**Article type:** Synthesis

**Article title:** Global analysis of ant elevational diversity

**Author names:** Tim Szewczyk1 and Christy M. McCain1,2

**Author research addresses:**

1Department of Ecology & Evolutionary Biology, University of Colorado, Boulder, CO 80309, USA

2CU Museum of Natural History, University of Colorado, Boulder, CO 80309, USA

**Correspondence author:** Tim Szewczyk

**Correspondence address:** MCOL 265 UCB, University of Colorado, Boulder, CO 80309-0265

**Correspondence e-mail**: timothy.szewczyk@colorado.edu

**Running head:** Ant elevational diversity

**Word count:** Abstract, body, & references: 6,782 words; abstract: 290 words

**Estimated pages required for figures:** 2

**Number of figures:** 5

**Number of tables:** 0

**Supplementary appendices:** 2

**For submission to:** *Journal of Biogeography*

**ABSTRACT**

**Aim** Ant diversity, like the diversity of many ectothermic insect taxa, is commonly thought to decrease with elevation. Here we use published data on ant diversity across elevational gradients to detail the observed diversity patterns and to test the predictions and interactions of four major diversity hypotheses: thermal energy, the mid-domain effect, area, and the elevational climate model.

**Location** Twenty elevational gradients from mountains across the globe.

**Methods** Of sixty-six published datasets taken from the literature, only those with standardized, comprehensive sampling were used. Datasets included both local and regional ant diversity and spanned 80º in latitude across six biogeographical provinces. We used a combination of simulations, linear regressions, and non-parametric statistics to test multiple quantitative predictions of each hypothesis. We used an environmentally and geometrically constrained model to test their interactions.

**Results** Ant diversity showed three distinct patterns across elevations: hump-shaped mid-elevation peaks in diversity are the most common pattern followed by low-elevation plateaus and monotonic decreases. The elevational climate model, which proposes that a combination of temperature and precipitation drives diversity, and area were partially supported as independent drivers. Thermal energy and the mid-domain effect were not supported as primary drivers of ant diversity globally. The interactions model supported the influence of multiple drivers, though not a consistent set of drivers. The complexity of the best fit environmental model was dependent on the level of precipitation.

**Main Conclusions** Well-sampled datasets show that ant diversity is predominantly highest at middle elevations. In contrast to many vertebrate taxa, global ant elevational diversity patterns are not driven by a simple combination of factors, but rather a complex interplay contingent on precipitation levels. Differences in ecology and natural history among taxa may be crucial to the processes influencing broad-scale diversity patterns.

**Keywords** EGCM, elevational climate model, environmentally geometrically constrained model, environmental gradient, Formicidae, insect, mid-domain effect, species area relationship, species richness, temperature

**INTRODUCTION**

Over the last two decades, a resurgence of interest in the patterns and drivers of diversity has shown that elevational diversity is quite variable within and among taxa (Rahbek, 1995; Brown, 2001; Bhattarai et al., 2004; McCain, 2009). Myriad hypotheses have been proposed to explain these broad-scale patterns (Pianka, 1966; Gaston, 2000). Global analyses of the diversity of vertebrate and plant taxa suggest some combination of the taxon's biology (Grytnes, 2003; McCain, 2009, 2010), geometric constraints (Rahbek, 1997), and the current climate (McCain, 2005, 2007a). In contrast, ant diversity is still thought to most often decrease with elevation, with other patterns viewed as exceptions (e.g., Fisher, 1998; Brühl et al., 1999; Malsch et al., 2008; Dunn et al., 2010; but see Burwell & Nakamura, 2011). Neither this general assumption nor the drivers of ant diversity have been tested rigorously across replicated gradients.

Elevational gradients provide compact, globally replicated systems for assessing the relative support for hypothesized diversity drivers (Rahbek, 1995; Lomolino, 2001; McCain & Grytnes, 2010). Because mountain ranges vary in characteristics such as climate and area distribution, comparisons among mountain ranges decouple variables and constraints (Lomolino, 2001). Global elevational gradients thus provide a robust system for evaluating diversity patterns and drivers (Lomolino, 2001; McCain, 2007a).

Though most focus has been on vertebrate and plant taxa, the majority of animal species are insects (McCoy, 1990; Beck & Chey, 2008; Diniz-Filho et al., 2010; Brehm et al., 2013). Ants in particular are ecologically diverse, relatively well-described, and include competitors, predators, scavengers, and seed-dispersers (Hölldobler & Wilson, 1990; Lach et al., 2010). Unlike most insect taxa, the ants used in species-level identifications are wingless workers. Their restricted mobility heavily reduces the impact of windblown accidentals in estimating a species' elevational range. Despite the diversity and ecological importance of insects and ants, there is little comprehensive understanding of their elevational or latitudinal diversity patterns (Rahbek, 2005; Diniz-Filho et al., 2010; McCain & Grytnes, 2010). Several factors have been implicated as drivers of ant diversity along elevational gradients, although no systematic testing of single factors or the complexity of their interactions exists to date.

**Hypotheses**

*Thermal Energy*

Thermal energy has seen support as a driver of ant diversity (Sanders et al., 2007; Malsch et al., 2008) with several proposed mechanisms. Warmer temperatures may allow longer foraging periods (Hölldobler & Wilson, 1990) or increased food resources through increased productivity (Kaspari et al., 2000). Alternatively, the metabolic theory of ecology (MTE) posits that metabolic rates drive ecological and evolutionary processes. Metabolic rates and chemical reactions increase with temperature, so speciation may increase correspondingly (Allen et al., 2002; Brown et al., 2004). Regardless of mechanism, temperature-based hypotheses all predict a close relationship between temperature and diversity across the elevational gradient (Pianka, 1966; Kaspari et al., 2000; Allen et al., 2002). Because temperature declines on average 6ºC for each 1000m gained in elevation (Barry, 1992), these hypotheses predict a corresponding monotonic decline in diversity from the mountain base to the summit.

