# Range size and ant communities across elevations

# Introduction

Patterns of species richness and community composition are directly determined by the distribution 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 macroscale distribution of ant diversity. Elevational gradients provide useful study systems to investigate these patterns and drivers (McCain, 2009a, 2010). Mountains, occurring on every continent, act as compact, globally replicated systems that vary across 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, and at different taxonomic levels, can yield insight into processes affecting ant species diversity across spatiotemporal scales.

Despite comprising the majority of animal species, insects have not received much focus in such macroecological studies (Diniz-Filho et al., 2010). However, with the astonishing array of insect diversity, no picture of biodiversity would be complete without including insects. Furthermore, understanding the processes underlying insect diversity may yield valuable insights into the processes that shape patterns biodiversity more broadly. Ants have a number of advantages for global studies of diversity. As predators, competitors, scavengers, and dispersers, they have major ecological impacts in a wide variety of systems (Hölldobler and Wilson, 1990). In contrast to many insect taxa, the individuals used for identification are wingless, restricting their movement from the nest and reducing the impact of accidentals. Additionally, because of the historic interest across many decades **CITE**, ants are relatively well-described taxonomically compared to other insect taxa. Nevertheless, we know little about the ranges and less about the basic natural history of many species (Lanan, 2014).

Ants are an incredibly diverse taxon by nearly any ecological metric. Dietary breadth ranges from the specialist predator species in the subfamily Amblyoponinae to generalist omnivores in the subfamily Myrmicinae. Nesting habits are variable, with differences in site preferences among genera, among species, and even variability within species **CITE**. Ant species may differ in worker body size **CITE**, colony size **CITE**, colony structure **CITE**, levels of aggression **CITE**, number of queens **CITE**, and degree of polymorphism **CITE** among other traits. Given this tremendous range of biological characteristics, it seems reasonable to expect that factors shaping the distribution of species vary among subfamilies or genera. Additionally, species richness is hugely disparate among subfamilies. In such a diverse and numerically heterogeneous taxon as ants, any patterns of species richness and compositional change may be driven primarily by the most speciose subfamily or genus rather than reflecting the tendencies of each subtaxon.

Understanding the distribution of biodiversity necessitates a comprehensive, global perspective. Here, I review the work to date on ant communities across elevations with specific regard to elevational range sizes, community composition, and species richness. Using well-sampled elevational datasets, I investigate these patterns at the species, genus, and subfamily level.

# Datasets

To identify ant elevational distribution datasets at local spatial scales, I performed a literature search with Web of Knowledge and Google Scholar, using combinations of the keywords 'ant', 'elevation\*', 'altitud\*', 'gradient', 'diversity', and 'insect'. This search primarily returned studies along discrete elevational transects with sampling sites interspersed along the gradient. To identify ant elevational distribution datasets at regional spatial scales, I searched for publications with 'ants of' in the title. This search returned guides to the ant fauna of a particular geopolitical region. Such guides typically compile museum records and collections from many years spread across the region, detailing the recorded occurrences of each ant species in the region. The elevational range of each ant species was interpolated. That is, each species was assumed present between the lowest and highest 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) sufficient, even sampling effort with standardized methods across the gradient; (2) sampling of 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, 1990, 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 found (Appendix). A number of publications used data from the literature or sampled geographically disparate sites, leaving 47 unique 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, and 16 of those provided species-level elevational range data. 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, tropic and temperate zones, mainland and island gradients, and wet and arid climates (Appendix).

I classified the ant elevational richness into five categories using definitions from the literature (McCain, 2009a, 2010). In decreasing patterns, diversity is highest at the lowest elevation and declines steadily with increasing elevation. In low plateau patterns, diversity is consistently high across at least the lowest 300m before declining monotonically. Mid-peaks show highest diversity >300m from the mountain base and with at least 25% greater diversity than at the base. Low plateaus with mid-peaks have highest diversity at least 300m from the base with high diversity across the lowest 300m. In increasing patterns, diversity increases with elevation. No pattern was recorded when none of these definitions were met and the richness showed no consistent pattern across elevations. Though more patterns are possible (McCain, 2009a), the datasets here were characterized well by these five patterns.

# Elevational range size

Temperatures vary across seasons more dramatically in temperate locations than in tropical locations. Consequently, tropical organisms experience a narrower range of temperatures annually and are expected to have narrower thermal tolerances (Janzen, 1967). On mountains, where temperature declines rapidly with elevation, this results in smaller elevational ranges in tropical species (Janzen, 1967; Ghalambor et al., 2006; McCain, 2009b). Latitudinal trends in thermal tolerances and elevational range sizes have been shown in both vertebrate and invertebrate taxa (McCain, 2009b; Sunday et al., 2011; Sheldon and Tewksbury, 2014; Sheldon et al., 2015). Specifically in ants, small elevational range sizes have been noted along several tropical mountains, with many species detected at just one elevation (Olson, 1994; Samson et al., 1997; Fisher, 1998; Brühl et al., 1999; Longino and Colwell, 2011).

