Ants, elevation, phylogenetic diversity and community structure

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Abstract.   Testing the degree of support for macroecological patterns requires that the data behind these hypotheses be available for examination and re-testing. Using geographically wide-spread incidence matrices and a multi-gene phylogeny for ants (Hymenoptera: Formicidae), I calculated phylogenetic measurements of alpha and beta diversity and elevation to test the degree of support for the expected relationships between diversity and elevation (negative) and between phylogenetic clustering and elevation (positive). Whether diversity was estimated morphologically or phylogenetically, the elevational decay of alpha diversity was more frequently a linear decline than a mid-elevation peak. However the expectation that phylogenetic community structure would more likely be clustered with increasing elevation was not supported. This might be due to the fact that the physiological limitations filtering the taxa present are expressed at the species level and are thus beyond the resolution of this phylogeny. Trends linking elevational decay in beta diversity to temperature and precipitation were weak, but the results do support Janzen's 1967 prediction that communities on tropical mountains were less similar to each other than in temperate mountain communities. At the genus level, these data suggest that there is no general pattern regarding whether environmental/habitat filters (clustering) or inter-specific competition (dispersion) filter the taxa present. Instead, this analysis suggests that the community assemblages are not significantly different from random across elevation or temperature. These findings reinforce how important it is to support intuition with data and how critical it is to make data public and accessible so that hypotheses can be re-examined and tested.

Key words: environmental filter; Formicidae; phylogenetic clustering; public data.

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INTRODUCTION

Diversity in montane areas declines at higher elevations as a result of the increased frequency of cooler temperatures and continuously wet substrates combined with reduced solar radiation and smaller area. (Olson 1994, Flenley 1995). Since the work of Grinnell and Storer (1924) in Yosemite National Park, California and Whittaker (1952) in the Great Smoky Mountain National Park in the first half of the 20th century, through to multiple analyses being prepared and published (or re-collected) today, discerning elevational gradients of alpha and beta diversity are of increasing importance as the isotherms on these montane areas are radically changing (Mountain Research Initiative 2015).

While diversity is expected to be negatively correlated with elevation, the actual situation can be more complex than is often appreciated. For example, the relationship between elevation and diversity for hyperdiverse taxa, where both monotonic declines and mid-elevation peaks in diversity have been reported, can be particularly

complex (Fischer et al. 2011). Delineating these diversity patterns can be slowed by the inertia caused by the taxonomic impediment prevalent in hyperdiverse groups (Adams et al. 2014). When such diversity necessitates the use of provisional taxonomic identifications it results in an inability to compare between studies.

Within hyperdiverse taxa, species level identifications are frequently characterized with provisional names (Groc et al. 2010). However, within many groups, like the ants (Hymenoptera: Formicidae), genus-level identification is much more likely to be un-ambiguous and still phylogenetically informative (Groc et al. 2010). Thus, not only are generic identifications a taxonomic grade much more likely to be directly comparable across studies, but genus level data are phylogenetically valuable. The most extensive phylogeny for the ants (Moreau et al. 2006), is resolved at the genus level. Using this phylogenetic hypothesis permits the calculation of phylogenetic diversity using the most reliable, and valuable, taxonomic information from each study.

In addition to their well supported phylogeny, the ants were selected for this work due their large impact on ecological services in both temperate and tropical environments (Andersen et al. 2004, Del Toro et al. 2012). In addition, ants have been widely used both in studies of elevation/diversity and in studies that utilized phylogenetic measures of diversity and community structure (Smith et al. 2005, 2009, 2014, Lessard et al. 2009, Smith and Fisher 2009, Machac et al. 2011, Donoso 2014). I calculated phylogenetic estimates of diversity derived from a common and public phylogeny as a bridge between multiple independent studies which had each examined diversity patterns across elevational gradients. I defined phylogenetic diversity as the sum of all phylogenetic branches connecting species together within a community. In this sense, it is differentiated from a more classical presentation of Faith's phylogenetic diversity where the sum of the branch lengths present at a site would include a reference to a larger regional phylogeny. Cadotte et al. (2010) categorized this style of phylogenetic diversity measurement as Community Phylogenetic Diversity and proposed that this was the more appropriate measure of phylogenetic diversity for assessing species coexistence since community processes operate on extant members (Cadotte et al. 2010).

Severe environmental conditions such as reduced temperature and increased precipitation have been hypothesized (Machac et al. 2011) to act as a strict filter on total diversity and the members of the regional species pool such that the resultant high-elevation community would be phylogenetically clustered to contain only those taxa capable of dealing with this stress. My objective was to ask three questions. First, are patterns of diversity congruent between taxonomically derived incidence matrices and when diversity is measured phylogenetically? Second, does calculating beta diversity phylogenetically result in altered estimates of overlap between elevations? Third, are communities increasingly phylogenetically clustered with increasing elevation? Since the relationship between diversity and elevation is indirect; temperature and precipitation data for each site was extracted from the WorldClim dataset (Version 1.4, release 3; Hijmans et al. 2005) to compare with diversity.