*Mid-domain Effect*

The mid-domain effect (MDE) is a null model based on the geometric constraints imposed by a bounded domain (Colwell & Hurtt, 1994; Colwell & Lees, 2000). On elevational gradients, the simulated random placement of observed elevational ranges between the mountain base and summit results in highest diversity at the middle elevation with symmetric declines toward each boundary (Colwell & Lees, 2000; McCain, 2004; Dunn et al., 2007). If ant elevational diversity is driven by the MDE, such simulations should predict empirical diversity and mean range size across the gradient (Arita, 2005).

*Area*

The geographical area hypothesis, based on the species-area relationship, predicts that as the area in an elevational band increases, diversity in that band should increase (Terborgh, 1973; Rosenzweig, 1992). Typically, this relationship is linear on a log-log scale (Rosenzweig, 1995; Rahbek, 1997; McCain, 2007b). Over broad spatial scales, larger areas allow for larger ranges, decreasing extinction probability and increasing speciation probability through the introduction of a barrier (Rosenzweig, 1995 and references therein). Over narrow spatiotemporal scales, larger areas will likely include more habitats, increasing the probability of detecting additional species from adjacent habitats (Terborgh, 1973; Rosenzweig, 1995; Romdal & Grytnes, 2007). However, the effect of area may be greater over larger spatial scales since sampling area is standardized in local studies (McCain, 2007b; Karger et al., 2011).

*Elevational Climate Model*

The elevational climate model (ECM) approximates productivity and proposes that the combination of temperature and precipitation drives diversity, predicting highest diversity at the warmest, wettest elevations (McCain, 2007a). The diversity pattern predicted by the ECM consequently depends on the local mountain climate. On arid mountains, water availability is typically highest at middle elevations due to the dry climate at the base and increased runoff toward the summit (Mollhagen & Bogan, 1997; Brown, 2001). Thus, water limitation restricts diversity toward the base while temperature restricts diversity toward the summit, resulting in a mid-elevation diversity peak. On mountains in wet climates water is plentiful, so temperature drives diversity, resulting in highest diversity at the base and declining diversity toward the summit (McCain, 2007a). The ECM offers testable predictions while fine-scale, reliable global productivity data are lacking.

Our aim is a synthetic understanding of both the patterns in elevational ant diversity and what environmental factors, independently and simultaneously, are key drivers of ant diversity. We first test the common assumption that ant diversity decreases with increasing elevation by reanalyzing published studies of montane ant diversity. We also assess the impact of sampling completeness and bias, such as undersampling at low elevations, elevationally-biased sampling, and large-scale deforestation effects (McCain, 2005; Nogués-Bravo et al., 2008; McCain & Grytnes, 2010). With well-sampled ant datasets, we evaluate various predictions of diversity theory, including energetic, mid-domain effect, area, climate hypotheses, and their interactions.

**MATERIALS AND METHODS**

**Data**

To identify local-scale datasets of ant diversity along elevational transects, we conducted literature searches (2012-2013) using combinations of 'ant', 'elevation(-al)', 'altitud(-inal)', 'gradient', 'diversity', and 'insect' as keywords using Web of Knowledge and Google Scholar. To locate regional-scale datasets of ant diversity, we searched for publications with 'ants of' in the title; this search returned guides to the ant fauna of a geopolitical region, typically compiled from museum records and data collected over many years, detailing each recorded occurrence of each ant species in that region.

To identify robust datasets, we required that a study describe ant diversity along an elevational gradient or within a mountainous region and meet five *a priori* criteria: (1) high sampling effort with standardized methods across elevations; (2) sampling of ≥ 70% of the elevational gradient; (3) sampling within the lowest 400m of the gradient; (4) no sampling gaps > 500m in elevation; and (5) relatively little anthropogenic disturbance (e.g., widespread deforestation). These criteria were adapted from previous studies (e.g., McCain, 2009, 2010) and are necessary to ensure an accurate description of the naturally occurring pattern (McCoy, 1990, 2002; McCain, 2005; Rahbek, 2005; Nogués-Bravo et al., 2008; McCain & Grytnes, 2010). Because the diversity patterns differ primarily across the lower portion of the mountain (Fig. 1), violations of the second criterion were allowed when the unsampled region was primarily at high elevations where declining diversity had been sufficiently demonstrated.

Elevational ranges of ant species in each study were interpolated. That is, a species was assumed present at all elevations between the lowest and highest observed elevations. Although interpolation may artificially inflate the reported diversity at middle elevations (Grytnes & Vetaas, 2002), the majority of species in these datasets were detected at all sampled elevational bands within their elevational range. The impact of interpolation was minimal and did not alter any overall diversity patterns. We therefore employed interpolation uniformly. Each elevational gradient was divided into 100m bands (i.e., 0−99m, 100−199m, etc.), and diversity was estimated as the number of species' ranges in each band.

Sampling methods varied among studies, though most used mini-Winkler traps, pitfall traps, or both (Appendix S1). If authors reported data from both standardized and non-standardized methods (e.g., haphazard hand collection), only the former was included in this reanalysis. In some cases, authors reported diversity based on rarefaction methods. While rarefaction better accounts for rare or difficult to detect species and may allow more accurate comparisons (Colwell & Coddington, 1994; Gotelli & Colwell, 2001; Chao & Jost, 2012), many studies did not report these values and did not provide sufficient information for their calculation. Additionally, rarefied richness does not allow for hypothesis testing using species ranges (e.g., MDE). Therefore, we used only interpolated diversity.

