# 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). Documenting how ant communities change along elevational gradients, and at different taxonomic levels, may 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; Beck et al., 2012). Given the astonishing array of insect diversity, no picture of biodiversity would be complete without including insects. Ants are particularly valuable 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 with consequently restricted movement from the nest, reducing the impact of accidentals. Additionally, because of the historic interest across many decades, 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 specialist predators 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 differ in worker body size **CITE**, degree of polymorphism **CITE**, colony size **CITE**, colony structure **CITE**, level of aggression **CITE**, and number of queens **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, 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 in ants at the species, genus, and subfamily level, and evaluate latitudinal trends.

# 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 particular geopolitical regions. Such guides typically compile museum records and many years of collections across the region, detailing the recorded occurrences of each ant species. Elevational ranges were 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.

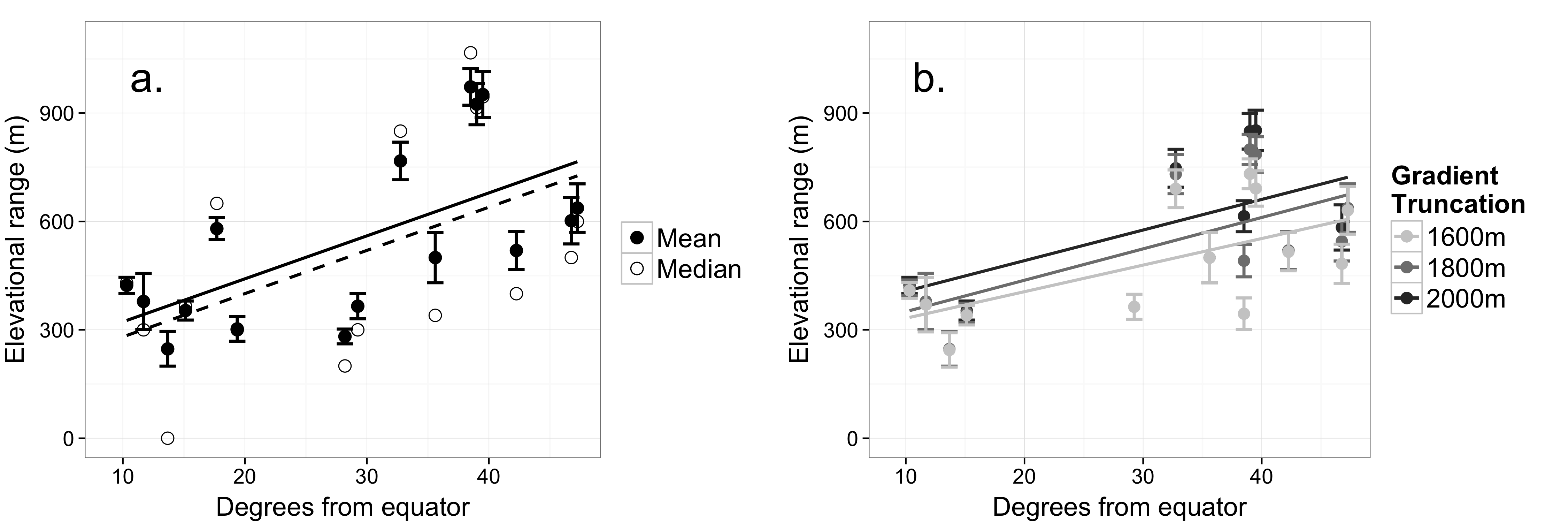
A total of 68 candidate datasets were identified (Appendix). A number of publications used data from the literature or sampled geographically disparate sites, leaving 47 unique datasets that detailed ant distributions or richness within a single region or along a gradient. There were 20 that met all five *a priori* sampling criteria, with 16 of those providing 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, tropical 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, declining steadily with increasing elevation. In low plateau patterns, diversity is consistently high across at least the lowest 300m before declining. 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 likewise have highest diversity at least 300m from the base, but with high diversity across the lowest 300m. In increasing patterns, diversity increases with elevation. No pattern was recorded when the richness showed no consistent pattern across elevations.

# Elevational range size

Seasonal temperature variation is more dramatic 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, 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 detected 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 elevation (Olson, 1994; Samson et al., 1997; Fisher, 1998; Brühl et al., 1999; Longino and Colwell, 2011).

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 analyzed 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 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, 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.

**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 (*n*=16; mean: *P*=0.009, *R2*=0.353; median: *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).