METHODS

Studies that had measured ant diversity (species richness) and elevation, and regional surveys that included measures of richness and elevation, were selected from the literature. From this larger pool there were eighteen studies that had reported their findings in sufficient detail that I could re-create their species/elevation incidence matrix (Fig. 1; Supplement). The eighteen published datasets of ant communities and elevation (representing 265 sites with 2,054 species from 159 genera) were made in Madagascar (Fisher 1998), five regions within the United States (Tennessee (Lessard et al. 2007), Arizona (Andersen 1997), Colorado (Gregg 1963), New England (Del Toro 2013) and Georgia (Ipser et al. 2004)), Norway (Hågvar 2005), Mongolia (Pfeiffer et al. 2003), Austria (Glaser 2006), two locations in Costa Rica (Barva transect, Longino and Colwell 2011; Area de Conservación Guanacaste, Smith et al. 2014), Colombia (van der Hammen and Ward 2005), Guyana (Lapolla et al. 2007), Brazil (Araújo and Fernandes 2003), Egypt (Orabi et al. 2011), India (Sabu et al. 2008), Malaysia (Brühl et al. 1999) and the Philippines (Samson et al. 1997).
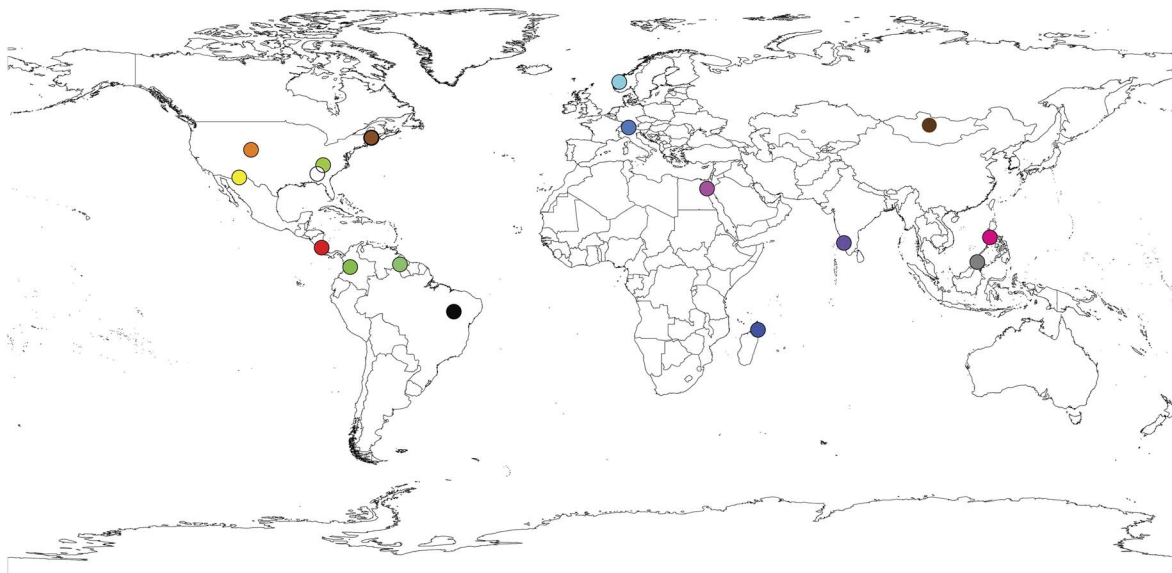
Fig. 1. Sampling localities of the eighteen published ant diversity and elevation incidence matrices examined: Madagascar (Fisher 1998), Great Smoky Mountains National Park in Tennessee (Lessard et al. 2007), the Chiricahua Mountains in Arizona (Andersen 1997), Colorado, USA (Gregg 1963), Georgia, USA (Ipser et al. 2004), New England, USA (Del Toro 2013), Norway (Hågvar 2005), Mongolia (Pfeiffer et al. 2003), Austria (Glaser 2006), Costa Rica (Atlantic, Longino and Colwell 2011; Pacific, Smith et al. 2014), Colombia (van der Hammen and Ward 2005), Guyana (Lapolla et al. 2007), Brazil (Araújo and Fernandes 2003), Egypt (Orabi et al. 2011), India (Sabu et al. 2008), Malaysia (Brühl et al. 1999) and the Philippines (Samson et al. 1997). The map was made using www.simplemappr.net.

The analyses

Alpha diversity (species richness) and beta diversity (Jaccard index; Magurran and McGill 2011) were calculated based on the incidence matrix from the original publication in EstimateS (v 9.1; Colwell and Elsensohn 2014). Some taxonomic updates were necessary so that the species names in each publication matched the taxonomy used in the Moreau et al. phylogeny tip-labels. For example, *Veromessor lobognathus* was changed to *Messor lobognathus* in Gregg (1963; although a recent myrmicine phylogeny has ressurected the genus; Ward et al. 2014). In one case, similar (adjacent) elevations were combined (van der Hammen and Ward 2005). In another two cases multiple, overlapping, sampling sites were binned into 100 m sampling intervals (Ipser et al. 2004, Del Toro 2013). When multiple elevations were binned, trends were also calculated for the individually reported sites. In one case (Pfeiffer et al. 2003), the elevations were extracted from Google Earth (Google Earth

2012) based on the latitude and longitude provided in the publication. Finally, where only one species was recovered from a mid-elevation location (Ipser et al. 2004; 214 m; suggesting reduced sampling intensity) or where notably fewer species than adjacent locations were recorded (Fisher 1998; 600 m) this elevation was removed from the matrix as an outlier.

The phylogeny

There is a well-supported, multi-gene phylogeny for ants at the genus level (congruent maximum parsimony, maximum likelihood and Bayesian analyses based on 4,572 base pairs (bp) from six genes: 1 mitochondrial (COI), 2 rDNA (18S and 28S) and three single, or low, copy number nuclear markers (wingless (wg), Abdominal-A (abd-A) and long-wavelength Rhodopsin (LR); Moreau et al. 2006). The Moreau et al. phylogeny is archived on Treebase (Piel et al. 2003; S1573, however the tree used here included branch lengths and is available from the primary

author's website: www.moreaulab.org/molecular-microbial-resources/). The Moreau et al. phylogeny was trimmed using the R (R Core Team) packages ape (Paradis et al. 2004) and picante (Kembel et al. 2010) so that the phylogeny contained only those genera found at each of the geographic locations, thus making 18 site-level phylogenies (Fig. 2).

Phylogenetic community structure

To compare each published incidence matrix phylogenetically, the reported matrix was reduced to genus/elevation and this new matrix was then used to calculate phylogenetic measures of diversity (total branch length among all taxa in a sample; PD), the nearest taxon index (the mean nearest phylogenetic taxon distance for the taxa in each sample (MNTD) compared to randomly generated null phylogenies (NTI)) and the Net Relatedness Index (the mean phylogenetic distance for the taxa in each sample (MPD) compared to the randomly generated null phylogenies and incidence matrices (NRI; Webb et al. 2002; Fig. 2; Supplement). I also created incidence matrices for each location where abundance was coded as the species richness within each genus. All measures of phylogenetic community structure were calculated using phylocom (version 4.1, Webb et al. 2008) and the picante (Kembel et al. 2010) package in R. In each case, the observed phylogenetic distribution was tested against null distributions generated according to all possible models implemented in phylocom. These categories, as coded as in phylocom, are (0) phylogeny shuffle where genus labels are randomized across the entire phylogeny; (1) random draws from sample pool genus richness of each sample is maintained but the genus occurring in each sample are randomized based on those species actually occurring in at least one sample; (2) random draws from sample pool is similar to (1) however the genus in each community become random draws from the entire phylogeny and (3) the independent swap algorithm where number of genera per sample and frequency of occurrence of each genus across samples are held constant as genus co-occurrences in samples are randomized. The abundance matrices based calculations of NRI were only tested according to the independent swap algorithm. Phylogenetic estimates of beta diversity (phylobetadiversity)

were calculated as the mean nearest taxon distance—an estimate of the phylogenetic distance between pairs of species drawn from two elevations (comdistnt in phylocom). Morphological or phylogenetic estimates of diversity were compared to elevational separation using a Mantel test. To examine the relationship between phylogenetic community structure and temperature, values of NRI and NTI were compared to the average mean temperature values for the exact locations if reported, or for the site if not.