Ant elevational diversity was classified into five broad patterns using previous definitions (Fig. 1)(McCain, 2009, 2010). Decreasing patterns show highest diversity in the lowest elevational band with diversity declining as elevation increases. Low plateaus have consistently high diversity across at least the lowest 300m followed by a monotonic decline in diversity. Mid-elevation peaks have the highest diversity at middle elevations (> 300m from the base) and with 25% greater diversity than at the base. Increasing patterns have increasing diversity with increasing elevation. Lastly, no pattern was detected when none of these definitions was met. More patterns are possible (McCain, 2009), but the observed ant patterns were characterized by these five classifications.

For area analyses, digital elevation models (DEMs) were downloaded from CGIAR-CSI (srtm.csi.cgiar.org). These rasters are derived from the USGS/NASA SRTM data at ~90m x 90m resolution with a vertical error of < 16m. Using ArcGIS, rasters were converted into an Albers Equal Area projection centred on each study site. For regional studies, the boundary of the study area was the corresponding geopolitical region. For local studies, the study area boundary was determined by using mountain ridges and major watersheds to isolate the focal mountain within a 30km buffer around the sampling locations (McCain, 2007b). Alternative delineation methods and buffer sizes did not qualitatively alter area profiles. To estimate the area within each 100m elevational band, we calculated the area of the hypotenuse plane of each raster cell and then, within each 100m band, summed the calculated areas of all cells.

Rasters of climate data at 1km x 1km resolution were downloaded from WorldClim (worldclim.org) and converted into Albers Equal Area projections as above. Only mean annual temperature and annual precipitation were used because of high collinearity among other variables. Though the resolution is relatively coarse, the quality was consistent at a global scale. Additionally, finer resolution would likely have little qualitative effect because the climatic variables were averaged within each 100m band in a study area. Studies were classified into two broad climate categories based on the climate of the mountain base (arid: humidity index < 0.5, wet: humidity index > 0.5; UNEP's (1997) World Atlas of Desertification).

**Hypothesis Tests**

*Thermal Energy*

If thermal energy is the primary driver of ant diversity, then diversity should decline monotonically on each elevational gradient, mirroring the declining temperature. Decreasing patterns should consequently be most common regardless of other mountain characteristics. Simple linear regressions were used to test for a positive, linear relationship between mean annual temperature and diversity for each study. Two predictions of the metabolic theory of ecology (MTE) were tested: (1) a linear relationship according to the equation *ln(S) = b\*(kT)-1 + c*, where *S* is the diversity within an elevational band, *k* is Boltzmann's constant (*k = 8.62x10-5 eV\*K-1*), and *T* is the annual mean temperature in Kelvin, and (2) a slope of -0.7 < *b* < -0.6 (Brown et al., 2004; Hawkins et al., 2007a; McCain & Sanders, 2010). To test the MTE predictions, we followed the methods of Hawkins *et al.* (2007a) and McCain & Sanders (2010), combining all ant datasets and using a simple linear regression. All temperature analyses were repeated using area-standardized diversity (below).

*Mid-domain Effect*

To test the MDE predictions, we randomized the placement of elevational ranges using the observed range size distribution within the boundaries of each elevational gradient (R Development Core Team 2012). Four studies did not provide the elevational range of each species and were not included in tests of the MDE predictions (Appendix S1). In 100,000 simulations for each study, we calculated diversity as the number of ranges occurring in each elevational band and mean range size as the average size of those ranges. The predictive ability of the MDE was assessed with simple linear regressions of the observed and mean predicted values and by calculating the proportion of observed values falling within the middle 95% of the simulated values. The MDE may only be evident when diversity is standardized for area at each elevation (McCain, 2005, 2007b). This was tested only with simple linear regressions of area-standardized diversity (detailed below) and mean predicted values because area-standardized diversity values are not on a natural scale, precluding direct comparisons of magnitude.

*Area*

To test the strength of the species-area relationship, we used simple linear regressions after log-transforming diversity and area (Arrhenius, 1921; Rosenzweig, 1995; Rahbek, 1997). The area hypothesis also predicts that standardizing diversity for elevational area should alter both the diversity pattern and the elevation of the diversity peak (McCain, 2007b). To standardize for area, we first estimated an overall *z* for montane ants using *S = cAz* with all studies combined. This method reduces bias from extreme *z* values occasionally observed on mountains (McCain, 2007b). Using this averaged *z*, we calculated area-standardized diversity for each elevation in each study as *S/Az*, where *S* and *A* are the interpolated diversity and area for a given elevational band. The area-standardized diversity patterns were then characterized using the descriptions above. Varying *z* beyond the 95% confidence limits had little qualitative effect on the resulting patterns. A paired t-test was used to determine whether area-standardization altered the elevation of the diversity peak. To test whether the species-area relationship was stronger in regional studies than in local studies (Karger *et al.*, 2011), we used a Mann-Whitney U-test to compare coefficients of determination.

*Elevational Climate Model (ECM)*

We tested four predictions of the ECM. First, to test the prediction that mid-peaks are more common on arid than wet mountains, we used a Fisher's Exact Test to detect if wet and arid climates were positively associated with high diversity at the base (decreasing and low plateaus) and low diversity at the base (mid-peaks) respectively. Second, to test whether temperature predicts diversity better on wet than arid mountains, we used simple linear regressions and compared the coefficients of determination with a Mann-Whitney U-test. Third, to evaluate whether diversity at the mountain base is higher on wet than arid mountains, we compared the proportion of diversity at the base using a Mann-Whitney U-test. Using proportions allows for better comparison of the diversity pattern shape and accounts for large diversity differences across studies. Fourth, to test whether precipitation limits diversity at the base of arid mountains, we correlated base precipitation with the proportion of diversity at the base using Spearman's Rho.