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. 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 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 elevational pattern of each can clarify the importance of ecological filtering, biotic interactions, and neutral processes in structuring ant communities (Svenning et al., 2011).

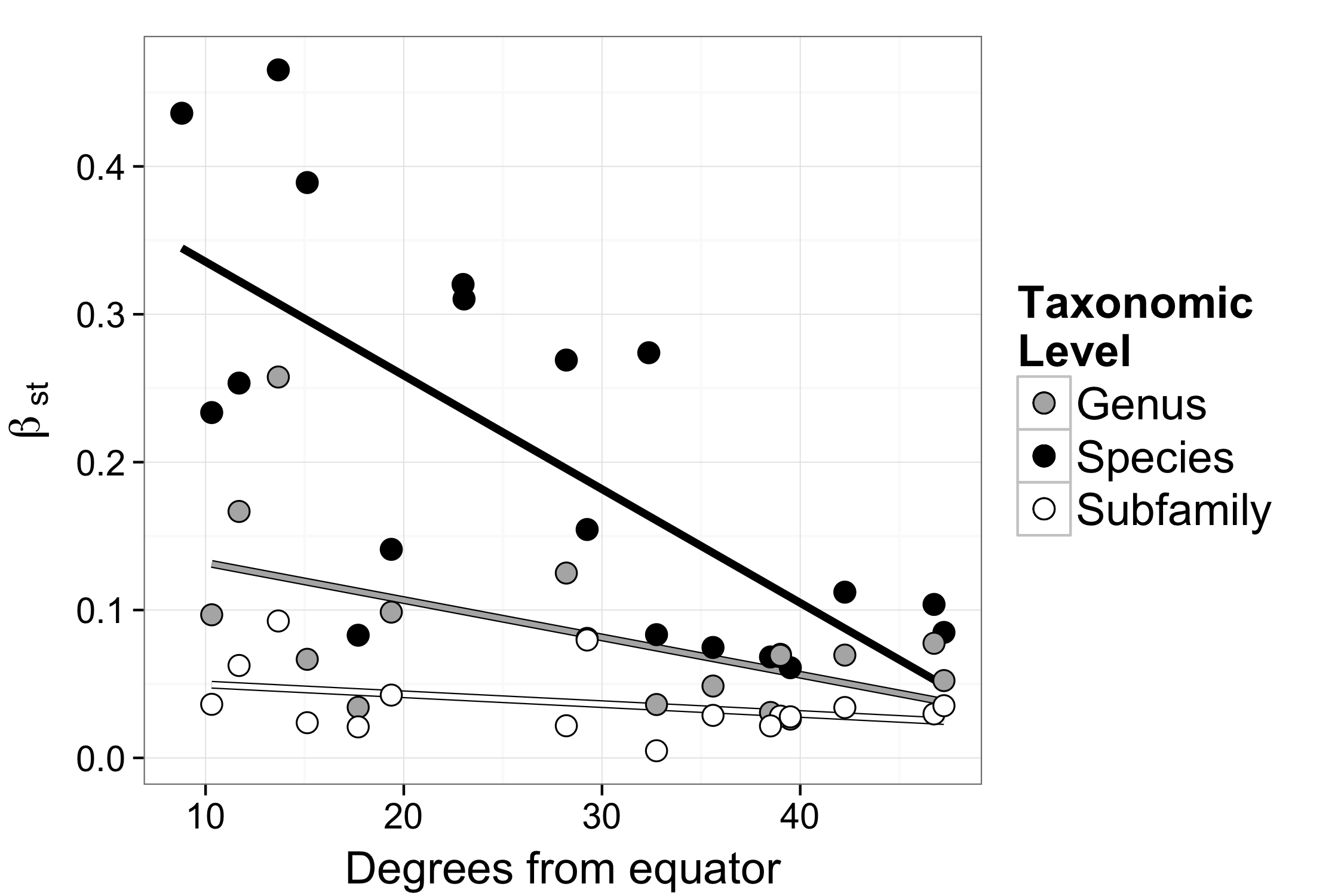
To compare gradient-wide beta diversity, I calculated overall beta diversity as (Tuomisto, 2010):

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:

