with latitude (Fig. 2, gray; *n*=16, *P*=0.03, *R2*=0.25). Generic composition changes more rapidly across elevations at low latitudes, though the trend is weaker than at the species level. The proportion of gradient-wide genus beta diversity due to turnover is significantly higher in temperate regions (Fig. 3; Wilcoxon rank sum test: *W*=49, *P*=0.042), though there is high variability among both temperate and tropical gradients. Nonetheless, at the gradient scale, genus communities vary due to roughly equal proportions of turnover and nestedness (Fig. 3; Paired t-test: *t15*=-0.67, *P*=0.51). Pairwise comparisons of all elevations along a given gradient show that the difference in genus composition results from both the replacement of one genus with another and the loss of genera without replacement.

Between elevationally adjacent sites, ant genera, like ant species, tend to be nested; adjacent communities differ due to the loss of genera between elevations rather than the replacement of one genus with another. Along many gradients, turnover at the genus level is nearly zero between the majority of adjacent elevations. The primary exceptions are in the Philippines (Samson et al. 1997), where turnover is higher than nestedness except at the highest elevations, and in the McPherson Range in Australia (Burwell and Nakamura 2011), where turnover is higher than nestedness along the lower half of the gradient.

### Subfamily level

At the subfamily level, gradient-wide beta diversity () shows no relationship with latitude (Fig. 2, white; *n*=16, *P*=0.15, *R2*=0.08). The proportion of gradient-wide subfamily beta diversity due to turnover does not differ between tropical and temperate mountains (Fig. 2b; Wilcoxon rank sum test: *W*=45; *P*=0.08). In fact, nearly all of the change in subfamily composition is due to nestedness rather than turnover (Fig. 3; Paired t-test: *t15*=-11.04, *P*<0.001). Subfamilies rarely replace one another along an elevational gradient, but rather the subfamily composition of each elevation is either identical to or a subset of the composition at other elevations.

There is no subfamily turnover along any gradient between adjacent elevations. The high degree of elevational overlap among subfamilies results in nested subsets of communities across elevations. Subfamilies are typically progressively excluded at higher elevations, consistent with environmental filtering (Dapporto et al. 2014). There is little evidence for competitive exclusion across elevations at the subfamily level.

Latitudinal trends in elevational beta diversity are contingent on taxonomic level. Tropical ant communities show more extreme differences across elevations. Beta diversity between adjacent elevations declines as taxonomic resolution decreases. Species dissimilarity is higher than genus dissimilarity which, in turn, is higher than subfamily dissimilarity.

Most dramatically, turnover across elevations declines at higher taxonomic levels irrespective of latitude. Communities become increasingly nested as the differences are due not to the replacement of one taxon with another, but to the loss or addition of taxa. This taxonomic trend may occur because competition is most intense among congeners, though heightened sensitivity to abiotic conditions at the species level and resultant elevational specialization could also produce this pattern (Machac et al. 2011; Dapporto et al. 2014).

# Richness patterns

### Species richness

Ant species richness shows a variety of patterns across elevational gradients. In the robust datasets, mid-peaks are most common (14/20), though decreasing (3/20) and low plateau (3/20) patterns also occur (Fig. 4, black bars). Despite strong latitudinal trends in range size and beta diversity, the richness pattern distribution of tropical gradients is not significantly different from that of temperate gradients (Fisher's Exact Test: *n*=20, *P*=0.30). At the species level, ant elevational richness varies among mountain ranges, but is frequently highest at intermediate elevations.

### Genus richness

The number of genera across elevations typically mirrors the number of species; the genus richness pattern is the same as the species richness pattern in 11 of the 16 gradients. The distribution of genus richness patterns does not differ significantly from the species richness patterns (Fig. 4, black and gray bars; Fisher's Exact Tests: *nspecies*=20, *ngenus*=16, *P*=0.28; *nspecies*=16, *ngenus*=16, *P*=0.39). The peak in genus richness tends to be less pronounced, resulting in several low plateau with mid-peak patterns that are not seen at the species level. The distribution of genus richness patterns does not vary significantly between tropical and temperate datasets (Fisher's Exact Test: *n*=16, *P*=0.11). The log number of species increases quite predictably with the log number of genera (*R2* mean: 0.96), lending further evidence that ant richness patterns are similar at the species and genus scales.