*Interactions: Environmentally and Geometrically Constrained Model*

To assess the effects of each hypothesized driver simultaneously, we used an environmentally and geometrically constrained model (EGCM) (Wang & Fang, 2012). The EGCM framework relies on the prediction that small-ranged species are less affected by the geometric constraints imposed by a bounded domain and therefore better reflect the influence of the environmental gradient. We explored range-size cutoffs of 1/4, 1/5, 1/6, and 1/7 of the mountain gradient to define the small-ranged species group. Excluding elevations near the boundaries (Wang & Fang, 2012), we used the small-ranged species at each cutoff to fit a model of log diversity predicted by log area, mean annual temperature, and annual precipitation, using AIC to determine the best model for each cutoff. We used the predictions from these models as probability distributions for 5,000 simulations, randomly placing the elevational midpoints of the large-ranged species along the corresponding gradient. We selected the optimal cutoff based on the strength of the fit between these simulations and the observed large-ranged species diversity for each transect (Wang & Fang, 2012). This analysis used the same subset of datasets used to evaluate the MDE.

**RESULTS**

*Datasets and Patterns*

Sixty-six datasets were identified as possible sources for ant diversity across elevations (Appendices S1 & S2). In two cases, the authors sampled both sides of a mountain range with no shared sample sites, so the two transects were treated as separate transects (Botes et al., 2006; Burwell & Nakamura, 2011). Forty-five datasets were unique and provided data on ant diversity for a single gradient or region. Only twenty of these datasets met the *a priori* sampling criteria. These twenty datasets, representing six biogeographical provinces and both temperate and tropical regions, were comprised of eleven local studies and nine regional studies (Fig. 2). Additionally, eight studies were in arid climates and twelve were in wet climates. Despite only detecting twenty sufficiently sampled gradients for ants, this is similar to some harder to survey vertebrate taxa, like bats (e.g., twenty-two bat datasets: McCain, 2007a). Insect diversity studies along gradients are still gaining interest, as vertebrate gradients have been surveyed for much longer (Diniz-Filho et al., 2010).

Robust ant diversity datasets showed three of the patterns detailed above. Most transects showed mid-elevation peaks, while monotonic declines and low plateaus occurred in equal proportion (Fig. 1a). The distribution of patterns was nearly identical between local and regional scales: both showed primarily mid-peaks with equal numbers of low plateau and decreasing patterns (Appendix S1).

The under-sampled datasets showed five patterns (Fig. 1b). Mid-peaks were most common as in the well-sampled gradients, though a substantial number of decreasing patterns were detected. These were observed largely in studies that did not sample within the lowest 400m. Low plateaus, increases, and no pattern occurred in equal, low numbers (Appendix S2).

*Thermal Energy*

Thermal energy was not well supported as an independent driver of ant diversity. Only 15% of studies detected a monotonic decrease with increasing elevation. No area-standardized patterns showed monotonic decreases. A positive, significant relationship with temperature was detected in 60% of studies, though the *r2* distribution was bimodal with many studies showing a very poor fit (Fig. 3a; *r2* mean = 0.465, median = 0.550). With area-standardization, 70% of studies showed a positive, significant relationship, though fits were similar (*r2* mean = 0.462, median = 0.458). Additionally, the individual relationships were predominantly curvilinear rather than linear as predicted by a strong temperature driver. In support of the first prediction of the MTE, a linear relationship between log-transformed diversity and the inverse of temperature fit the data better than a curvilinear relationship (delta AIC = 12.06), but the slope did not fall within the predicted bounds (*P* < 0.001, 95% CI: -0.487 < *β* < -0.258, predicted: -0.7 < *β* < -0.6). Area-standardized diversity showed similar results (P < 0.001, 95% CI: -0.384 < *β* < -0.198).

*MDE*

There was little support for the MDE. The MDE generally predicted diversity poorly with either the proportional or linear model method (Fig. 4a, b; proportion of points within 95% bands: mean = 0.257, median = 0.218; linear models: *r2* mean = 0.354, median = 0.274). Standardizing for area slightly improved the linear model fit (*r2* mean = 0.396, median = 0.318). The MDE predicted mean range size somewhat better than it did diversity, but overall fits were still generally low (Fig. 4c, d; proportion within 95% bands: mean = 0.335, median = 0.278; linear models: *r2* mean = 0.384, median = 0.387).

*Area*

There was mixed support for the area hypothesis. A positive, significant relationship between area and diversity was seen in 80% of studies (Fig. 3b; *r2* mean = 0.585, median = 0.685). With area standardization, the diversity pattern changed in 50% of studies and the diversity peak shifted significantly upward (*P* = 0.01, *t19* = 2.77), though only 35% of studies showed a shift > 300m. The effect of area did not differ with scale (*P* = 0.82, *W* = 46).

*ECM*

There was mixed support for the ECM. Mid-peaks were not more likely on arid mountains (Fig. 2; *P* = 0.32, *ω* = 4.63). However, temperature predicted diversity significantly better on wet mountains (Fig. 3a; *P* = 0.003, *W* = 85), and a significant relationship between temperature and diversity was detected on 83% of wet mountains and 25% of arid mountains. The proportion of diversity at the base was significantly higher on wet mountains (*P* = 0.025, *W* = 19). There was no significant correlation on arid mountains between the proportion of diversity at the base and the precipitation at the base (*P* = 0.096).

*Interactions: EGCM*

Small-ranged species diversity was predicted reasonably well by the best environmental models (*r2* mean = 0.661, median = 0.723, range = 0.189–0.982). The large-ranged species diversity pattern was very well predicted by the EGCM simulations in most studies, though the fit was rather poor in two studies (*r2* mean = 0.843, median = 0.957, range = 0.197–0.988). Additionally, inclusion of geometric constraints improved fit in 62.5% of studies. Each possible environmental model was the optimal model for at least one study (Fig. 5). With the exception of one dataset, the optimal models for all wet-based mountains included just one environmental variable. In contrast, the optimal models for all arid-based mountains included multiple variables.

**DISCUSSION**

Accounting for sampling bias, ants do not uniformly nor commonly decline in diversity with increasing elevation as previously thought. In fact, ant diversity most commonly shows mid-elevation peaks, with low plateaus and decreasing patterns occurring less frequently (Fig. 1a). None of the four broad drivers assessed individually were universally supported. Rather, evaluation of interactions showed support for the influence of multiple drivers, though not a consistent set of drivers.