However, because the largest possible elevational range size is the entire gradient, comparisons among gradients may be sensitive to gradient height (McCain, 2009b). To minimize the influence of disparate gradient heights, I analysed truncated gradients (McCain, 2009b) in addition to complete gradients (*ncomplete*=16). All datasets were truncated at a certain height and gradients below this threshold were excluded. Mean elevational ranges were then calculated along each truncated gradient. Three truncation heights were used: 1600m (*n*=13), 1800m (*n*=12), and 2000m (*n*=10).

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). Ant elevational ranges do, therefore, appear to be larger in the tropics, consistent with other taxa (McCain, 2009b; Sheldon and Tewksbury, 2014; Sheldon et al., 2015) and with the seasonality hypothesis (Janzen, 1967). Additionally, there is a marginal latitudinal decline in the proportion of species detected in a single elevational band (*n*=16, *P*=0.05, *R2*=0.193). However, this latitudinal trend in elevational range size does not hold at larger taxonomic scales. Neither the mean genus elevational range nor the mean subfamily elevational range change across latitudes (genus: *n*=16, *P*=0.22; subfamily: *n*=16; *P*=0.40). This suggests that, while individual species may be constrained by thermal tolerance, the variability in thermal tolerance among species within each genus is great enough to encompass the increased annual variation at high latitudes.

Because high elevations, like high latitudes, also experience increased climatic variability, the mean elevational range size may increase with elevation (Stevens, 1992). To avoid the disproportionate influence and non-independence of large-ranged species (Rohde et al., 1993; Gaston et al., 1998; McCain and Bracy Knight, 2013), I estimated mean range size at each elevation using both the midpoint method, where mean range size is estimated as the average range of all species whose midpoints occur at that elevation, and the quartile method, which uses only species with ranges < 1/4 of the gradient. (Rohde et al., 1993; McCain and Bracy Knight, 2013). Contrary to expectations, there is little evidence of a consistent trend in ant species range size along elevational gradients using either method (midpoint: increase with *P*< 0.05 in 2/16 gradients, *R2* mean: 0.15, median: 0.03; quartile: increase with *P*< 0.05 in 3/16 gradients, *R2* mean: 0.20, median: 0.14).

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

# Species composition & beta diversity

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). Total beta diversity can be partitioned into turnover and nestedness to compare the proportion of compositional change resulting from the replacement or addition of species, respectively (Baselga, 2010). Turnover and nestedness are likely driven by different processes. Understanding the pattern of each across elevations can clarify the importance of ecological filtering, biotic interactions, and neutral processes **CITE**(Svenning et al., 2011).

To compare gradient-wide beta diversity, I calculated overall beta diversity as (Tuomisto, 2010):

where is the total richness along the gradient and is the average richness of the sampled elevational bands. Because this method is affected by the number of sampled elevational bands, I standardized as:

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

### Species

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 does not vary significantly between tropical and temperate mountains (Fig. 3; Wilcoxon rank sum test: *W*=41, *P*=0.26). Overall, 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). That is, when all pairs of elevations are compared, communities at two different elevations each commonly have distinct species.

This is not the case, however, at a narrower spatial resolution. Rather, nestedness dominates between adjacent elevations along most gradients (STATS). This seemingly contradictory pattern emphasizes the importance of spatial scale to patterns of beta diversity. Comparing sites across the entire gradient, species replace each other and high elevation communities are distinct from low elevation communities. However, this replacement occurs gradually across elevations. Species are more often distributed individually, with overlapping ranges, rather than occurring as distinct abutting communities. In exception, turnover is quite high between adjacent elevations for a large portion of several tropical gradients (Samson et al., 1997; Fisher, 1998; Longino and Colwell, 2011), consistent with a high degree of elevational specialization resulting from some combination of competition and abiotic constraints.

### Genus

At the genus level, declines with latitude (Fig. 2, gray; *n*=16, *P*=0.03, *R2*=0.25). The genus composition changes more rapidly across elevations at lower latitudes, though the trend is weaker than at the species level. The proportion of gradient-wide beta diversity at the genus level due to turnover is significantly higher in temperate regions (Fig. 3; Wilcoxon rank sum test: *W*=49, *P*=0.042). However, there is high variability in the genus turnover proportion among both temperate and tropical gradients; this apparent difference may be spurious. At the gradient scale, genus turnover and genus nestedness are comparable along most gradients (Fig. 3; Paired t-test: *t15*=-0.67, *P*=0.51). When all elevations along a given gradient are compared pairwise, the difference in genus composition results from both the replacement of one genus for another and the loss of genera without replacement.