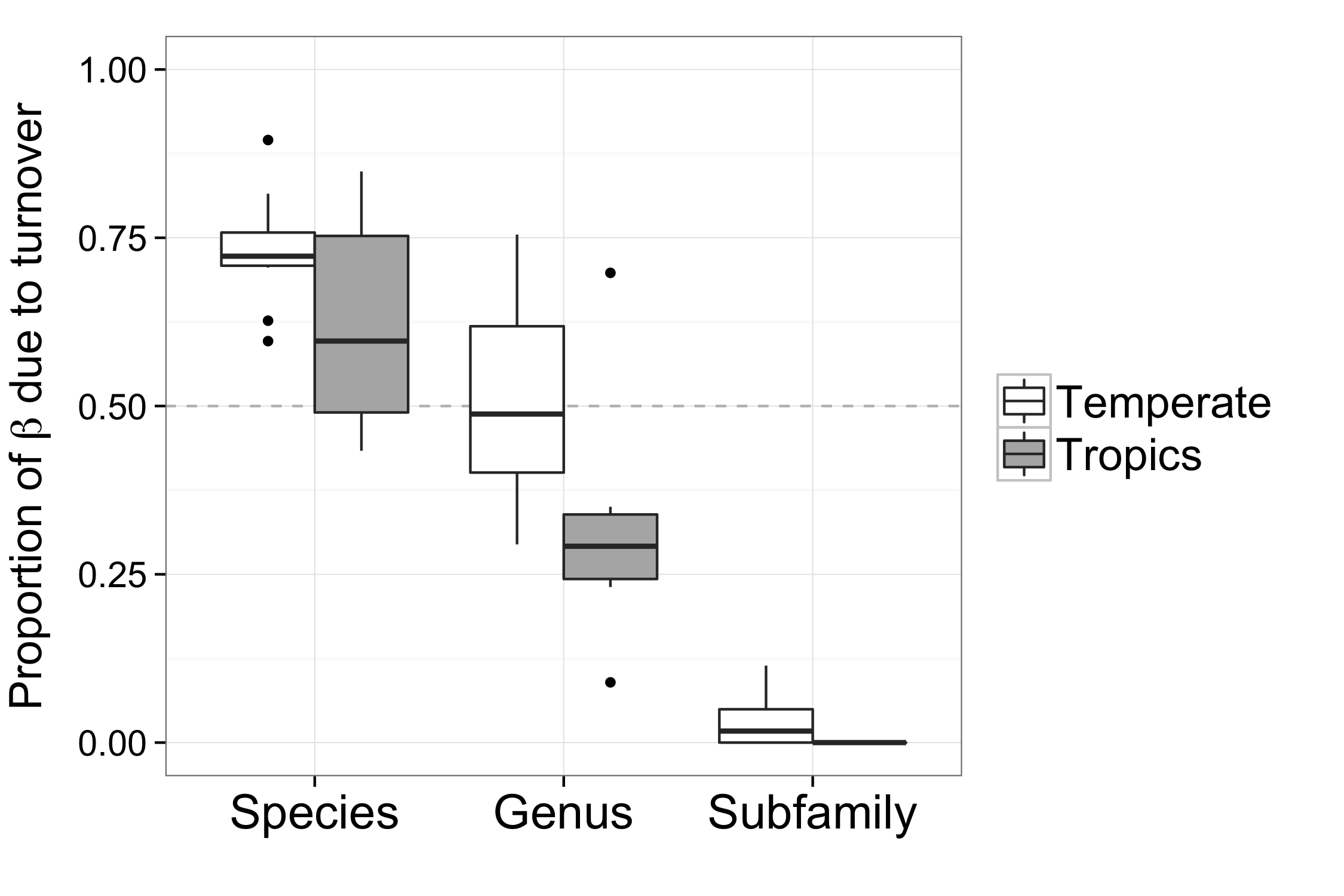
where *N* is the number of elevational bands (Chao et al., 2012). To explore gradient-wide turnover and nestedness as well as the change in ant communities between adjacent sites along each gradient, I used the Sørensen-family metrics in the R package *betapart* to calculate beta diversity, turnover, 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 when comparing not the entire gradient (gradient-wide beta) but changes along the gradient between elevational bands (elevational beta). 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. But 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, gradient-wide beta () also declines with latitude (Fig. 2, gray; *n*=16, *P*=0.03, *R2*=0.25). The genus 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). 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 typically comparable (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.

**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 decreases at higher taxonomic levels. At 0.5 (dotted line), turnover and nestedness contribute equally to the change in community composition.

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.