Additional factors not evaluated here may affect patterns of ant diversity. Habitat complexity, vegetation structure, and leaf litter depth have been suggested in several systems (Lassau & Hochuli, 2004; Sarty et al., 2006; Pacheco & Vasconcelos, 2011; Bharti et al., 2013). Complications arise, however, both in identifying and quantifying the relevant habitat features (McCain & Grytnes, 2010), particularly in analyses spanning the globe. Biotic interactions have long been speculated to affect patterns of diversity (Lomolino, 2001), though the extent to which local interactions among individuals affect large scale patterns of diversity remains unclear (Ricklefs, 2004; Cerdá et al., 2013). Detailed data on potential competitors along each elevational gradient, paired with sufficient knowledge of species-specific interactions, are required to assess this hypothesis. Finally, evolutionary history may impact diversity patterns (Willig et al., 2003); rigorous evaluation relies on the development of species-level, time-calibrated phylogenies. Additionally, evolutionary models predict consistent elevational diversity patterns within regions and primarily mid-elevation peaks in diversity (McCain, 2009; Colwell & Rangel, 2010), rather than the variation observed.

A sizable proportion of studies employ sampling regimes that fail to ensure an accurate description of the diversity across the gradient (Appendix S2). In this analysis, only 44% of the unique datasets met the *a priori* criteria. Similar proportions of sufficiently sampled studies have been found for birds (41%: McCain, 2009), bats (44%: McCain, 2007a), vertebrate ectotherms (51%: McCain & Sanders, 2010), reptiles (67%: McCain, 2010), and small non-volant mammals (73%: McCain, 2005). Of the ant datasets that were excluded due to sampling issues, 64% either did not sample >70% of the gradient or did not sample the lowest 400m (Appendix S2). Ignorance at the base of the mountain biases observations toward declining diversity (Fig. 1b; Appendix S2) regardless of the true pattern because diversity typically decreases beyond a certain elevation (Rahbek, 2005; Nogués-Bravo et al., 2008). The use of rigorous *a priori* standards is crucial to understanding and disentangling the drivers of diversity.

It is commonly thought that temperature should be a major driver of ant diversity (e.g., Fisher, 1998; Brühl et al., 1999; Sanders et al., 2007; Malsch et al., 2008; Dunn et al., 2010; Munyai & Foord, 2012). However, energetic hypotheses were not supported generally and support did not improve with area-standardization. Across a latitudinal gradient, local ant diversity has been found to be consistent with one formulation of the MTE (Kaspari et al., 2004), though the controversial hypothesis has not seen broad support (Hawkins et al., 2007b; McCain & Sanders, 2010). We fail to find convincing evidence for the MTE or for a simple linear relationship with thermal energy. Ants may behaviourally moderate the temperatures they experience through nesting site and architecture (Lach et al., 2010) or by altering temporal patterns of foraging (Hölldobler & Wilson, 1990). Soil temperature may more closely approximate the temperatures experienced by many ants. Nevertheless, soil temperature would still be expected to decline with elevation, failing to explain the prevalence of mid-elevation peaks. Alternatively, the effect of temperature may be contingent upon water availability. Energy and water, well-established physiological constraints, have been implicated as important drivers of diversity and abundance in both plants and animals (Kaspari et al., 2000; Hawkins et al., 2003; Bhattarai et al., 2004). These effects may occur directly through physiology or indirectly through effects on productivity and food resources (Gaston, 2000; Kaspari et al., 2000; Hawkins et al., 2003; McCain, 2007a, 2009). However, while ant diversity across elevations was somewhat consistent with the ECM, the effects of temperature and precipitation appear to be more nuanced.

Area likewise was not consistently supported, though it predicted diversity well along the majority of transects. Though effects of area are expected to be stronger at a regional scale, no difference was detected. This suggests that local studies along elevational gradients may occur at intermediate scales for ants, resulting in similar dynamics in local and regional studies (McCain & Grytnes, 2010). Alternatively, the local species richness may be influenced by regional area indirectly via the regional species pool (Rosenzweig & Ziv, 1999; Romdal & Grytnes, 2007). The predictions of the area hypothesis were not supported across all gradients, however. The strong fit to the species-area relationship may, therefore, be spurious. No support was found for the MDE, whether assessed independently or with area-standardized diversity. The MDE has had a controversial history with highly variable predictive ability across multiple taxa (e.g., Sanders, 2002; McCain, 2003, 2005, 2009; Colwell et al., 2004). Studies evaluating elevational gradients globally, however, have generally found poor support for the MDE (Dunn et al., 2007; McCain, 2007a, 2009, 2010; Beck & Chey, 2008).

Diversity hypotheses are not mutually exclusive and likely act in tandem to shape the patterns observed across elevational gradients (Willig et al., 2003; Dunn et al., 2007; Wang & Fang, 2012). The EGCM predicted diversity quite well along most gradients and fit generally improved with the inclusion of geometric constraints. This suggests that geometric constraints due to the mid-domain effect may play a role in shaping overall ant diversity on most gradients by impacting the distribution of large-ranged species. However, no single environmental model was supported globally (Fig. 5). Rather, the best environmental model was highly variable among gradients and each combination of variables was selected for at least one gradient. With current data, the forces that shape ant diversity across elevations globally appear to be complex with no universal model. Alternatively, ant diversity may be driven by processes like biotic interactions that are currently untestable.

Both the EGCM and independent hypothesis tests indicate a dichotomy based on the precipitation levels at the mountain base, however. Under the assumption that small-ranged elevational specialists reflect the environmental influences driving the diversity of all ant species along a gradient (Wang & Fang, 2012), there appears to be one dominant factor driving ant diversity on each wet-based gradient. In roughly equal proportions, this was either area or temperature. In contrast, the best environmental models for arid climates always included multiple variables. This suggests a broad influence of precipitation and geometric constraints with the diversity pattern further modified by area, temperature, or a combination depending on the gradient.

