



Elevational gradients in phylogenetic structure of ant communities reveal the interplay of biotic and abiotic constraints on diversity

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A central focus of ecology and biogeography is to determine the factors that govern spatial variation in biodiversity. Here, we examined patterns of ant diversity along climatic gradients in three temperate montane systems: Great Smoky Mountains National Park (USA), Chiricahua Mountains (USA), and Vorarlberg (Austria). To identify the factors which potentially shape these elevational diversity gradients, we analyzed patterns of community phylogenetic structure (i.e. the evolutionary relationships among species coexisting in local communities). We found that species at low-elevation sites tended to be evenly dispersed across phylogeny, suggesting that these communities are structured by interspecific competition. In contrast, species occurring at high-elevation sites tended to be more closely related than expected by chance, implying that these communities are structured primarily by environmental filtering caused by low temperatures. Taken together, the results of our study highlight the potential role of niche constraints, environmental temperature, and competition in shaping broad-scale diversity gradients. We conclude that phylogenetic structure indeed accounts for some variation in species density, yet it does not entirely explain why temperature and species density are correlated.

A fundamental pattern in biogeography is that both the number of species in a local community (i.e. species density; Gotelli and Colwell 2001) and the composition of communities vary, often systematically, along elevational gradients (Rahbek 2005, McCain 2009). The question, of course, is what drives that variation? Despite a growing number of ecological and evolutionary hypotheses to explain elevational diversity gradients (Sanders 2002, Colwell et al. 2004, Smith et al. 2007, Wiens et al. 2007, Kozak and Wiens 2010, and citations therein), the causes remain poorly understood.

One promising approach to infer the underlying processes shaping spatial variation in community composition is the use of phylogenetic tools (Cavender-Bares et al. 2009). Modern approaches build on the earlier use of taxonomic similarity to understand the assembly of communities (Elton 1946, Simberloff 1970). For example, if species within the same genus are more functionally and ecologically similar to one another than distantly related species, observed genus-to-species ratios that are higher than expected (i.e. when compared to a null model) might indicate that competition structures communities. The availability of well-sampled phylogenies has allowed the development of a framework (Webb 2000, Webb et al.

2002) which combines the approach of Elton (1946) with the information now available from phylogenetic trees. The framework allows inferring the potential mechanisms that underlie community phylogenetic structure, i.e. phylogenetic relationships among species coexisting within a community. After the actual phylogenetic structure of local communities is assessed, it is compared with structure of communities randomly assembled (i.e. following a specific null model) from the larger, regional species pool. Webb et al. (2002) argued that if the species occurring in a local community are clustered in the phylogeny (i.e. more phylogenetically related than in the null model communities) then the underlying cause of structure is likely to be environmental filtering on shared physiological tolerances, assuming that niches are conserved (Webb et al. 2002, Losos 2008). Alternatively, when species are overdispersed in the phylogeny (i.e. species are less related than in the null model communities) then either interspecific competition or trait convergence is implicated as the structuring force. A lack of a phylogenetic structuring suggests that neutral processes shape the community (Kembel and Hubbell 2006). However, it is worth noting as a caveat that other processes have also been proposed to lead to patterns similar to clustering/overdispersion (e.g. density-dependent

interactions, facilitation during succession; Cavender-Bares et al. 2009).

A growing number of studies have used community phylogenetic approaches to better understand spatial variation in community composition (Stevens 2006, Emerson and Gillespie 2008, Graham and Fine 2008, Algar et al. 2009, Cavender-Bares et al. 2009, Vamossi et al. 2009). Yet, only two studies, to our knowledge, have tested whether the phylogenetic structure of local communities might vary along elevational gradients or whether the drivers of diversity along elevational diversity gradients can be inferred by employing a community phylogenetics perspective (Bryant et al. 2008, Graham et al. 2009). Bryant et al. (2008) examined the phylogenetic structure of microbial and plant communities at five sites along a single elevational gradient in the Rocky Mountains, USA, and found that the microbial communities tended to be phylogenetically clustered throughout the entire elevational gradient, but the plant communities were overdispersed at higher elevations. Graham et al. (2009) examined the phylogenetic structure of 189 hummingbird communities in the Andes in Ecuador and found that communities were overdispersed in lowlands, suggesting an important role of interspecific competition.