To test whether there was more or less PD than expected (based on the relationship between taxonomic richness and PD across elevation) I compared the residuals of a linear regression of PD against taxonomic richness (genus or species) to elevation. If there was greater PD at high elevations than predicted by either taxonomic measure of richness I would expect a positive relationship between the residuals and elevation. In addition, I examined the pattern of residuals from each of the highest elevation sites from each locality.

Latitude and environmental variables

Once taxonomic and phylogenetic measures of alpha and beta diversity were estimated, these values were compared to the average absolute latitude of the study location (from polar to equatorial). This allowed me to test the prediction there would be reduced beta diversity in the tropical (latitude 0–23°) vs. temperate mountains (Janzen 1967, Ghalambor et al. 2006, Rosner 2013). As a proxy for direct measurements of environmental variables at each location, the patterns of phylogenetic alpha and beta diversity were compared to large scale environmental data resources via the 1 square kilometer grid WorldClim data (version 1.4, release 3; Hijmans et al. 2005) using DIVA-GIS (version 7.5; Hijmans et al. 2001). The observed values of beta diversity were then compared to a principal estimate of temperature (BIO1 = average annual temperature or BIO2; mean diurnal range (mean of monthly; max temp − min temp)) and precipitation (mean annual). To aid in visualising the relationship between beta diversity and these environmental data, the points were smoothed using the nonparametric method LOESS (Cleveland and Loader 1996).

Fig. 2. Plots of the Moreau et al. (2006) phylogeny trimmed to include only those genera recorded at each elevation in each of 18 published incidence matrices. The tip colors correspond to the localities in Fig. 1. The sampled elevations proceed from top left to bottom right, (so the lowest elevation measured is represented by tips colors of the top left tree and the highest measured elevation is the bottom right tree). The community present at each sampling elevations is indicated by the array of colored dots. Thus, the phylogenetic diversity of any elevation is the summed branch length between all colored tips while the phylogenetic community structure is the mean phylogenetic distance between the dots, relative to the mean and standard deviation of possible associations distributed randomly across the phylogeny. Consult the Supplement for the complete incidence data for the elevational range covered by each study that was used to calculate PD, NRI and NTI. (A) Atlantic Costa Rica (Longino and Colwell 2011), (B) Mongolia (Pfeiffer et al. 2003), (C) Colorado (Gregg 1963), (D) Colombia

RESULTS

The analyses

There is not currently the sample size available to test differences between positive and negative latitude (sixteen of the eighteen studies were from above the equator with only sites from Brazil and Madagascar having negative latitude) and thus all calculations of latitude here are based on absolute latitude. Of the 2,054 species contained in the 18 studies, more than half (1,191, or 57.98%) had provisional species names. In only one case was the genus not named (1/159, or 0.6%). When alpha diversity (species richness) was calculated from the original incidence matrix, half the studies (9/18) displayed a monotonic, negative decline of diversity with elevation (i.e. the most diverse site was the lowest elevation and the linear regression with $p = 0.1$); five studies (5/18) displayed a mid-elevation peak (i.e. the most diverse site was neither the highest nor the lowest elevation with a p-value for the quadratic term in a polynomial regression ($p < 0.1$) and the Akaike's information criterion (AIC) of a polynomial regression was lower than that for a linear regression) while 4 displayed no significant relationship at all (Table 1). When diversity was calculated phylogenetically, 10 studies displayed a negative relationship between elevation and alpha diversity, 4 displayed a mid-elevational peak and 4 showed no significant relationship (Table 1, Fig. 3; Appendix: Figs. A1, A2). For those sites where multiple elevation sites were binned into 100 m units, patterns were similar, so for simplicity I only report the binned results. Both taxonomic and phylogenetic methods of estimating alpha diversity supported the observation that the highest elevation sites had lower diversity than mid- or low elevation localities.

There was no relationship between the residuals of taxonomic richness (species or genus richness) and PD against elevation (Supplement). The residuals of the relationship between PD and species richness were positive in all cases (18/18) for each of the highest elevation and in nearly all (17/18) for the lowest elevation sites for each study. However, in only 8 of 18 cases were there positive residuals in the relationship between PD and genus richness for the highest and lowest elevation sites (Supplement; Appendix: Fig. A3).

The phylogenetic measure of beta diversity changed sharply with elevational separation (note that phylobetadiversity is opposite in value to Jaccard; Appendix: Fig. A4; Fig. 4). In most cases (15/18) the relationship between Jaccard and elevation (Mantel r statistic) was stronger than for phylobetadiversity and elevation while the number of significant relationships was slightly higher for phylobetadiversity than for Jaccard (9:7; Appendix: Table A1).

Phylogenetic community structure

Patterns with all four null models were similar—and for simplicity only those obtained using the independent swap algorithm are reported. The relationship between phylogenetic clustering (NRI or NTI) and elevation displayed no apparent or significant trend towards increased phylogenetic clustering with increasing elevation in the ant communities included here (NRI: $R^2 = 0.043$, $p = 0.57$, NTI: $R^2 = 0.084$, $p = 0.259$; Fig. 5). In only 2 cases was there a positive and significant relationship between elevation and structure in the direction predicted (Austria (NTI; $R^2 = 0.201$, $p = 0.035$), Tennessee (NTI; $R^2 = 0.36$, $p = 0.009$); Table 2; Appendix A: Fig. A5)). There was no relationship between low elevation sites and phylogenetic dispersion. These patterns were the same whether phylogenetic community structure indices were calculated with incidence or abundance matrices (Supplement).

(continuation of Fig. 2 legend)

(van der Hammen and Ward 2005), (E) Madagascar (Fisher 1998), (F) the Chiricahua Mountains in Arizona (Andersen 1997), (G) Norway (Hågvar 2005), (H) Brazil (Araújo and Fernandes 2003), (I) Great Smoky Mountains National Park in Tennessee (Lessard et al. 2007), (J) India (Sabu et al. 2008), (K) Egypt (Orabi et al. 2011), (L) the Philippines (Samson et al. 1997), (M) Malaysia (Brühl et al. 1999), (N) Guyana (Lapolla et al. 2007), (O) Austria (Glaser 2006), (P) Georgia (Ipser et al. 2004), (Q) New England, USA and (R) Area de Conservacion Guanacaste (ACG) Costa Rica.