However, between elevationally adjacent sites, ant genera, like ant species, tend to be nested (STATS) and 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. With common interpretations of turnover and nestedness **CITE**, the high nestedness with low turnover along most gradients suggests that environmental filtering is more important than biotic interactions in determining the ant genus communities across elevations.

### Subfamily

At the subfamily level, shows no relationship with latitude (Fig. 2, white; *n*=16, *P*=0.15, *R2*=0.08). The change in subfamily composition across elevations does not vary consistently with latitude. The proportion of gradient-wide beta diversity due to turnover at the subfamily level is not different between tropical and temperate mountains (Fig. 2b; Wilcoxon rank sum test: *W*=45; *P*=0.08) and 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). That is, subfamilies rarely replace one another among sites, but rather the subfamily composition of each elevation is most often either identical to or a subset of the composition at other elevations.

Between adjacent elevations, there is no subfamily turnover along any gradient. Instead, there is a high degree of elevational overlap among subfamilies, resulting in subfamily communities that are subsets across elevations. Often, subfamilies are progressively excluded as elevation increases, likely due to environmental filtering. With highly nested subfamily communities, there is little evidence for competitive exclusion across elevations at the subfamily level.

Thus, latitudinal trends in elevational beta diversity are contingent on taxonomic level. Community differences across elevations are most extreme between tropical ant species. Furthermore, beta diversity between adjacent elevations declines as taxonomic resolution decreases. The species dissimilarity is higher than genus dissimilarity (stats for *Betagenus* and *Betaspecies*) which, in turn, is higher than subfamily dissimilarity (stats for *Betasubfamily* and *Betagenus*). 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 of taxa. This may occur because of competitive exclusion between congeners across elevations, though heightened sensitivity to abiotic conditions at the species level and consequent elevational specialization could also produce this pattern.

# Richness patterns

### Species richness

In the robust datasets, ant species richness most often peaks at intermediate elevations (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 than that of temperate gradients (Fisher's Exact Test: *n*=20, *P*=0.30). In the excluded datasets, the patterns were more variable. In addition to the mid-peaks, decreases, and low plateaus seen in the robust datasets, there were also gradients with increasing richness and with no identifiable pattern. Furthermore, decreasing patterns were nearly as common as mid-peaks in the excluded datasets. Some of these decreasing patterns, however, are likely an artefact of sampling bias. Of the excluded gradients that detected decreases, the majority did not sample within the lowest 400m, potentially failing to capture the portion of the gradient across which the common patterns differ the most. Ant species richness, therefore, shows a variety of elevational patterns, with richness often highest at intermediate elevations.

### Genus richness

The number of genera across elevations typically mirrors the number of species, with the genus richness pattern the same as the species richness pattern in 11/16 gradients. Moreover, the distribution of genus richness patterns does not differ significantly from the species richness patterns (Fig. 4, gray and black bars; Fisher's Exact Tests: *nspecies*=20, *ngenus*=16, *P*=0.28; *nspecies*=16, *ngenus*=16, *P*=0.39), though there is a tendency for the peak in genus richness to be less pronounced, resulting in several low plateaus with mid peaks that were 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 number of species increases quite predictably with the number of genera (STATS), lending further evidence that the richness patterns are nested taxonomically.

### Subfamily richness

The number of ant subfamilies shows less distinct patterns elevationally than the number of species or genera due to the smaller number of subfamilies, though they are generally coarsely similar to the species and genus richness patterns. The distribution of subfamily richness patterns is not significantly different from that of the species richness patterns (Fig.4, white and black 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 (Fig. 4, gray and black bars; Fisher's Exact Test: *n*=16; *P*=0.84). Like the species and genus patterns, 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 number of subfamilies does predict the number of species (STATS), though of course less reliably than the number of genera.

Ant richness, therefore, is commonly high at intermediate elevations at the species, genus, and subfamily levels. Consequently, it appears that the underlying ecological or evolutionary factors driving richness are creating similar patterns at multiple taxonomic scales. It may seem intuitive that the number of species would increase with the number of genera, though in fact the species community can be over- or underdispersed phylogenetically (Webb et al., 2002), with the degree phylogenetic dispersion possibly arising from a balance between 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 ant species across the many genera and subfamilies along each gradient may be responding similarly to the combination of processes affecting speciation and community assembly. Nonetheless, given the disparate number of species within each ant genus or subfamily, the pattern of species richness across communities on an elevational gradient may simply result from the richness pattern of the most speciose genus or subfamily along the gradient.

# Dominant taxa

### Most speciose genus

The most speciose genus in each dataset comprises 7–31% of the total species richness along the 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 does not vary predictably across latitudes (*n*=16, *P*=0.15, *R2*=0.08).