Ant diversity is similar to that of other taxa in that a variety of elevational patterns is seen globally. The diversity patterns of vertebrate taxa investigated so far, however, seem to be driven by a relatively simple combination of factors. The elevational diversity patterns of birds, bats, and small non-volant mammals are all likely shaped by both temperature and precipitation (McCain, 2005, 2007a, 2007b, 2009), though each taxon shows a different overall distribution of diversity patterns. Reptile diversity is more closely tied to temperature, though precipitation and area seem to play a role as well (McCain, 2010; McCain & Sanders, 2010). As ectotherms, ant diversity would intuitively be affected largely by temperature. Nevertheless, the robust patterns of ant diversity across elevational gradients instead suggest a complex interplay of multiple drivers.

In conclusion, ant diversity shows a variety of patterns across elevations globally, most often peaking at mid-elevations. These patterns, in contrast to those of vertebrate taxa, are likely driven by the complex interplay of multiple factors dependent on the precipitation regime. Thus ant gradients, combined with other taxon-scale analyses, suggest that the taxon’s ecology and natural history may be critical to the processes influencing broad-scale patterns. The rigorous analysis of more insect and invertebrate taxa at a global extent in addition to a focus on gathering key data to test other potential drivers (e.g., biotic interactions and natural history) will provide the perspective required to understand how diversity is distributed and how to better predict future changes.

**ACKNOWLEDGEMENTS**

The authors are indebted to the researchers whose work is re-analysed herein. Jan Beck, and the members of the McCain lab provided excellent advice for improving analyses and manuscript drafts.

**REFERENCES**

Allen A., Brown J., & Gillooly J. (2002) Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. *Science*, **297**, 1545–1548.

Arita H.T. (2005) Range size in mid-domain models of species diversity. *Journal of Theoretical Biology*, **232**, 119–26.

Arrhenius O. (1921) Species and area. *Journal of Ecology*, **9**, 95–99.

Barry R.G. (1992) *Mountain weather and climate.* Routledge, London.

Beck J. & Chey V.K. (2008) Explaining the elevational diversity pattern of geometrid moths from Borneo: a test of five hypotheses. *Journal of Biogeography*, **35**, 1452–1464.

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

Bhattarai K.R., Vetaas O.R., & Grytnes J.A. (2004) Fern species richness along a central Himalayan elevational gradient, Nepal. *Journal of Biogeography*, **31**, 389–400.

Botes A., McGeoch M.A., Robertson H.G., van Niekerk A., Davids H.P., & Chown S.L. (2006) Ants, altitude and change in the northern Cape Floristic Region. *Journal of Biogeography*, **33**, 71–90.

Brehm G., Strutzenberger P., & Fiedler K. (2013) Phylogenetic diversity of geometrid moths decreases with elevation in the tropical Andes. *Ecography*, **36**, 1247–1253.

Brown J. (2001) Mammals on mountainsides: elevational patterns of diversity. *Global Ecology and Biogeography*, **10**, 101–109.

Brown J., Gillooly J., Allen A., Savage V., & West G. (2004) Toward a metabolic theory of ecology. *Ecology*, **85**, 1771–1789.

Brühl C.A., Mohamed M., & 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.J. & 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.

Cerdá X., Arnan X., & Retana J. (2013) Is competition a significant hallmark of ant (Hymenoptera: Formicidae) ecology? *Myrmecological News*, 131–147.

Chao A. & Jost L. (2012) Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. *Ecology*, **93**, 2533–2547.

Colwell R.K. & Coddington J.A. (1994) Estimating terrestrial biodiversity through extrapolation. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, **345**, 101–118.

Colwell R.K. & Hurtt G.C. (1994) Nonbiological gradients in species richness and a spurious Rapaport effect. *American Naturalist*, **144**, 570–595.

Colwell R.K. & Lees D.C. (2000) The mid-domain effect: geometric constraints on the geography of species richness. *Trends in Ecology & Evolution*, **15**, 70–76.

Colwell R.K., Rahbek C., & Gotelli N.J. (2004) The mid-domain effect and species richness patterns: what have we learned so far. *American Naturalist*, **163**, E1–E23.

Colwell R.K. & Rangel T.F. (2010) A stochastic, evolutionary model for range shifts and richness on tropical elevational gradients under Quaternary glacial cycles. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, **365**, 3695–707.

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

Dunn R.R., McCain C.M., & Sanders N.J. (2007) When does diversity fit null model predictions? Scale and range size mediate the mid-domain effect. *Global Ecology and Biogeography*, **16**, 305–312.

Dunn R.R., Sanders N.J., Guenard B., & Weiser M.D. (2010) Geographic gradients in the diversity, abundance, size, and ecological consequences of ants. *Ant Ecology* pp. 38–58.

Fisher B.L. (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. (2000) Global patterns in biodiversity. *Nature*, **405**, 220–7.

Gotelli N.J. & Colwell R.K. (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, **4**, 379–391.

Grytnes J.A. (2003) Species-richness patterns of vascular plants along seven altitudinal transects in Norway. *Ecography*, **26**, 291–300.

Grytnes J.A. & Vetaas O.R. (2002) Species richness and altitude: a comparison between null models and interpolated plant species richness along the Himalayan altitudinal gradient, Nepal. *The American Naturalist*, **159**, 294–304.

Hawkins B.A., Albuquerque F.S., Araújo M.B., Beck J., Bini L.M., Cabrero-Sanudo F.J., Castro-Parga I., Diniz-Filho J.A.F., Ferrer-Castán D., Field R., & others (2007a) A global evaluation of metabolic theory as an explanation for terrestrial species richness gradients. *Ecology*, **88**, 1877–1888.