### Subfamily

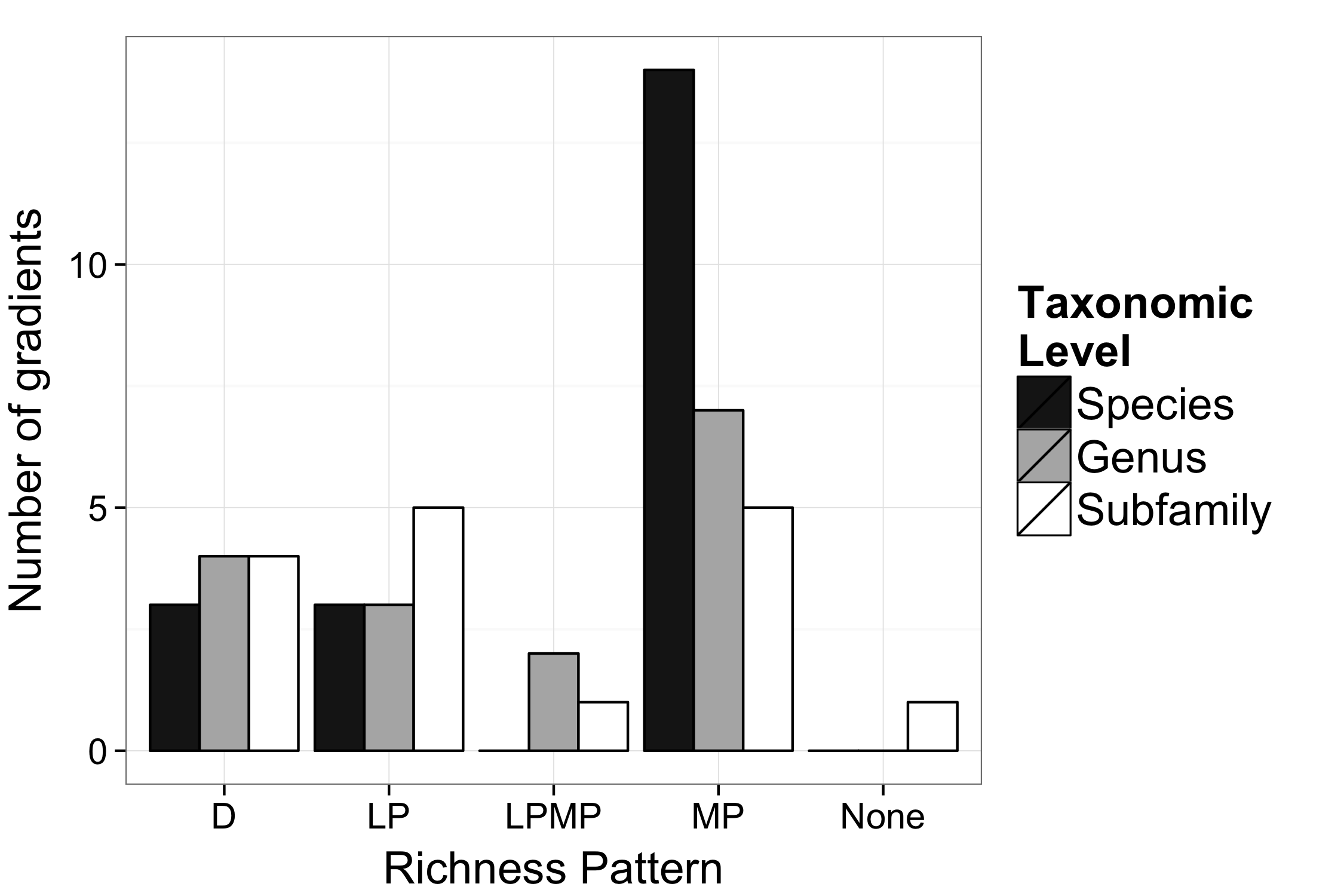
At the subfamily level, shows no relationship with latitude (Fig. 2, white; *n*=16, *P*=0.15, *R2*=0.08). The change in subfamily composition across elevations does not vary consistently with latitude. The proportion of gradient-wide subfamily beta diversity due to turnover is not different between tropical 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 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 communities that are subsets across elevations. Often, subfamilies are progressively excluded at higher elevations, 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

Ant species richness shows a variety of patterns across elevational gradients. In the robust datasets, 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 from that of temperate gradients (Fisher's Exact Test: *n*=20, *P*=0.30). In the excluded datasets, the patterns are more variable, with mid-peaks, decreases, low plateaus, increases, and no identifiable pattern reported. Furthermore, decreasing patterns were roughly as common as mid-peaks in these datasets. This is likely an artefact of sampling bias, however. Of the excluded gradients detecting decreases, the majority did not sample within the lowest 400m, failing to capture the portion of the gradient where the common patterns differ the most. At the species level, therefore, ant elevational richness is variable among mountain ranges, though frequently highest at intermediate elevations.