### Subfamily richness

The richness pattern of ant subfamilies along each gradient coarsely resembles the species and genus richness patterns, though it is less distinct due to the smaller number of subfamilies. The distribution of subfamily richness patterns is not significantly different from that of the species richness patterns (Fig.4, black and white bars; Fisher's Exact Tests: *nspecies*=20, *nsubfamily*=16, *P*=0.10; *nspecies*=16, *nsubfamily*=16, *P*=0.20) nor from that of the genus richness patterns (Fig. 4, gray and white bars; Fisher's Exact Test: *n*=16, *P*=0.84). As at the species and genus levels, the distribution of subfamily richness patterns does not vary significantly between tropical and temperate gradients (Fisher's Exact Test: *n*=16, *P*=0.28). The log number of subfamilies predicts the log number of species, though less reliably than does the number of genera (*R2* mean: 0.79).

Ant richness is often high at intermediate elevations. This is true at the species, genus, or subfamily level. The underlying ecological or evolutionary factors driving richness may create similar patterns all multiple taxonomic levels. While it may seem intuitive that the number of species would increase with the number of genera, in fact species communities can be phylogenetically over- or under-dispersed (Webb et al. 2002). The degree of? phylogenetic dispersion likely arises from the interplay of environmental filtering, neutral processes, and competition (Webb et al. 2002; Kembel and Hubbell 2006; Machac et al. 2011). The similarity in richness patterns across taxonomic levels suggests that species across the many genera and subfamilies of ants along each gradient respond similarly to the combination of processes affecting speciation and community assembly.

# Dominant taxa

### Most speciose genus

The numerical dominance of the most speciose genus is highly variable among mountain ranges. The most speciose genus along each gradient comprises 7–31% of the total species richness of the average gradient (mean ± SE: 20.0 ± 1.57%). These genera include *Camponotus* (Sabu et al. 2008), *Formica* (Gregg 1963; Allred 1982; Wheeler and Wheeler 1986; Hellrigl 2003; Glaser 2006), *Lasius* (Karaman 2011), *Pheidole* (Moody and Francke 1982; Van Pelt 1983; Samson et al. 1997; Fisher 1998; Araújo and Fernandes 2003; Burwell and Nakamura 2011; Longino and Colwell 2011), *Stenamma* (Lessard et al. 2007), and *Strumigenys* (Sarnat and Economo 2012). The proportion of species within the most speciose genus in a regional community does not vary predictably across latitudes (*n*=16, *P*=0.15, *R2*=0.08).

The species richness of the most speciose genus strongly predicts richness across elevations (*R^2* mean: 0.79). This single genus does not solely drive the overall pattern. Instead, the species richness pattern of the most speciose genus typically mirrors the richness pattern of the remaining species. The richness of the most speciose genus predicts the richness of the remaining genera quite well on average (Fig. 5a; *R2* mean: 0.69), though the relationship varies among gradients (*b* mean: 3.5, standard deviation: 2.9, range: -0.9–10.8). Many of the non-dominant genera are neither speciose nor widespread enough to reliably reveal a species richness pattern. Those that are tend to show an elevational richness pattern that is qualitatively similar to the overall pattern for that gradient and to that of the most speciose genus on the gradient.

### Most speciose subfamily

The numerical dominance of the most speciose subfamily is highly variable among mountain ranges. The most speciose subfamily along each gradient comprises 39–73% of the total species richness (mean ± SE: 54.5 ± 2.04%). Along a given gradient, one of two subfamilies are dominant: Formicinae (Gregg 1963; Allred 1982; Wheeler and Wheeler 1986; Hellrigl 2003; Glaser 2006) or Myrmicinae (Moody and Francke 1982; Van Pelt 1983; Samson et al. 1997; Fisher 1998; Araújo and Fernandes 2003; Lessard et al. 2007; Sabu et al. 2008; Burwell and Nakamura 2011; Karaman 2011; Longino and Colwell 2011; Sarnat and Economo 2012). There is no latitudinal trend in the proportion of species contained within the most speciose subfamily (*n*=16, *P*=0.38, *R2*=0.06).