Hawkins B.A., Diniz-Filho J.A.., Bini L.M., Araújo M.B., Field R., Hortal J., Kerr J.T., Rahbek C., Rodríguez M.Á., & Sanders N.J. (2007b) Metabolic theory and diversity gradients: Where do we go from here? *Ecology*, **88**, 1898–1902.

Hawkins B.A., Field R., Cornell H. V., Currie D.J., Guégan J.-F., Kaufman D.M., Kerr J.T., Mittelbach G.G., Oberdorff T., O’Brien E.M., Porter E.E., & Turner J.R.G. (2003) Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, **84**, 3105–3117.

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

Karger D.K., Kluge J., Krömer T., Hemp A., Lehnert M., & Kessler M. (2011) The effect of area on local and regional elevational patterns of species richness. *Journal of Biogeography*, **38**, 1177–1185.

Kaspari M., O’Donnell S., & Kercher J.R. (2000) Energy, density, and constraints to species richness: Ant assemblages along a productivity gradient. *The American Naturalist*, **155**, 280–293.

Kaspari M., Ward P.S., & Yuan M. (2004) Energy gradients and the geographic distribution of local ant diversity. *Oecologia*, **140**, 407–413.

Lach L., Parr C., & Abbott K. (2010) *Ant Ecology.* Oxford University Press, USA, New York.

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

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

Malsch A., Fiala B., Maschwitz U., Mohamed M., Nais J., & Linsenmair K. (2008) An analysis of declining ant species richness with increasing elevation at Mount Kinabalu, Sabah, Borneo. *Asian Myrmecology*, **2**, 33–49.

McCain C.M. (2003) North American desert rodents: a test of the mid-domain effect in species richness. *Journal of Mammalogy*, **84**, 967–980.

McCain C.M. (2004) The mid-domain effect applied to elevational gradients: species richness of small mammals in Costa Rica. *Journal of Biogeography*, **31**, 19–31.

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

McCain C.M. (2007a) Could temperature and water availability drive elevational species richness patterns? A global case study for bats. *Global Ecology and Biogeography*, **16**, 1–13.

McCain C.M. (2007b) Area and mammalian elevational diversity. *Ecology*, **88**, 76–86.

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

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

McCain C.M. & Grytnes J.A. (2010) Elevational gradients in species richness. *Encyclopedia of Life Sciences* pp. 1–10.

McCain C.M. & Sanders N.J. (2010) Metabolic theory and elevational diversity of vertebrate ectotherms. *Ecology*, **91**, 601–609.

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

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

Mollhagen T.R. & Bogan M.A. (1997) Bats of the Henry Moutains region of southeastern Utah. *Occasional Papers of the Museum of Texas Tech University*, **170**, 1–13.

Munyai T.C. & 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., & Rahbek C. (2008) Scale effects and human impact on the elevational species richness gradients. *Nature*, **453**, 216–219.

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

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

Programme U.N.E. (1997) World atlas of desertification / UNEP ; co-ordinating editors, Nick Middleton and David Thomas. .

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

Rahbek C. (1997) The relationship among area, elevation, and regional species richness in neotropical birds. *The American Naturalist*, **149**, 875–902.

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

Ricklefs R.E. (2004) A comprehensive framework for global patterns in biodiversity. *Ecology Letters*, **7**, 1–15.

Romdal T. & Grytnes J. (2007) An indirect area effect on elevational species richness patterns. *Ecography*, **30**, 440–448.

Rosenzweig M.L. (1992) Species diversity gradients: We know more and less than we thought. *American Society of Mammalogists*, **73**, 715–730.

Rosenzweig M.L. (1995) *Species Diversity in Space and Time.* Cambridge University Press, Cambridge.

Rosenzweig M.L. & Ziv Y. (1999) The echo pattern of species diversity: pattern and processes. *Ecography*, 614–628.

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

Sanders N.J., Lessard J.-P., Fitzpatrick M.C., & Dunn R.R. (2007) Temperature, but not productivity or geometry, predicts elevational diversity gradients in ants across spatial grains. *Global Ecology and Biogeography*, **16**, 640–649.

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

Terborgh J. (1973) On the notion of favorableness in plant ecology. *The American Naturalist*, **107**, 481–501.

Wang X. & Fang J. (2012) Constraining null models with environmental gradients: a new method for evaluating the effects of environmental factors and geometric constraints on geographic diversity patterns. *Ecography*, **35**, no–no.

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

**SUPPORTING INFORMATION**

Additional Supporting Information may be found in the online version of this article:

**Appendix S1:** Details and references of ant elevational gradients used in analyses

**Appendix S2:** Details and references of ant datasets excluded from analyses

**BIOSKETCH**

**Tim Szewczyk** is a PhD student in Christy McCain’s lab at the University of Colorado at Boulder in the Department of Ecology & Evolutionary Biology who is interested in biogeography and ecology at a large spatiotemporal scale with a focus on biodiversity, insects, and metacommunities. He is also interested in models and simulations in ecology as well as montane ecology.

**Christy McCain** is an Assistant Professor in the Department of Ecology & Evolutionary Biology and Curator of Vertebrates in the Museum of Natural History at the University of Colorado at Boulder. Christy is an ecologist focusing on large-scale ecological patterns with particular emphasis on species richness, abundance, and distribution patterns along ecological gradients. She is also interested in macroevolution, montane biogeography, climate change, conservation, and theoretical and empirical aspects of the causes and maintenance of species diversity.

Editor: Melodie McGeoch

**Figure Legends**

**Figure 1** (a) The number of well-sampled ant studies showing each of the diversity patterns (*n* = 20). Mid-peaks were most common with equal numbers of decreasing and low plateau patterns observed (see text for definitions). Regional (gray bars) and local (black bars) scales did not differ in the pattern distribution. (b) Unique datasets that did not meet the *a priori* criteria (*n* = 25; see text) showed five patterns: mid-peaks and decreasing patterns were most common with equal numbers of low plateaus, increasing patterns, and no pattern (see text for definitions). Most studies that did not sample within the lowest 400m (black bars) reported monotonic decreases while studies that sampled within the lowest 400m (gray bars) reported other patterns.