Table 1. The relationships between species richness, phylogenetic diversity and elevation for the eighteen publications surveyed here. Original data from the studies (species richness) evaluated using species richness displayed no relationship (4), linear decline with elevation (9) or a mid-elevation peak (5). When diversity is measured phylogenetically, the pattern evident in some individual cases changed however the proportion of times the relationship between diversity and elevation was not evident (4), declining linearly (10) or peaking at mid-elevations (4) was approximately the same. Asterisk indicates a significant relationship.

Country	Elevation range (m)	Relationship between elevation and species richness	p (linear)	AIC (linear)	p (quadratic)	AIC (quadratic)
A) Species richness						
Austria	400–2100	monotonic decline	0.000*	110.7855	0.812	112.7156
Brazil	800–1500	monotonic decline	0.000*	47.14866	0.104	44.51337
Colombia	500–2700	mid-elevation peak	0.040*	308.8983	0.022*	118.5063
Costa Rica, Atlantic	50–2000	monotonic decline	0.000*	70.51171	0.529	71.72685
Costa Rica, Pacific	0–1500	mid-elevation peak	0.432	74.69442	0.046*	69.73791
Egypt	90–1730	no relationship	0.467	16.25602	0.557	17.16426
Guyana	20–1300	no relationship	0.119	60.55191	0.926	62.53494
India	300–1650	no relationship	0.786	308.8983	0.194	310.4467
Madagascar	25–1985	mid-elevation peak	0.087*	72.30321	0.005*	59.26718
Malaysia	560–2300	monotonic decline	0.000*	78.50889	0.005*	67.91631
Mongolia	1000–2000	no relationship	0.309	46.76471	0.519	48.12831
Norway	0–1000	monotonic decline	0.005*	53.46252	0.539	54.90995
Philippines	250–1750	mid-elevation peak	0.012*	52.30409	0.039*	45.97784
USA, Arizona	1400–2600	monotonic decline	0.085*	62.21146	0.741	64.0179
USA, Colorado	1000–4267	mid-elevation peak	0.009*	210.2118	0.000*	195.8596
USA, Georgia	0–1055	monotonic decline	0.045*	66.35017	0.336	66.71938
USA, New England	6–1020	monotonic decline	0.000*	86.74925	0.798	88.65335
USA, Tennessee	379–1651	monotonic decline	0.000*	118.5399	0.397	119.6806
B) Phylogenetic diversity						
Austria	400–2100	monotonic decline	0.000*	253.9231	0.311	254.6488
Brazil	800–1500	monotonic decline	0.000*	48.7154	0.036*	42.98825
Colombia	500–2700	monotonic decline	0.014*	308.8983	0.544	310.4467
Costa Rica, Atlantic	50–2000	monotonic decline	0.000*	114.1713	0.317	114.1982
Costa Rica, Pacific	0–1500	mid-elevation peak	0.274	139.3365	0.097*	136.4971
Egypt	90–1730	mid-elevation peak	0.288	74.73754	0.049*	65.01489
Guyana	20–1300	no relationship	0.086*	111.6272	0.463	112.5605
India	300–1650	no relationship	0.432	308.8983	0.155	310.4467
Madagascar	25–1985	mid-elevation peak	0.010*	117.9435	0.067*	113.3615
Malaysia	560–2300	monotonic decline	0.000*	142.9337	0.476	144.1056
Mongolia	1000–2000	no relationship	0.283	151.2113	0.125	149.6165
Norway	0–1000	monotonic decline	0.022*	157.8659	0.588	159.436
Philippines	250–1750	monotonic decline	0.054*	104.9709	0.217	103.4068
USA, Arizona	1400–2600	no relationship	0.159	138.3317	0.802	140.2202
USA, Colorado	1000–4267	mid-elevation peak	0.000*	384.3878	0.001*	373.538
USA, Georgia	0–1055	monotonic decline	0.030*	140.3709	0.211	139.6175
USA, New England	6–1020	monotonic decline	0.005*	186.0234	0.588	187.5932
USA, Tennessee	379–1651	monotonic decline	0.000*	341.775	0.655	343.5356

Latitude and environmental variables

Between-site similarity, calculated taxonomically using the Jaccard Index or using phylobetadiversity, was lower in tropical mountains compared to temperate ones (morphospecies Jaccard $t = -6.215$, df $= 600.9$, $p < 0.001$; phylobetadiversity $t = 8.325$, df $= 560.6$, $p < 0.001$; Fig. 6; Appendix: Fig. A6). The WorldClim data from each of the 18 site locations was used as a simplification for the variable patterns occurring within each site location. When alpha and beta diversity values were compared to environmental co-variates extracted from the WorldClim data set (at 1 km^2 resolution) there was a significant relationship between both the mean annual temperature ($R^2 = 0.107$, df $= 1$, $p < 0.001$) and mean annual precipitation ($R^2 = 0.1$, df $= 1$, $p < 0.001$) with phylobetadiversity while only mean annual temperature was significantly related with Jaccard ($R^2 = 0.109$, df $= 1$, $p < 0.001$; Fig. 7). The relationship between each measure of beta diversity and all 19 environmental variables is presented in Appendix: Fig. A6 and the Supplement. There was no relationship between phylogenetic community structure (NRI or NTI)
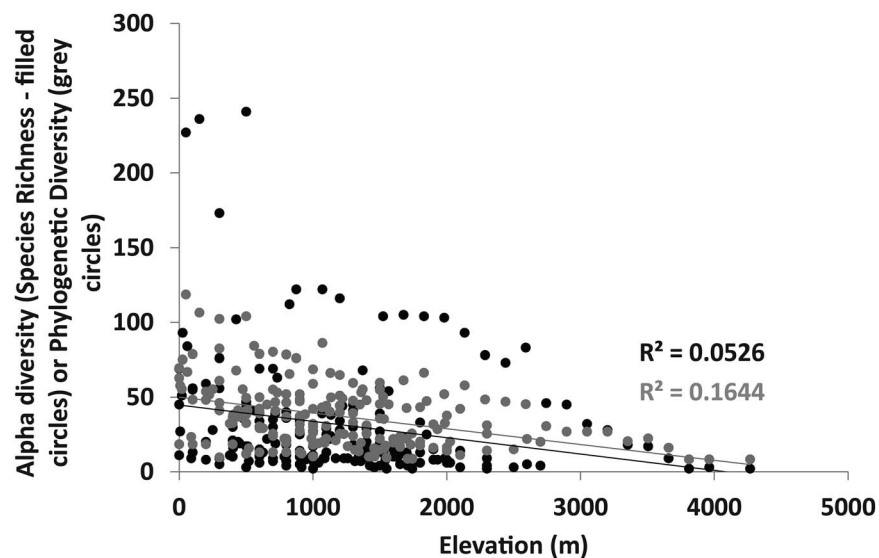
Fig. 3. Alpha diversity declines sharply at high elevations for both species richness (black) and phylogenetic diversity (grey). From mid to low elevations the pattern is variable with evidence of both monotonic decline and mid-elevation peaks (Table 1). The strength of a linear negative relationship is stronger for phylogenetic diversity. The Supplement contains the data and trends for each of the studies combined in this figure.