### Genus richness

**Fig. 4** Robust patterns of ant elevational richness patterns across taxonomic scales. 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).

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 11/16 gradients. Moreover, 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), though there is a tendency for the peak in genus richness to be less pronounced, resulting in several low plateaus with mid-peaks 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 ant richness patterns are similar at the species and genus scales.

### Subfamily richness

The richness pattern of ant subfamilies along each gradient is coarsely similar to the species and genus richness patterns, though the patterns are 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 number of subfamilies does predict the number of species (STATS), though less reliably than does the number of genera.

Ant richness, therefore, is often high at intermediate elevations whether measured at the species, genus, or subfamily level. Consequently, it appears that the underlying ecological or evolutionary factors driving richness are creating similar patterns at multiple taxonomic scales. While it may seem intuitive that the number of species would increase with the number of genera, in fact species communities can be over- or under-dispersed phylogenetically (Webb et al., 2002), with the degree phylogenetic dispersion likely arising 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 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 may simply result from the richness pattern of the most speciose genus or subfamily along the gradient.

# Dominant taxa

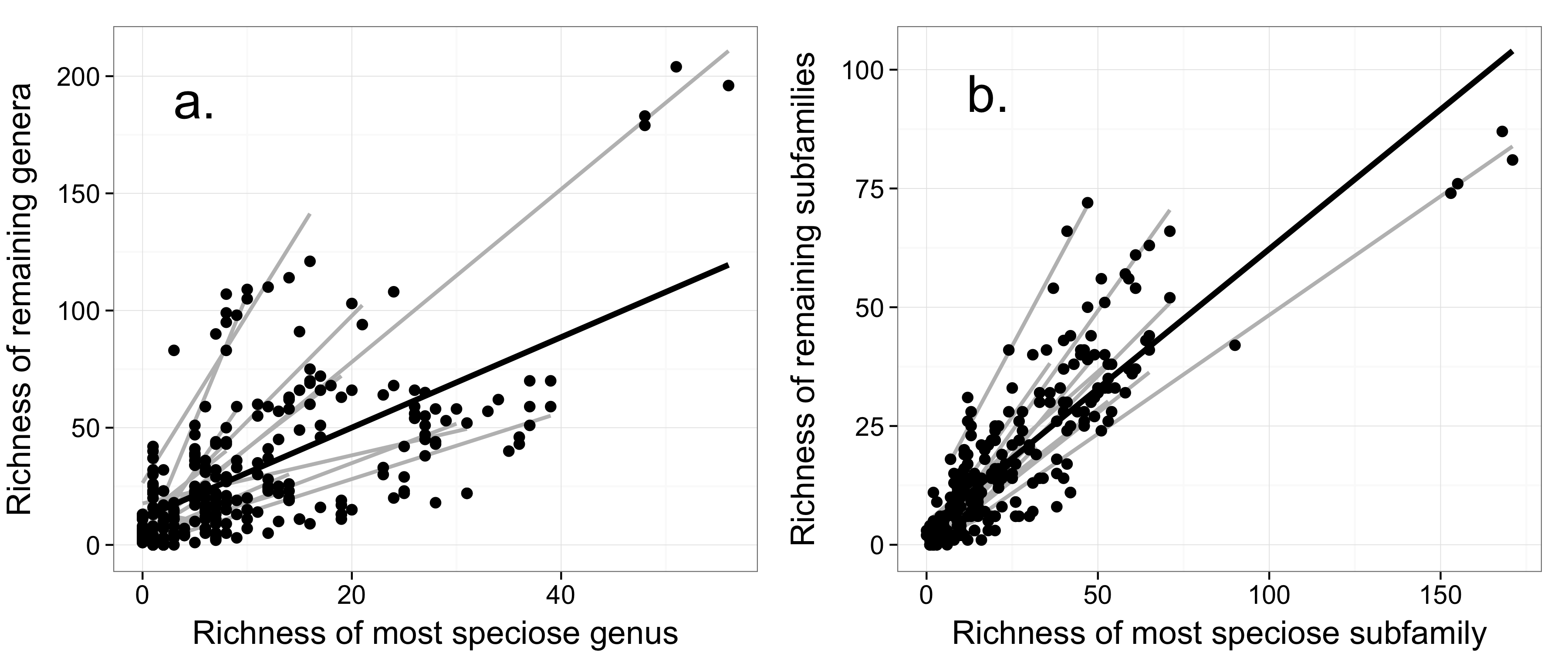
### Most speciose genus

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 that 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).