The community phylogenetics approach hinges on an important assumption – that closely related species share similar traits and functions. This assumption has been called phylogenetic conservatism, niche conservatism, or evolutionary stability (Losos 2008). Importantly, neither the Bryant et al. (2008) nor the Graham et al. (2009) study tested for phylogenetic conservatism. Moreover, the Bryant et al. (2008) and the Graham et al. (2009) focused on single elevational gradients such that the generality of the patterns they documented is hard to assess.

In this study, we examine patterns of ant species density and community phylogenetic structure along three elevational gradients. We tested two predictions: 1) communities at high-elevation sites would be phylogenetically clustered, as would be expected if traits are conserved and only closely related species of a subset of lineages possessed the traits which allowed them to persist at cold, high-elevation sites, and 2) communities at low-elevation sites would be phylogenetically overdispersed in the phylogeny, as would be expected if interspecific competition rather than environmental filtering shaped the composition of local communities. Finally, we assessed whether the elevational pattern in phylogenetic structure is sufficient to explain patterns in species density, or whether environmental gradients have effects on species density above and beyond the effects of phylogenetic structure.

Methods

The data

We obtained data on the identities and occurrences of species within local communities from two published studies (Chiricahua Mountains, USA: Andersen 1997; Vorarlberg Mountains, Austria: Glaser 2006) and our own work (southern Appalachian Mountains, USA: Sanders et al. 2007). Importantly, each of the datasets consists of samples from local communities along extensive elevational gradients (Table 1); the data are not interpolated ranges or derived from niche models. For detailed information on geography of montane systems and sampled sites, see Supplementary materials Appendix 1.

Constructing phylogenies

We constructed three phylogenies, one for each of the montane systems, based on published genus-level phylogenies (Brady et al. 2006, Moreau et al. 2006). We adopted the molecular datasets from these studies from the TreeBase database <www.treebase.org>. Nine of the 175 species considered here lacked species- and genus-level molecular data. In these few cases (5% of all species in this study), species were substituted with closely related taxa with relationships derived from Bolton's (2003) classification. We extended the molecular dataset using 80 additional sequences (using the same genes as in the Brady et al. (2006) and Moreau et al. (2006) studies) available for particular species in GenBank in order to incorporate within-genus variability and to resolve some of the genus-level polytomies (especially in the genera *Pheidole* and *Camponotus*). These additional sequences, their GenBank codes, as well as the substituted taxa are listed in the Supplementary materials Appendix 2. We aligned the edited sequences in MAFFT, ver. 6 (Katoh et al. 2002). To reconstruct the phylogenies, we employed a maximum likelihood approach with topology constraint in PAUP 4.0 (Swofford 1993). The tree topology, on which molecular data were forced, corresponded with the genus-level phylogeny of Bolton (2003), Brady et al. (2006), and Moreau et al. (2006). We estimated branch lengths on the basis of substitution rates in a combined molecular dataset. For more details, see Supplementary materials.

Assessing phylogenetic structure of communities

Prior to examining the phylogenetic structure of communities, we tested for niche conservatism/phylogenetic conservatism. Based on our understanding of the natural

Table 1. Location, number of sites, and elevational span sampled for the community data used in the analyses. The entire elevational extent of Chiricahua Mts: 1100–2900 m, Vorarlberg Mts: 350–3000 m, Smoky Mts: 250–2000 m. More information on geography of the montane systems and sites sampled is given in the Supplementary material Appendix 1.

Author	Montane system	Location	No. of sites	Elevation range (m)
Andersen (1997)	Chiricahua Mts	Arizona, USA	9 sites	1400–2600
Glaser (2006)	Vorarlberg	Austria	18 sites	400–2100
Sanders et al. (2007)	Smoky Mts	Tennessee/N Carolina, USA	29 sites	379–1828

history of ants and previous studies, we tested for conservatism in three traits: habitat associations (woodlands, shrublands, meadows and grasslands), nest site (in soil, under rocks, mounds and ground nests, rotting wood, canopy and trees), and worker size (measured as the Weber's length of thorax). Each of these three suites of traits represents a significant axis of the ecological niche of ants and can be related to interspecific competition (worker size, nest site) or environmental tolerance (habitat association, nest site). We employed the random tree-length distribution algorithm for discrete traits (Cubo et al. 2005) that randomly permutes taxa (and their character values) along the phylogeny, while holding the topology as well as the branch lengths constant. Each character is mapped on the phylogeny through the maximum parsimony procedure. Afterwards, the number of character steps along the actual phylogeny is contrasted with the distribution of the number of steps in the 10 000 randomly constructed phylogenies. In the case of continuous characters, we used squared-length parsimony (Cubo et al. 2005). We performed these analyses in Mesquite 2.7 (Maddison and Maddison 2002). Our results were not affected by the bias potentially introduced by phylogenetic signal in occurrence frequencies (i.e. closely related species appear in many communities as present) (Kembel 2009) because we employed a null model that takes into consideration the prevalence of species in the communities and samples them accordingly (see below, Gotelli 2000).