and average annual temperature (Fig. 7).

Discussion

"…phylogenies describe patterns, onto which evolutionary processes usually map only imperfectly."

—Losos (2011:724)

Expectation of phylogenetic clustering

As Losos noted (2011), we should test for a phylogenetic effect directly rather than assuming it a priori. In the growing field of phylogenetic community structure analysis, evidence for clustering is common. Indeed, one literature review of a wide variety of taxa (Vamosi et al. 2009) found that more than half of the studies examined evidence for phylogenetic clustering (59%). Thus, the expectation was that this meta-analysis would provide further evidence of phylogenetic clustering within ant communities at high elevations. While there are certainly instances of clustering at high elevations (Machac et al. 2011, Smith et al. 2014), it does not follow that we should expect it in all cases. Further, we should also ensure that phylogenetic community

analyses are able to explicitly test the hypotheses that closely related species are, in fact, ecologically similar. As Graham et al. noted in a recent review (2014) we know remarkably little regarding which traits or adaptations allow certain species to survive at various elevations. The results of this analysis do not support the intuitive and generally accepted nature of the trend for ants with regards to increased phylogenetic clustering with elevation or temperature. At the genus level, these data suggest that neither habitat (clustering) nor competition (dispersion) filter the taxa present—rather this analysis suggests that the community assemblages are not significantly different from random across elevation or temperature.

Pragmatically measuring diversity (i.e. without a solidified taxonomic framework) is a familiar circumstance to most biologists (particularly those who work with hyperdiverse or understudied taxa and/or areas). However, one result of such pragmatic unit assignment is an inevitably reduced capacity to compare between studies, regions, researchers or collection times. Recently, others have begun to accrue data which suggests that simply measuring diversity via richness may not, necessarily represent evolu-
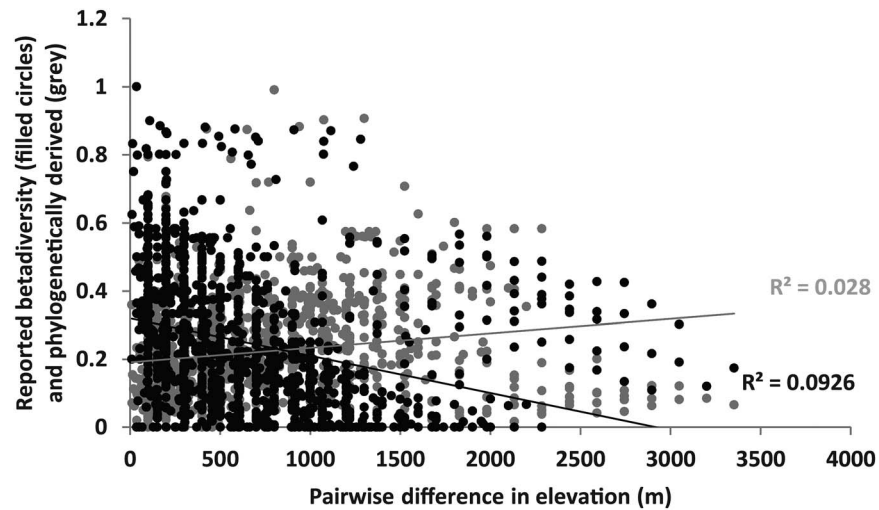
Fig. 4. Beta diversity measured as reported in the original publication (black circle) and phylogenetic measure of beta diversity (grey circles). Increasing elevational distance between sites strongly affects each measure. Note that the measure of phylobetadiversity is expressed as the opposite to the Jaccard and thus increasing values indicate reduced similarity.

tionary history (Rolland et al. 2012). Measuring diversity using phylogenetic measures (such as PD) is one way to entrench the measurement of evolutionary history with the measurement of

diversity. Where the two measures were compared, some found congruence between the measures (Smith and Fisher 2009) while others have revealed divergent patterns (Forest et al.
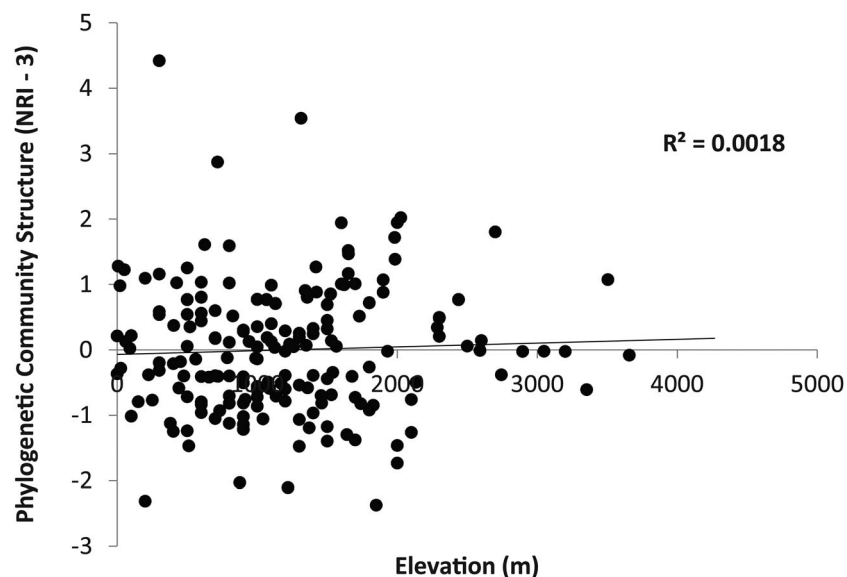

Fig. 5. While there are cases where highest elevation communities are phylogenetically clustered, across the entire data set, high elevation ant communities are not significantly more likely to be phylogenetically clustered than low or mid elevations. For individual comparisons across all 18 studies and null models see Table 2 and Appendix: Fig. A8.