**Figure 2** The distribution of ant study sites (circles), the three main elevational richness patterns for each hemisphere (bars), and the number of patterns on wet and dry based mountains (black & white). (D = decreasing, LP = low plateau, MP = mid-elevational peak; see text for definitions).

**Figure 3** Regression analyses of the temperature-diversity and species-area relationships using the well-sampled ant datasets. (a) Fits to the temperature-ant diversity relationship (*n* = 20) with mean *r2* = 0.465 ± 0.076 (SE). Wet mountains showed a significantly better fit than did arid mountains (*r2wet* = 0.635 ± 0.078, *n* = 12; *r2arid* = 0.210 ± 0.095, *n* = 8; *P* = 0.003). (b) Fits to the species-area relationship (*n* = 20) with mean *r2* = 0.585 ± 0.068 (SE).

**Figure 4** Evaluation of mid-domain effect (MDE) predictions (*n* = 16). MDE simulations poorly predicted diversity both in (a) the proportion of observed values falling within the 95% predictive bands (mean = 0.257 ± 0.044 (SE)) and in (b) the *r2* values from linear regressions (mean *r2* = 0.354 ± 0.067). Mean range size was poorly predicted by the MDE simulations measured both by (c) the mean range sizes falling within the 95% predictive bands (mean = 0.335 ± 0.055) and by (d) linear regressions (mean *r2* = 0.384 ± 0.059).

**Figure 5** EGCM optimal environmental models for the best cutoff of each transect in wet and arid climates (*n* = 16). These models were fit using only small-ranged species in each transect. In the full model, log diversity in each elevational band was predicted by log area (A), mean annual temperature (T), and annual precipitation (P). With one exception, all wet mountain ant diversity was best predicted by one environmental variable, most often either area or temperature. In contrast, arid mountain ant diversity was best predicted by models including two or three variables, most often with area and temperature included.

Figure 1

Mac HD:Users:fossegrimen:Dropbox:Thesis:Manuscripts:2013 AntMeta:JBiogeog_Resub:WorkingDraft:Figures:Fig1.pdf

Figure 2

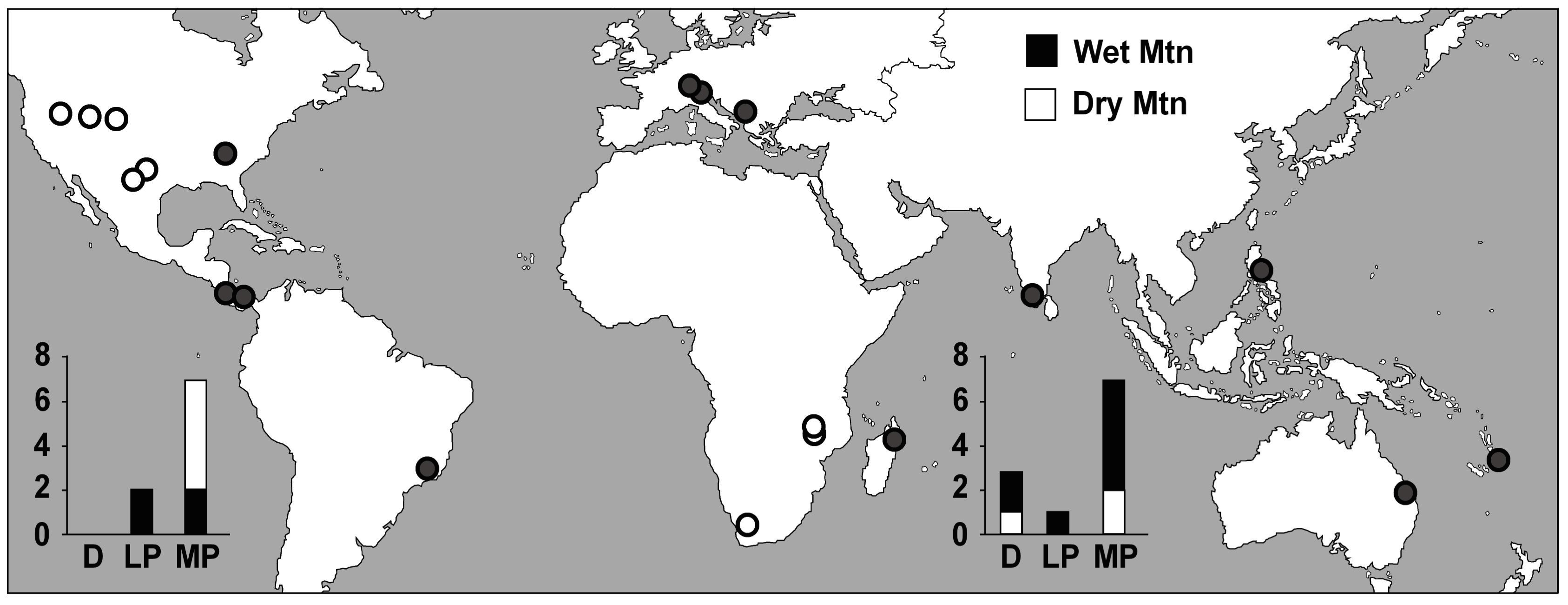


Figure 3

Mac HD:Users:fossegrimen:Dropbox:Thesis:Manuscripts:2013 AntMeta:JBiogeog_Resub:WorkingDraft:Figures:Fig3.pdf

Figure 4

Mac HD:Users:fossegrimen:Dropbox:Thesis:Manuscripts:2013 AntMeta:JBiogeog_Resub:WorkingDraft:Figures:Fig4SM.pdf

Figure 5