As with the dominant genus, the species richness of the most speciose subfamily is remarkably similar both to the richness of all species (*R2* mean: 0.97) and to the richness of species in non-dominant subfamilies (Fig. 5b; *R2* mean: 0.81) across elevations. The total species richness pattern is not simply a product of the most speciose subfamily. Rather, the dominant subfamily shows the same richness pattern as the remaining subfamilies, and the richness pattern of each subfamily is often qualitatively similar to the overall richness pattern and to the pattern of the most speciose subfamily.

Ant species richness patterns across elevations are not driven by a single subtaxon, but rather emerge from the congruent, nested richness patterns of many genera and subfamilies. The richness pattern within each subtaxon tends to be broadly similar to that of the whole. This suggests that the key factors shaping the richness of ants across a given elevational gradient may act on the majority of ant subtaxa similarly, regardless of ecological differences.

# Research gaps

Sampling within the lowest 400m is critical to reliably detect the underlying pattern because elevational richness patterns tend to differ primarily towards the mountain base (Diniz-Filho et al. 2010). Additionally, though a multitude of hypotheses have been proposed as drivers of ant community structure and diversity along elevational gradients (Samson et al. 1997; Botes et al. 2006; e.g., Longino and Colwell 2011), the data required to rigorously evaluate many of these hypotheses are lacking at a broad scale. In particular, habitat complexity, such as vegetation structure or leaf litter depth, has been suggested as a driver of ant diversity (Lassau and Hochuli 2004; Sarty et al. 2006; Pacheco and Vasconcelos 2011; Bharti et al. 2013). Such data have not been widely collected across elevational gradients with ant species data. Further, we know little about the ranges and less about the basic natural history of many ant species (Lanan 2014). Dietary, foraging, and nesting habits can vary dramatically within a genus and even within a species (Hölldobler and Wilson 1990). Understanding how biotic interactions and variation in their strength affect ant communities across elevations relies on thoroughly detailing behavior and interactions across a wide taxonomic variety of ant species. Ant communities can also vary substantially across seasons and years (Bishop et al. 2014), variation that has rarely been accounted for. A greater focus on seasonal and annual fluctuations will inform mechanistic approaches to understanding patterns of ant communities. Finally, a recent phylogenetic analysis of tropical ants across elevations found that the ant communities were phylogenetically clustered, suggesting a strong role of environmental filtering (Smith et al. 2014). Increased focus on phylogenetic patterns may help to disentangle the interplay of ecological and evolutionary processes in shaping ant communities (Machac et al. 2011; Smith et al. 2014).

# Conclusion

Ant elevational ranges are narrowest at tropical latitudes, leading to higher gradient-wide beta diversity and high species turnover in the tropics. This trend becomes less distinct at higher taxonomic levels where elevational ranges become broader and communities become increasingly nested. The elevational species richness patterns do not vary systematically across latitudes in contrast to elevational ranges and beta diversity. Elevational species richness is a conglomerate property across subfamilies and genera rather than a function of only the most speciose subtaxon. The richness patterns along a given gradient are broadly similar among species, within and among genera, and within and among subfamilies. Similar factors likely influence the elevational distribution of ant species across many genera and subfamilies despite dramatic biological differences. Thus, while range sizes and changes in species composition are inherently linked to variation in species richness, they are not as directly relevant to richness patterns at the scale of elevational gradients.

# Acknowledgments

I am indebted to the authors whose work is reanalyzed here. I would also like to thank Dr. Christy McCain, Dr. Michael Breed, Kevin Bracy Knight, Holly D’Oench, and Helen McCreery for their insightful comments and helpful advice.

# Table Caption

**Table 1** Robust datasets used for analyses. References marked with an asterisk (\*) did not provide species-level range data. D = decreasing; LP = low plateau; MP = mid-peak.

# Figure Legends

**Fig. 1** Ant species elevational range sizes increase with latitude. (a) Both the mean (solid; ± 1 standard error) and median (open) elevational range size increases with distance from the equator along complete gradients (mean: *n*=16, *P*=0.009, *R2*=0.353; median: *n*=16, *P*=0.04, *R2*=0.208). (b) This trend does not appear to be driven by the height of the mountain. The mean elevational range size increases with latitude with all three truncation heights (1600m subset: black, *n*=13, *P*=0.021, *R2*=0.344; 1800m subset: dark gray, *n*=12, *P*=0.012, *R2*=0.437; 2000m subset: light gray, *n*=10, *P*=0.033, *R2*=0.384).