Table 2. The relationship between phylogenetic community structure (NRI and NTI) and elevation. There is no prevalent trend towards increased phylogenetic clustering with increasing elevation. In only 2 cases was this relationship significant. Asterisk indicates a significant relationship.

Source	Country	Elevation range (m)	Elevation and structure (NRI)	Linear R^2	p (linear)	Elevation and structure (NTI)	Linear R^2	p (linear)
Glaser, 2006	Austria	400–2100		0.064	0.162	+	0.201	0.035*
Araújo and Fernandes 2003	Brazil	800–1500		−0.161	0.869	−	0.550	0.021*
van der Hammen and Ward 2005	Colombia	500–2700		0.027	0.237		0.013	0.281
Longino and Colwell 2011	Costa Rica, Atlantic	50–2000		0.114	0.241		−0.088	0.504
Smith et al. 2014	Costa Rica, Pacific	0–1500	−	0.514	0.027*		−0.166	0.955
Orabi et al. 2011	Egypt	90–1730		−0.305	0.816		−0.276	0.739
Lapolla et al. 2007	Guyana	20–1300		−0.031	0.407		−0.199	0.955
Sabu et al. 2008	India	300–1650		−0.246	0.678		0.340	0.179
Fisher 1998	Madagascar	25–1985		−0.121	0.638		−0.110	0.599
Brühl et al. 1999	Malaysia	560–2300		0.049	0.273		−0.142	0.961
Pfeiffer et al. 2003	Mongolia	1000–2000		−0.090	0.627		−0.111	0.757
Hågvar 2005	Norway	0–1000	−	0.605	0.024*	−	0.655	0.017*
Samson et al. 1997	Republic of the Philippines	250–1750		0.597	0.078		0.372	0.164
Andersen 1997	USA, Arizona	1400–2600		−0.165	0.938		−0.147	0.758
Gregg 1963	USA, Colorado	1000–4267		−0.015	0.404		−0.058	0.920
Ipser et al. 2004	USA, Georgia	0–1055		−0.163	0.902		0.005	0.349
Del Toro 2013	USA, New England	6–1020		−0.047	0.479		−0.086	0.658
Lessard et al. 2007	USA, Tennessee	379–1651		0.060	0.162	+	0.296	0.009*

2007, Cadotte et al. 2009). The accumulation or paucity of phylogenetic diversity is linked to the gain or loss of deeper evolutionary history—and as such we should consider global patterns of the distribution of this diversity carefully. I used phylogenetic methodology as a bridge between 18 independent studies of ants and elevation, where more than 50% of the species were named using interim epithets, to assess the expected patterns of alpha and beta diversity across elevation. Phylogenetic diversity did not uniformly decline with increasing elevation. Both monotonic decline and mid-elevational peaks were found, but the proportion of those showing a monotonic decline increased when alpha diversity was measured phylogenetically. All higher elevation communities were not found to be phylogenetically clustered. In fact there were only 2 of 18 studies that showed phylogenetic clustering at high elevations. Phylogenetic estimates of betadiversity were congruent with taxon-based estimates. Trends of the elevational decay of beta diversity with elevation are similar when either measured taxonomically or phylogenetically—though taxonomic (i.e. species level) decay is stronger. Patterns of beta diversity for tropical mountains were different from temperate mountains. Measured taxonomically or phylogenetically, between site similarity decreased more rapidly with elevational separation in tropical than temperate mountains.

In three cases the sites analysed here overlapped with those included in the recent Machac et al. review (2014; Arizona, Austria and Tennessee). Although methodology used to calculate phylogenetic community structure differed, the results were congruent—a strong positive relationship between NTI and elevation in Tennessee (Lessard et al. 2007) and Austria (Glaser 2006) and no significant relationship across the elevational gradient in Arizona originally described by Andersen (1997). However, the pattern throughout the other locations is much more ambiguous and it is only when the cases from Machac et al. are included in a larger dataset it becomes apparent that they are the only cases of a positive relationship between community structure and elevation. Machac et al. (2011) reported a distinct boundary at elevations that had an average annual temperature of 10°C. When the average annual temperature was colder than this the communities tended to display phylogenetic
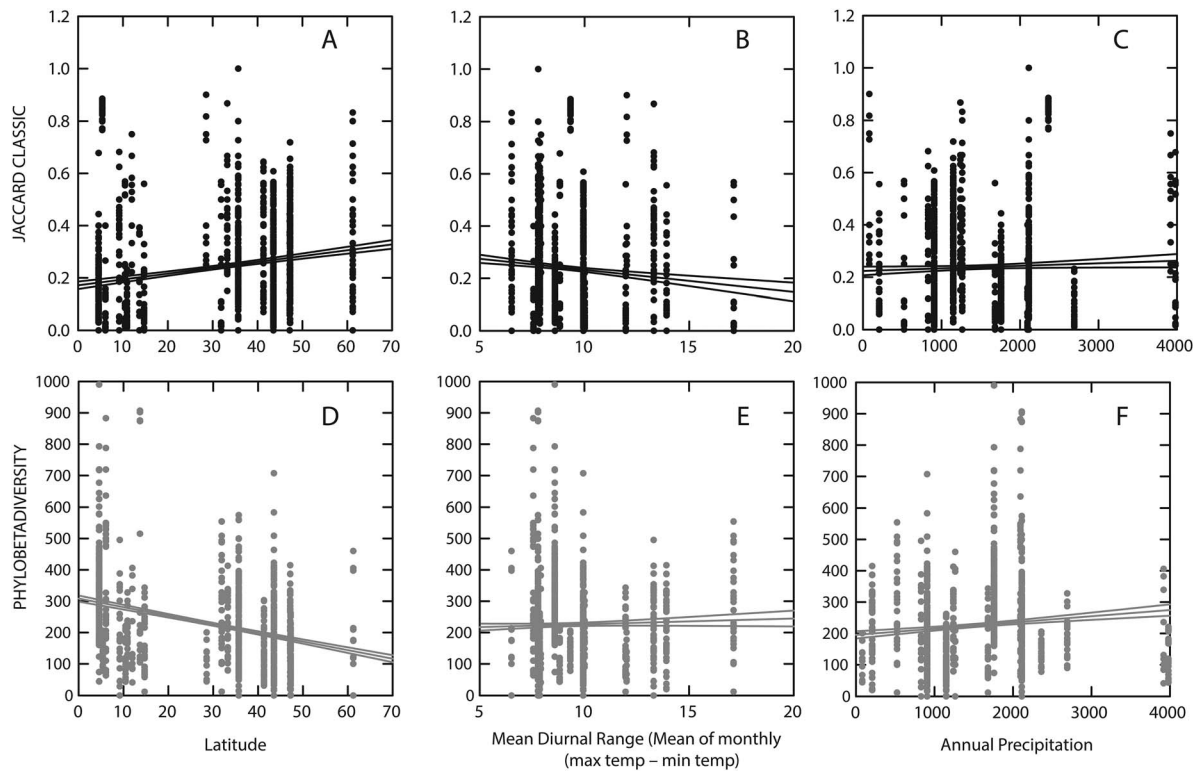
Fig. 6. The average between community similarity measured morphologically (A, B and C) or phylogenetically (D, E and F) compared to latitude (A and D) and temperature (B and E) and precipitation (C and F). Beta diversity measured using the classic Jaccard Index for the taxonomic level reported in the study shown in black, or using a measure of phylobetadiversity (the phylogenetic distance between samples, based on phylogenetic distances of taxa in one sample to the taxa in the other uses the nearest taxon method) based on the observed incidence matrix from that study and the phylogeny of Moreau et al. (2006) (shown in grey). Communities on tropical mountains are less similar to each other than communities on temperate mountains. The complete list of nineteen full variables are displayed in Appendix: Fig. A5 and all raw data are presented in the Supplement.