After testing for niche/phylogenetic conservatism, we estimated the phylogenetic structure of each community from the three montane systems using two indices: mean phylogenetic distance (MPD) and mean nearest neighbor distance (MNND; Webb et al. 2002). MPD is an estimate of the average phylogenetic relatedness (on basis of branch lengths) between all possible pairs of taxa in a local community. MNND, in contrast, is an estimate of the mean phylogenetic relatedness between each taxon in a local community and its nearest relative. We then calculated standardized NRI and NTI indices. The NRI and NTI describe the difference between average phylogenetic distances (MPD and MNND, respectively) in the observed and randomly generated null communities, standardized by the standard deviation of phylogenetic distances in the null communities (Webb et al. 2008). We used R 2.8 to calculate NRI and NTI (Kembel et al. 2009). Since values of NRI and NTI were highly correlated ($r = 0.837$, $p < 0.001$), we report only NRI values in subsequent analyses. To assess whether the observed NRI values differed significantly from zero, we compared them to NRI values of null communities generated by Gotelli's swap algorithm (Gotelli 2000); i.e. the occurrence matrix is randomized holding the number of species per sample and the frequency of occurrence of each species across samples constant.

The phylogeny used for the calculation of NRI was not fully resolved and branch-length estimates were not available for all of the taxa. Therefore, we examined the impact of the phylogeny's resolution (defined as branch lengths availability) on NRI by estimating three different distances: species-level distances, genus-level distances, and simple Grafen's (1989) distances based on the tree topology. We then calculated new NRI values using these

distances for each of the three montane systems and mutually compared them.

Environmental variables

To examine the relationship between ant species density and climate, we extracted information on annual precipitation and annual mean temperature for each community in each montane region from the WorldClim v1.4 database (www.worldclim.org; Hijmans et al. 2005) using ArcView GIS (ver. 3.2, Esri 1992–2000; ESRI, Redlands, CA). WorldClim data pose some problems, especially in montane systems, because the resolution of the data is 1 km^2 . Considerable variation in temperature can occur within one square kilometer, especially in montane systems. As a check of the potential bias of using WorldClim data, we examined whether mean annual temperature data obtained from WorldClim were correlated with mean annual temperature data obtained from measurements of temperature from dataloggers arranged along the elevational gradient in the Smokies. Ideally, we would have measured temperature and precipitation data in each of the montane systems. However, because the WorldClim temperature data were correlated with the measured temperature data ($r = 0.998$, $p < 0.001$), and measured climate data were unavailable for two of the three gradients, we instead use WorldClim data. We also note that such an approach is common to other studies of elevational diversity gradients (McCain 2009) such that our work should be directly comparable. We chose these focal environmental variables because they are often strongly correlated with ant species density (Kaspari et al. 2000, Sanders et al. 2007, Dunn et al. 2009).

Analyses

We related elevation and the climate variables (mean annual temperature, annual precipitation) to species density (the number of species occurring in a local community) and to phylogenetic structure (NRI) of local communities using linear mixed-effect models. In the model, identity of a montane system was treated as a random effect, and elevation, mean annual temperature, annual precipitation, and all their combinations as explanatory variables. We used the maximum likelihood procedure to fit each model, and we compared those models via Bayesian information criterion (BIC).

As temperature appeared to be the best predictor of both species density and community phylogenetic structure, we conducted further analyses to tease apart the mechanisms linking these variables. The effects of temperature on NRI and species density could operate in one of two ways. First, temperature could influence phylogenetic structure and phylogenetic structure could in turn influence species density. In this scenario, species density patterns are simply a consequence of species of a few clades possessing the traits necessary to persist in harsh conditions, such as the cold. Or second, temperature could influence species density via mechanisms independent of phylogenetic structure. Any of a variety of effects are possible, including effects on speciation rates (Davies et al. 2004) or abundance mediated

effects on extinction (Willig et al. 2003). To distinguish between these possibilities, we assessed whether the effect of phylogenetic structure (estimated as NRI) on species density was significant even when the effect of temperature was already included as an explanatory variable in the model predicting species density. This outcome would indicate that phylogenetic structure has a direct effect on species density. Alternatively, if phylogenetic structure is not related to species density after temperature is included in the model, the result implies that phylogenetic structure may influence patterns of species density, but is insufficient as a complete explanation for them. All the analyses were conducted in R 2.8 (Pinheiro and Bates 2000).