The species richness of the most speciose genus, of course, strongly predicts richness across elevations (STATS). However, the overall pattern is not driven solely by this single genus. Instead, the species richness pattern of the most speciose genus is typically similar to the richness pattern of the remaining species. Along most gradients, the richness of the most speciose genus predicts the richness of the remaining genera quite well (Fig. 5a; STATS), though the relationship is variable among gradients (STATS: slope ranges). Many of the non-dominant genera are neither speciose nor widespread enough to reliably discern a species richness pattern. Those that are, however, tend to show a qualitatively similar elevational richness pattern both to the overall pattern and to that of the most speciose genus.

### 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 within the most speciose subfamily is remarkably similar across elevations both to the richness of all species (STATS) and to the richness of species in non-dominant subfamilies (Fig. 5b; STATS). Thus, 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. Furthermore, the richness pattern of each subfamily is often qualitatively similar to the overall richness pattern and to the pattern of the most speciose subfamily.

**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, 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.

Ant species richness patterns across elevations are not, therefore, driven by a single subtaxon, but rather emerge from the congruent, nested richness patterns of each genus and subfamily. The richness pattern within each subtaxon tends to be broadly similar to that of the whole. Moreover, the number of genera and, to a lesser extent, the number of subfamilies 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 the majority of ant taxa similarly, regardless of ecological differences. Thus, while range sizes and changes in species composition are inherently tied to variation in species richness, they perhaps are not as directly relevant to richness patterns 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 (Pianka, 1966; Willig et al., 2003). However, the consistent and reliable data needed to rigorously evaluate many of thesehypotheses are lacking at a broad scale. Habitat complexity, and in particular 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. 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.

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# References

Allred, D. 1982. Ants of Utah. *The Great Basin Naturalist* **42**: 415–511

Anderson, M.J., Crist, T.O., Chase, J.M., Vellend, M., Inouye, B.D., Freestone, A.L., Sanders, N.J., Cornell, H.V., Comita, L.S., Davies, K.F., Harrison, S.P., Kraft, N.J.B., Stegen, J.C., Swenson, N.G., and Others 2011. Navigating the multiple meanings of beta diversity: a roadmap for the practicing ecologist. *Ecology Letters* **14**: 19–28

Araújo, L.L., and Fernandes, G.G. 2003. Altitudinal patterns in a tropical ant assemblage and variation in species richness between habitats. *Lundiana* **4**: 103–109

Baselga, A. 2010. Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography* **19**: 134–143

Baselga, A. 2012. The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. *Global Ecology and Biogeography* **21**: 1223–1232

Baselga, A., and Orme, C.D.L. 2012. Betapart: An R package for the study of beta diversity. *Methods in Ecology and Evolution* **3**: 808–812

Beck, J., Ballesteros-Mejia, L., Buchmann, C.M., Dengler, J., Fritz, S.A., Gruber, B., Hof, C., Jansen, F., Knapp, S., Kreft, H., Schneider, A.-K., Winter, M., and Dormann, C.F. 2012. What’s on the horizon for macroecology? *Ecography* **35**: 673–683

Bharti, H., Sharma, Y., Bharti, M., and Pfeiffer, M. 2013. Ant species richness, endemicity and functional groups, along an elevational gradient in the Himalayas. *Asian Myrmecology* **5**: 79–101

Bishop, T.R., Robertson, M.P., Rensburg, B.J. van, and Parr, C.L. 2014. Elevation-diversity patterns through space and time: Ant communities of the Maloti-Drakensberg Mountains of southern Africa

Brühl, C.A., Mohamed, M., and Linsenmair, K.E. 1999. Altitudinal distribution of leaf litter ants along a transect in primary forests on Mount Kinabalu, Sabah, Malaysia. *Journal of Tropical Ecology* **15**: 265–277

Burwell, C., and Nakamura, A. 2011. Distribution of ant species along an altitudinal transect in continuous rainforest in subtropical Queensland, Australia. *Memoirs of the Queensland Museum* **55**: 391–412

Chao, A., Chiu, C.H., Hsieh, T.C., and Inouye, B.D. 2012. Proposing a resolution to debates on diversity partitioning. *Ecology* **93**: 2037–2051