clustering, and warmer than this communities tended to be phylogenetically overdispersed. This suggested a shift from inter-specific competition in warmer environments to the environmental filtering of harsh abiotic variables in cold environments. However, when examined over a larger number of studies, the apparent lack of relationship with temperature shown here does not support Machac et al.'s conclusion regarding the predictability of the variation in ant communities along an elevational gradient—specifically in their inference of a boundary at 10°C where community composition switches from one of competitive interactions to habitat filtering.

There is much evidence that insect communities change with elevation (Mani 1962). In a meta-analysis of 204 elevation/diversity studies,

Rahbek (2005) found that a mid-elevation peak in diversity was more prevalent (50% cases) than a monotonic decline (25%). Specifically with ants, there is evidence from multiple localities around the world of an effect of elevation on community composition. All methods tested here agree that high-elevations are less diverse than mid- or low elevations. Fifty percent (9/18) of the published comparisons of species richness with elevation displayed a linear decline. When alpha diversity was estimated phylogenetically, some individual cases changed, however the proportion of cases that displayed a linear negative relationship with elevation did not (55.5%, 10/18). The residuals of species richness and PD across elevation displayed no relationship when examined across all sites (Supplement). Interestingly however, all the
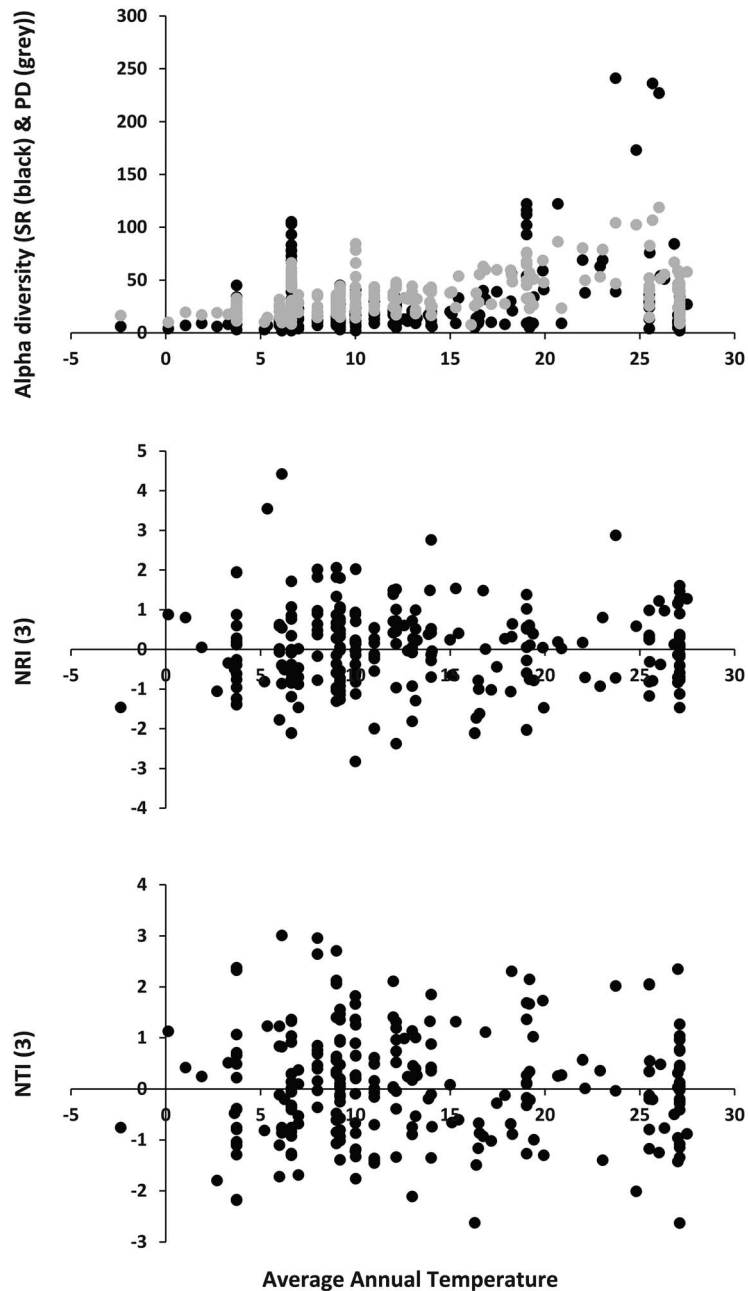
Fig. 7. There is no significant relationship between phylogenetic community structure and average annual temperature (°C).

highest elevation sites had higher PD than expected based on species richness (positive residuals). Furthermore, the same was true for 17 of 18 of the lowest elevation sites. This suggests that, while high elevation locations do have lower diversity (Fig. 3), these sites likely contain greater evolutionary history than is predicted by their species richness alone. One factor that may entangle morphological and phylogenetic estimates of diversity is the uneven representation of species within genera and the presence or absence of those genera within the