**Fig. 2** Gradient-wide beta diversity decreases with latitude. Total species beta diversity across each elevational gradient, standardized for the number of sampled elevations, declines with latitude (black; *n*=20, *P*<0.001, *R2*=0.49). This pattern diminishes at broader taxonomic scales with a weaker trend for genus beta diversity (gray; *n*=16, *P*=0.03, *R2*=0.25) and no trend for subfamily beta diversity (white; *n*=16, *P*=0.15, *R2*=0.08).

**Fig. 3** Proportion of gradient-wide beta diversity due to turnover decreases with taxonomic resolution. In both temperate (white) and tropical (gray) gradients, the proportion of beta diversity due to turnover (i.e., replacement) rather than nestedness decreases at higher taxonomic levels. At 0.5 (dotted line), turnover and nestedness contribute equally to the change in community composition.

**Fig. 4** Robust patterns of ant elevational richness patterns across taxonomic scales. Observed patterns included declines (D), low plateaus (LP), low plateaus with mid-peaks (LPMP), mid-peaks (MP), and no pattern (None). A variety of species richness patterns (black, *n*=20) occur, though mid-elevational peaks are most common. The pattern distribution is similar for both species (black) and genus (gray, *n*=16) richness (Fisher's Exact Test: *nspecies*=20, *ngenus*=16, *P*=0.28). Though the subfamily (white, *n*=16) richness patterns are less discernible due to the small number of subfamilies along many gradients, the distribution of patterns is not significantly different (Fisher's Exact Tests: *nspecies*=20, *nsubfamily*=16, *P*=0.10; *ngenus*=16, *nsubfamily*=16, *P*=0.84).

**Fig 5** Richness of the most speciose genus or subfamily predicts the richness of the remaining species. (a) The elevational richness pattern of the most speciose genus is nested within the richness pattern of the remaining species for most gradients. The trend is apparent with all datasets combined (black line) and within each gradient (gray lines). There is, however, much variability in the slope of the relationship among gradients. (b) The nestedness of the richness patterns becomes stronger at the subfamily level. The relationship is strong with all datasets combined (black line) and much less variable among transects (gray lines) compared to the genus level.

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| Reference | Study Area | Lat. (º) | Richness Pattern |
| Allred (1982) | Utah, USA | 39.5 | MP |
| Araujo & Fernandes (2003) | Espinhaco, Brazil | -19.4 | LP |
| Botes et al. (2006)\* | Cederburg Wilderness, South Africa | -32.4 | MP |
| Burwell & Nakamura (2011) | McPherson Range, Australia | -28.2 | D |
| Fisher (1998) | Ambohitsitondroina, Madagascar | -15.1 | MP |
| Glaser (2006) | Voralberg, Austria | 47.3 | LP |
| Gregg (1963) | Colorado, USA | 39.0 | MP |
| Hellrigl (2003) | South Tirol, Italy | 46.8 | MP |
| Karaman (2011) | Montenegro | 42.3 | D |
| Lessard et al. (2007) | Smoky Mtns, Tennessee, USA | 35.6 | MP |
| Longino & Colwell (2011) | Volcan Barva, Costa Rica | 10.3 | LP |
| Moody & Francke (1982), Cockendolpher & Francke (1990) | West Texas, USA | 32.8 | MP |
| Munyai & Foord (2012)\* | Soutpansberg, South Africa | -23.0 | D |
| Munyai & Foord (2012)\* | Soutpansberg, South Africa | -23.0 | MP |
| Olson (1994)\* | Bocas del Toro, Panama | 8.8 | MP |
| Sabu et al. (2008) | Western Ghats, India | 11.7 | MP |
| Samson et al. (1997) | Mt Isarog, Philippines | 13.7 | MP |
| Sarnat & Economo (2012) | Fiji | -17.7 | MP |
| Van Pelt (1983) | Chisos Mtns, Texas, USA | 29.3 | MP |
| Wheeler & Wheeler (1986) | Nevada, USA | 38.5 | MP |

*Table 1.*



Figure 1.



Figure 2.



Figure 3.



Figure 4.



Figure 5.

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