While the overall richness pattern is predicted well by the richness pattern of the most speciose genus (STATS), the overall pattern is not driven solely by a single genus. Rather, the species richness pattern of the most speciose genus is generally similar to the richness pattern of the remaining species; the richness of the most speciose genus predicts the richness of the remaining genera quite well along most gradients (Fig. 5a; STATS), though there is a fair amount of variability in the slopes among gradients (STATS: slope ranges). Many of the non-dominant genera (at least in terms of richness) do not have enough species or are not widespread enough to reliably discern a richness pattern. Those that are, however, tend to show a qualitatively similar elevational richness pattern both to the overall pattern and to the most speciose genus.

### Most speciose subfamily

The most speciose subfamily along each gradient comprises 39–73% of the total species richness (mean ± SE: 54.5 ± 2.04%). The dominant subfamily in terms of richness is either 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 significant latitudinal trend in the proportion of species in the most speciose subfamily (*n*=16, *P*=0.38, *R2*=0.06).

As with the most speciose genus, the species richness pattern within the most speciose subfamily tends to be remarkably similar to both the overall species richness pattern and the richness pattern of the remaining species (Fig. 5b; STATS). The elevational species richness pattern is not simply the result of the most speciose subfamily. Rather, the dominant subfamily shows the same richness pattern as the remaining subfamilies. As with the richness patterns of individual genera, the richness pattern of each subfamily along a gradient is often qualitatively similar to the overall richness pattern and to the pattern of the most speciose subfamily. The patterns are largely nested.

Ant species richness patterns across elevations are not, therefore, driven by a single genus or a single subfamily. Despite often comprising a sizable proportion of species, the most speciose genus or subfamily along a gradient most often shows a similar richness pattern across elevations as the remaining species. Though there is, of course, variability, the richness pattern within each genus or subfamily tends to be broadly similar to the whole. Moreover, the number of genera tends to correspond with the number of species across elevations. This suggests that the key factors shaping the richness of ants across a given elevational gradient may act on all ant taxa similarly, regardless of ecological differences. In contrast to the dramatic latitudinal differences in beta diversity and elevational range size, ant species richness patterns do not appear to vary consistently with latitude. Thus, while range sizes and changes in species composition are inherently tied to variation in species richness, they perhaps are not as directly related at the scale of elevational gradients.

# Research gaps

Many hypotheses have been proposed as drivers of ant community structure, richness, and diversity along elevational gradients, ranging from current climate to area to competition to habitat structure **CITE**(Pianka, 1966; Willig et al., 2003). However, the consistent and reliable data needed to rigorously evaluate these varied hypotheses are lacking at a broad scale. Habitat complexity, and in particular vegetation structure and leaf litter depth, has been suggested as a potential 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. Additionally, we know little of the basic biology for many species of ants. Dietary, foraging, and nesting habits can vary dramatically within a genus and even within a species **CITE**. Understanding how biotic interactions, such as competition for space or food resources, and changes in their strength across elevations affect ant communities relies on thoroughly detailing behavior across a wide taxonomic variety of ant species. Finally, ant communities can 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

In summary, ant elevational ranges are narrowest at tropical latitudes, leading to higher gradient-wide beta diversity and high species turnover. This trend becomes increasingly less distinct at higher taxonomic levels where elevational ranges become broader and communities become increasingly nested. The elevational species richness patterns, which do not appear to be directly related to turnover, are a conglomerate property across subfamilies and genera rather than just a function of the most speciose subtaxon. The broad similarity of richness patterns along a given gradient, including among species, within and among genera, and within and among subfamilies, suggests that despite large biological differences, similar factors may influence the elevational distribution of ant species across many genera and subfamilies.

# Figure Legends

**Fig. 1** Elevational range sizes of ant species increases with latitude. (a) Both the mean (solid; ± 1 standard error) and median (open) elevational range increases with distance from the equator (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 beta diversity across each elevational gradient, standardized for the number of sampled elevations, declines with latitude (*n*=20, *P*<0.001, *R2*=0.49). That is, the differences among ant species communities across elevations is more extreme in the tropics.

**Fig. 3** Proportion of gradient-wide beta diversity due to turnover decreases with taxonomic resolution. In both temperate (white) and tropic (gray) gradients, the proportion of beta diversity due to turnover decreases at higher taxonomic levels. At 0.5 (dotted line), turnover and nestedness contribute equally to the change in community composition. The ant communities differ primarily due to the sequential addition or loss of taxa across elevations rather than due to the replacement of one taxon with another.

**Fig. 4** Robust patterns of ant elevational richness patterns across taxonomic scales. A variety of species (black, *n*=20) richness patterns 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 Exat 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 gradients (gray lines). There is much variability in the slope of the relationship across gradients and, in one case, a negative relationship. (b) The apparent 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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