We note that spatial autocorrelation within montane systems can inflate type I errors in statistical tests. However, because interpreting the coefficients from spatial regression can be challenging at best (Bini et al. 2009), we do not use spatial regression techniques in these analyses (e.g. SAM – Rangel et al. 2006) and instead rely on BIC and R^2 values as estimates of goodness of fit.

Results

The three elevational gradients we considered consisted of 56 local ant communities with 175 ant species from seven subfamilies (Supplementary material Appendix 3). Along each of the gradients, ant species density decreased with elevation (Fig. 1).

Bayesian information criterion indicated that the best environmental predictor of ant species density was annual mean temperature ($BIC = 364.04$, positive relationship; Table 2). Only slightly less plausible were the models including elevation ($\Delta BIC = 0.11$; Table 2) and temperature + precipitation ($\Delta BIC = 0.64$; Table 2).

We found strong evidence for niche conservatism for each of the three traits we examined. The evolutionary stability of niches (represented by habitat associations, nest site, and worker size) was consistent among the montane

systems for each of the examined traits (10 000 randomizations, $p < 0.05$) (Table 4). In other words, not only were the traits examined here phylogenetically conserved, they were conserved everywhere.

NRI was correlated with temperature ($BIC = 338.95$, $R^2 = 0.36$; Table 3); the correlation was negative in each of the three montane systems (Fig. 2). This would be expected if environmental stress (due to lower temperatures at higher elevations) acted as a filter on lineages at high elevations and competition structured communities at low elevations. Besides temperature, the next best model of NRI with only a minor difference in BIC comprised elevation ($\Delta BIC = 0.68$; Table 3). Low-elevation communities tended to be significantly overdispersed (4 sites), whereas communities at higher elevations tended to be significantly clustered (7 sites) (Fig. 2).

Ant species density was significantly and positively correlated both with temperature ($p < 0.001$, $R^2 = 0.55$) and NRI ($p = 0.002$, $R^2 = 0.17$) in independent models (above). However, once temperature had been added in the model of species density, the contribution of NRI became insignificant ($p = 0.76$, $R^2_{NRI} < 0.01$). Conversely, even if the model of species density already comprised NRI, the effect of temperature remained significant ($p < 0.001$, $R^2_{temp} = 0.44$). These outcomes suggest that both the species density and community phylogenetic structure are mutually independent products of temperature variation.

The estimates of NRI are robust to phylogenetic resolution for the Smoky Mountains and Vorarlberg ant communities (Table 5). NRI for the communities from the Chiricahua Mountains varied with phylogenetic resolution, however, perhaps because there were only 9 sites sampled in the Chiricahuas and few genera were monotypic (as opposed to the Smoky Mountains and Vorarlberg) such that it was possible for polytomies within genera to have a greater effect. It could be argued that the species level phylogeny for the Smoky Mountains and Vorarlberg (due to its lower resolution) approaches the genus-level phylogeny; thus, resulting in a tight correlation between the respective NRI values. To avoid this artifact and examine