Moreau et al. phylogeny. For example, some species observed were members of genera that were not contained in the Moreau et al. phylogeny and in such cases the species were removed from the matrix and not included in phylogenetic calculations (Supplement). Removal prior to phylogenetic estimates might straighten the originally bow-shaped relationship if taxonomic exclusions were more prevalent at moderate elevations. However genera absent from the phylogeny were seen across the elevation gradient and there is no systematic evidence of this trend (the Supplement contains both original, reduced incidence and abundance matrices for all studies). One potential taxon that may be implicated in this pattern is the hyperdiverse, and widely distributed genus *Pheidole* (Wilson 2003). In the studies where *Pheidole* was present (13/18) species were found across most of the elevational range—and in some cases the species within *Pheidole* displayed a strong mid-elevation peak in diversity (e.g. Costa Rica; Longino and Colwell 2011, Smith et al. 2014). The phylogenetic measurements used here would miss such an increase in species-level phylogenetic diversity. The other likely explanation has to do with deeper than expected phylogenetic diversity at low elevations where, for instance, there are multiple instances where there are genera from subfamilies present at low elevations that are not evident at higher elevations (e.g. *Discothyrea* or *Proceratium* (Proceratiinae), *Mystrium* (Amblyoponinae), *Cerapachys* (Dorylinae) and numerous Ponerinae genera in Malaysia (Brühl et al. 1999) and *Tetraponera* (Pseudomyrmicinae) and various Ponerinae genera in the Phillipenes (Samson et al. 1997).

Massenerhebung and environmental variables

The Massenerhebung effect (Grubb 1971) predicts that the upper limits of montane cloud forest on small and/or isolated mountains will be lower due to decreased temperature and increased soil water content. From this observation, Janzen (1967) predicted that tropical organisms should respond to smaller bands of amenable conditions with smaller elevational ranges; and thus, mountain passes will be higher in the tropics. Janzen's predictions have generated much interest with regard to understanding how these species will respond to climate change

(Ghalambor et al. 2006, McCain 2009, Rosner 2013). An associated prediction from such extremely zoned elevational communities is that there ought to be a corresponding reduction in beta diversity (presuming reduced gene flow over time leading to allopatric speciation; Ghalambor et al. 2006). Thus, I expected lower pairwise estimates of beta diversity in tropical compared to temperate mountains. As stated by, Ghalambor, "*if Janzen is correct, tropical species should have narrower potential ranges than do temperate zone species*". The results of this meta-analysis support Janzen's prediction: communities on tropical mountains were less similar to each other than temperate mountain communities.

It is the abiotic factors that co-vary with elevation, not elevation itself, that affect diversity. Mountain-top environments tend to have greatly reduced temperature and increased precipitation levels compared to lower elevation environments (Barry 1992). This type of environment could (either or both) reduce the number of species colonizing or surviving—or strongly select for a subset of the regional species pool capable of living here. Trends linking elevational decay in beta diversity to environmental variables (temperature and precipitation) were not strong for either taxonomic or phylogenetic measures (Fig. 6; Appendix: Fig. A2, Table A1). Taxonomic measures of community similarity were higher at localities with higher temperatures while phylogenetic measures were higher with increased precipitation. Graham and Fine (2008) advocate for the use of phylogenetic measurements of beta diversity since such an explicitly evolutionary approach is likely to accurately reflect how a community changes along an environmental gradient. Here, phylogenetic trends of beta diversity parallel those of morphologically defined beta diversity across temperature and precipitation gradients—however the strength of the relationship is not strong. This is likely due to the taxonomic "grain" of the phylogeny and the resultant potential increase in resolution that the between-community analysis at a species level provides. If there is selection occurring at high-elevation sites that would promote the uniqueness of these communities and reduce beta diversity then, for the ants, this selection would likely be at the species level—

within individual genera (as was seen with the high-elevation genus *Adelomyrmex* in Pacific Costa Rica by Smith et al. (2014) and for the genera *Formica, Myrmica* and *Temnothorax* in the temperate studies reviewed by Machac et al. (2011)).

Conclusions

As the climate changes and as the field of phylogenetic community structure grows it is important that the predictions or expectations for diversity in montane environments are tested. In particular, it is important that the expectation of phylogenetic clustering due to strong environmental or ecological filtering at high environments (Fig. 1, panel 3, Graham et al. 2014) or the predictions that the tight physiological barriers experienced by insects (and in particular tropical insects) will result in smaller distributions and increased beta diversity in tropical versus temperate mountains (Rosner 2013) are supported by data. Determining the degree of support for such macroecological patterns, and the mechanism driving these patterns, is hindered when the data behind these hypotheses is not available for re-examination and re-testing. It is further challenged if the diversity of the taxonomic group in question necessitates the use of interim or provisional species names, thereby preventing the use of comparable species epithets between studies. The solution to the first problem is the consistent and expected public archiving of data (Roche et al. 2014). One solution to the second problem is to use phylogenetic measures of diversity and community structure (Webb et al. 2002) that are often based on deeper identification levels which are more dependable. Furthermore, phylogenetic methods extend diversity estimates beyond taxonomically-based measures of richness that may miss evolutionary history (Forest et al. 2007) or significant measures of ecosystem functioning (Cadotte et al. 2009).

The results presented here emphasize how the distribution of montane species is more than an ideal natural laboratory. Our world is increasingly dominated by anthropogenically changed climate (Stocker et al. 2013) and contemporary rates of extinction are estimated to be at least 1000x the background rate (Pimm et al. 2014). Tropical species, particularly the montane ones, have been amongst the first to respond to climate change by shifting their distributions upslope in response to increasing temperatures and aridity (Colwell et al. 2008). Tropical insect communities are characterized by extremely high diversity and endemism (Novotny and Miller 2014). Losing species (Dirzo et al. 2014) with such small distributions and high degrees of endemism will have a large effect on global diversity (Stocker et al. 2013). Thus, it is critically important that we are able to use all existing data to understand current diversity distributions in an evolutionary framework (Gonzalez and Peres-Neto 2015). When this is possible, we will be better able to understand how these distributions will change in a changing climate—and what we are likely to lose when they do.

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Supplemental Material

Ecological Archives

The Appendix and Supplement are available online: http://dx.doi.org/10.1890/ES14-00473.1.sm