Diniz-Filho, J.A.F., De Marco, P., and Hawkins, B.A. 2010. Defying the curse of ignorance: perspectives in insect macroecology and conservation biogeography. *Insect Conservation and Diversity* **3**: 172–179

Fisher, B. 1998. Ant diversity patterns along an elevational gradient in the Réserve Spéciale d’Anjanaharibe-Sud and on the western Masoala Peninsula, Madagascar. *Fieldiana Zoology* **90**: 39–67

Gaston, K.J., Blackburn, T.M., and Spicer, J.I. 1998. Rapoport’s rule: Time for an epitaph? *Trends in Ecology and Evolution* **13**: 70–74

Ghalambor, C.K., Huey, R.B., Martin, P.R., Tewksbury, J.J., and Wang, G. 2006. Are mountain passes higher in the tropics? Janzen’s hypothesis revisited. *Integrative and Comparative Biology* **46**: 5–17

Glaser, F. 2006. Biogeography, diversity, and vertical distribution of ants (Hymenoptera: Formicidae) in Vorarlberg, Austria. *Myrmecological News* **8**: 263–270

Gregg, R. 1963. *The Ants of Colorado*. University of Colorado Press, Denver, CO

Hellrigl, K. 2003. Faunistik der Ameisen und Wildbienen Südtirols (Hymenoptera: Formicidae et Apoidea). *Gredleriana* **3**: 143–208

Hölldobler, B., and Wilson, E.O. 1990. *The Ants*. Belknap Press of Harvard University Press, Cambridge

Janzen, D.H. 1967. Why Mountain Passes are Higher in the Tropics

Karaman, M. 2011. Zoogeography, diversity and altitudinal distribution of ants (Hymenoptera: Formicidae) in the Mediterranean and the oro-Mediterranean parts of Montenegro. *North-Western Journal of Zoology* **7**: 26–34

Kembel, S.W., and Hubbell, S.P. 2006. The phylogenetic structure of a neotropical forest tree community. *Ecology* **87**: 86–99

Lanan, M. 2014. Spatiotemporal resource distribution and foraging strategies of ants (Hymenoptera: Formicidae). *Myrmecological News* **20**: 53–70

Lassau, S., and Hochuli, D. 2004. Effects of habitat complexity on ant assemblages. *Ecography* **2**: 157–164

Legendre, P. 2014. Interpreting the replacement and richness difference components of beta diversity. *Global Ecology and Biogeography* 1–11

Lessard, J.J., Dunn, R.R., Parker, C.C., and Sanders, N.N. 2007. Rarity and diversity in forest ant assemblages of Great Smoky Mountains National Park. *Southeastern Naturalist* **0**: 215–228

Lomolino, M. 2001. Elevation gradients of species-density: historical and prospective views. *Global Ecology and Biogeography* **10**: 3–13

Longino, J.T., and Colwell, R.K. 2011. Density compensation, species composition, and richness of ants on a neotropical elevational gradient. *Ecosphere* **2**: art29

Machac, A., Janda, M., Dunn, R.R., and Sanders, N.J. 2011. Elevational gradients in phylogenetic structure of ant communities reveal the interplay of biotic and abiotic constraints on diversity. *Ecography* **34**: 364–371

McCain, C.M. 2005. Elevational gradients in diversity of small mammals. *Ecology* **86**: 366–372

McCain, C.M. 2009a. Global analysis of bird elevational diversity. *Global Ecology and Biogeography* **18**: 346–360

McCain, C.M. 2009b. Vertebrate range sizes indicate that mountains may be ‘higher’in the tropics. *Ecology Letters* **12**: 550–560

McCain, C.M. 2010. Global analysis of reptile elevational diversity. *Global Ecology and Biogeography* **19**: 541–553

McCain, C.M., and Bracy Knight, K. 2013. Elevational Rapoport’s rule is not pervasive on mountains. *Global Ecology and Biogeography* **22**: 750–759

McCain, C.M., and Grytnes, J.A. 2010. Elevational gradients in species richness. In: *Encyclopedia of Life Sciences*, pp. 1–10

McCoy, E. 1990. The distribution of insects along elevational gradients. *Oikos* **58**: 313–322

McCoy, E. 2002. The “veiled gradients” problem in ecology. *Oikos* **99**: 189–192

Moody, J., and Francke, O.F. 1982. *The ants (Hymenoptera, Formicidae) of western Texas Part I. Subfamily Myrmicinae*. Texas Tech Press, Lubbock, TX