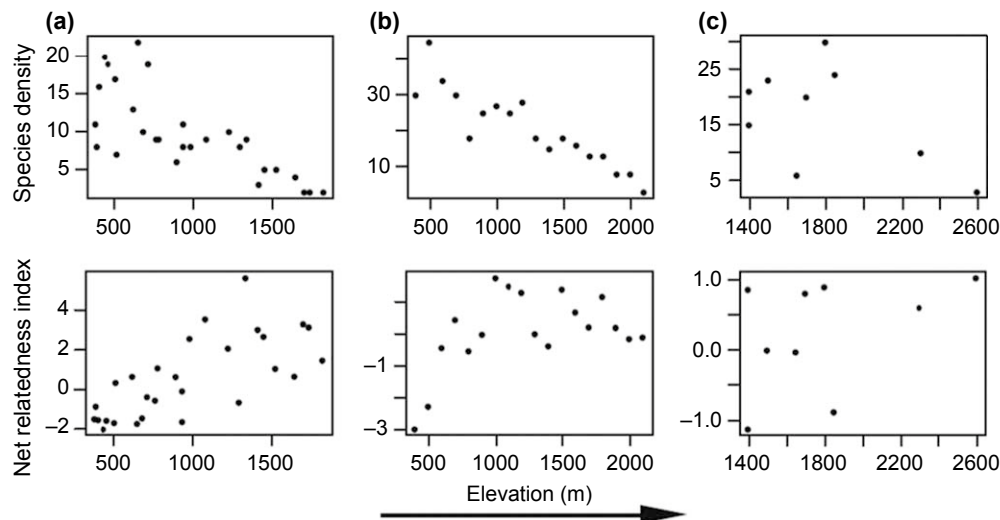


Figure 1. Community characteristics for (a) Smoky Mountains, (b) Vorarlberg, (c) Chiricahua Mountains. Species density (i.e. number of species in a local community) and net relatedness index (NRI) are plotted against elevation. Each point is a site sampled for ants.

Table 2. Models of ant species density. The most parsimonious model was identified via Bayesian information criterion (BIC). Abbreviations refer to temperature (Temp), precipitation (Precip), and elevation (Elev).

	BIC	logLik	DF	R ²
Null model	403.551	-195.765	—	—
Elevation	364.151	-174.061	51	0.546
Temperature	364.039	-174.005	51	0.547
Precipitation	393.806	-188.885	51	0.221
Temp+Precip	364.681	-172.322	50	0.574
Temp+Elev	367.173	-173.568	50	0.554
Precip+Elev	365.948	-172.956	50	0.564
Precip+Elev+Temp	368.110	-172.033	49	0.578

the robustness of NRI thoroughly, we additionally correlated genus-level NRIs and topology derived NRIs for Smoky Mts and Vorarlberg. Still, the NRIs were highly correlated (Smoky Mts: $F_{1, 26} = 335.400$, $p < 0.001$, $r = 0.962$; Vorarlberg: $F_{1, 16} = 43.620$, $p < 0.001$, $r = 0.846$) such that the incomplete phylogenetic resolution for a handful of species in this study is likely to have only marginal effects on our broad results. In addition, provided that the polytomies in some of the genera (e.g. *Pheidole*, *Camponotus*; Pie and Traniello 2007) represent rapid diversification events, additional resolution in these taxa should not affect the NRI estimates.

Discussion

We found that, across three elevational gradients in North America and Europe, ant species density is positively related to temperature. Such a result is not surprising. Numerous other studies have documented that species density is positively correlated with temperature (Hawkins et al. 2003). Temperature is often correlated with diversity, not just in ants but in many taxa, though the mechanisms that link temperature to diversity have been a topic of much discussion (Clarke and Gaston 2006, Storch et al. 2006, Hawkins et al. 2007, Hessen et al. 2007). Our results indicate that at high elevations and in cooler conditions, there are fewer species than in warmer, low-elevation sites. Those high-elevation species tend to come from fewer lineages than would be expected by chance. Only a few lineages appear to have traits that allow them to persist in colder, high elevation conditions.

Table 3. Models of community phylogenetic structure (represented by NRI values). The best model was identified via Bayesian information criterion (BIC). Abbreviations refer to temperature (Temp), precipitation (Precip), and elevation (Elev).

	BIC	logLik	DF	R ²
Null model	359.149	-173.564	—	—
Elevation	339.633	-161.802	51	0.348
Temperature	338.953	-161.462	51	0.356
Precipitation	347.040	-165.505	51	0.254
Temp+Precip	341.926	-160.945	50	0.368
Temp+Elev	342.618	-161.291	50	0.360
Precip+Elev	342.360	-161.162	50	0.363
Precip+Elev+Temp	345.321	-160.639	49	0.375

Table 4. Examination of the phylogenetic signal in relevant life history traits. If the number of parsimony character steps or “squared-length of the character” in case of continuous traits, i.e. worker size, (N_{steps}) is smaller than the lower borderline of the confidence interval (95% CI), the trait is phylogenetically conservative.