Munyai, T.C., and Foord, S.H. 2012. Ants on a mountain: spatial, environmental and habitat associations along an altitudinal transect in a centre of endemism. *Journal of Insect Conservation* **16**: 677–695

Nogués-Bravo, D., Araújo, M.B., Romdal, T., and Rahbek, C. 2008. Scale effects and human impact on the elevational species richness gradients. *Nature* **453**: 216–219

Olson, D.M. 1994. The distribution of leaf litter invertebrates along a neotropical altitudinal gradient. *Journal of Tropical Ecology* **10**: 129–150

Pacheco, R., and Vasconcelos, H.L. 2011. Habitat diversity enhances ant diversity in a naturally heterogeneous Brazilian landscape. *Biodiversity and Conservation* **21**: 797–809

Pianka, E. 1966. Latitudinal gradients in species diversity: a review of concepts. *American Naturalist* **100**: 33–46

Rahbek, C. 1995. The elevational gradient of species richness: a uniform pattern? *Ecography* **18**: 200–205

Rahbek, C. 2005. The role of spatial scale and the perception of large-scale species-richness patterns. *Ecology Letters* **8**: 224–239

Rohde, K., Heap, M., and Heap, D. 1993. Rapoport’s Rule Does Not Apply to Marine Teleosts and Cannot Explain Latitudinal Gradients in Species Richness

Sabu, T., Vineesh, P., and Vinod, K. 2008. Diversity of forest litter-inhabiting ants along elevations in the Wayanad region of the Western Ghats. *Journal of Insect Science* **8**: 1–14

Samson, D.A., Rickart, E.A., and Gonzales, P.C. 1997. Ant diversity and abundance along an elevational gradient in the Phillippines. *Biotropica* **29**: 349–363

Sanders, N. 2002. Elevational gradients in ant species richness: area, geometry, and Rapoport’s rule. *Ecography* **1**: 25–32

Sarnat, E., and Economo, E. 2012. *The ants of Fiji*. UC Publications in Entomology, University of California Press, Berkeley; Los Angeles, CA

Sarty, M., Abbott, K.L., and Lester, P.J. 2006. Habitat complexity facilitates coexistence in a tropical ant community. *Oecologia* **149**: 465–473

Sheldon, K.S., and Tewksbury, J.J. 2014. The impact of seasonality in temperature on thermal tolerance and elevational range size. *Ecology* **95**: 2134–2143

Sheldon, K.S., Leaché, A.D., and Cruz, F.B. 2015. The influence of temperature seasonality on elevational range size across latitude : a test using Liolaemus lizards. *Global Ecology and Biogeography* n/a–a

Smith, M.A., Hallwachs, W., and Janzen, D.H. 2014. Diversity and phylogenetic community structure of ants along a Costa Rican elevational gradient. *Ecography* no–o

Stevens, G.C. 1992. The Elevational Gradient in Altitudinal Range: An Extension of Rapoport’s Latitudinal Rule to Altitude. *The American Naturalist* **140**: 893–911

Sunday, J.M., Bates, A.E., and Dulvy, N.K. 2011. Global analysis of thermal tolerance and latitude in ectotherms. *Proceedings. Biological Sciences / The Royal Society* **278**: 1823–1830

Svenning, J.-C., Fløjgaard, C., and Baselga, A. 2011. Climate, history and neutrality as drivers of mammal beta diversity in Europe: insights from multiscale deconstruction. *The Journal of Animal Ecology* **80**: 393–402

Tuomisto, H. 2010. A consistent terminology for quantifying species diversity? Yes, it does exist. *Oecologia* **164**: 853–860

Van Pelt, A. 1983. Southwestern Association of Naturalists Ants of the Chisos Mountains, Texas (Hymenoptera: Formicidae). *The Southwestern Naturalist* **28**: 137–142

Webb, C., Ackerly, D., McPeek, M., and Donoghue, M. 2002. Phylogenies and community ecology. *Annual Review of Ecology and Systematics* **33**: 475–505

Wheeler, G., and Wheeler, J. 1986. *The ants of Nevada*. Natural History Museum of Los Angeles County, Los Angeles, CA

Willig, M., Kaufman, D., and Stevens, R. 2003. Latitudinal gradients of biodiversity: Pattern, process, scale, and synthesis. *Annual Review of Ecology, Evolution, and Systematics* **34**: 273–309