		N_{steps}	95% CI
Smoky Mts	nest site	18	(18; 24)
	habitat	6	(7; 9)
	worker size	7.9	(17.8; 175.7)
Vorarlberg Mts	nest site	25	(37; 44)
	habitat	16	(19; 27)
	worker size	10.7	(11.2; 233.9)
Chiricahua Mts	nest site	25	(27; 32)
	habitat	24	(25; 33)
	worker size	50.1	(55.7; 292.6)

By taking an explicit community phylogenetics approach, our work suggests that the factors that structure these ant communities may vary in predictable ways along environmental gradients. In 1960, Fischer wrote “much of the killing in high latitudes is done by the less selective inorganic forces . . . In the tropics on the other hand, the physical environment is more benign to most organisms, and the highly selective interorganic struggle for existence is more apparent.” Our results support Fischer’s assertion, but put it in the context of phylogenetic niche conservatism. Because traits of ants, like those of many taxa, are phylogenetically conserved, much of the “killing” at high elevations is not random phylogenetically, leaving species of those relatively few clades that have evolved the ability to deal with cold climates. In lowlands, competition appears to structure the communities rather than habitat filtering. Such mechanisms have long been suggested for both elevational and latitudinal gradients, but rarely tested (Bryant et al. 2008, Graham et al. 2009), especially among montane systems.

A question separate from whether environmental conditions affect phylogenetic structure in consistent ways (they do), is whether the patterns in phylogenetic structure are sufficient to account for patterns in species density or other measures of biological diversity. We found that while phylogenetic structure was correlated with ant species density, it was a poorer predictor of species density than was temperature. In other words, temperature appears to affect species density over and above its effects on phylogenetic structure. Bringing these results together, it seems that temperature may influence ant diversity both via its effects on phylogenetic structure (in essence a function of niche conservatism) as well as via other mechanisms, whether due to effects on abundance and ultimately extinction rates or some other link (Willig et al. 2003, Davies et al. 2004, Sanders et al. 2007). Finally, we need to consider the possibility that phylogenetic structure both influences and is influenced by species density.

It is interesting to consider just which ant taxa appear to have traits that allow them to pass through such an environmental filter in colder, high-elevation sites. Across these three disparate montane systems, species from the genera *Formica*, *Myrmica*, *Temnothorax* appear to be the most common at high-elevation sites (Supplementary material Appendix 3). Some of these genera possess traits

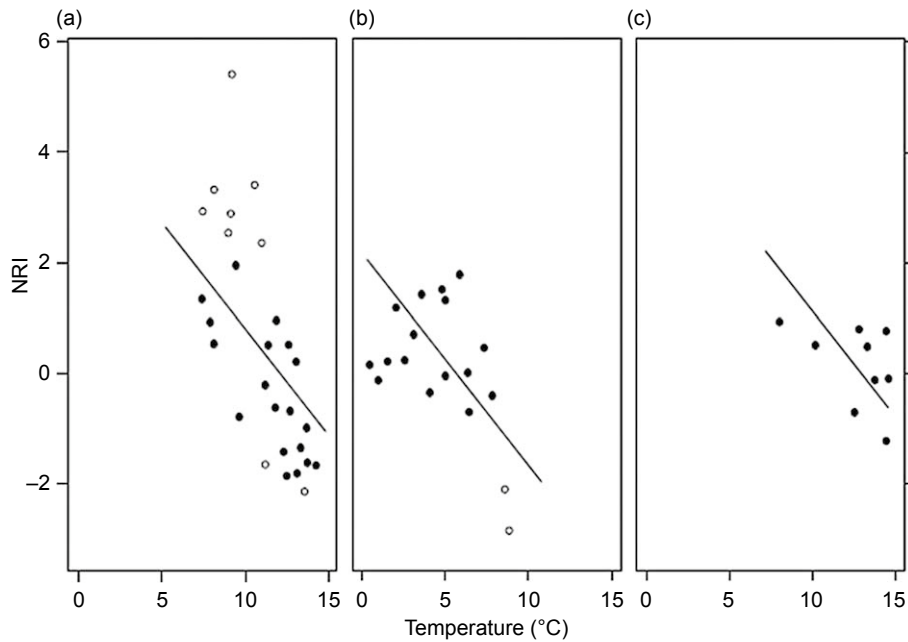


Figure 2. The relationship between phylogenetic community structure (NRI) and mean annual temperature ($F_{1, 51} = 24.33$, $p < 0.001$, $R^2 = 0.36$). The fitted relationship is depicted separately for (a) Smoky Mts, (b) Vorarlberg, (c) Chiricahua Mts. Significantly overdispersed/clustered communities are depicted as white points, and communities approaching random phylogenetic structure as black points.

that might facilitate overwintering (Kaspari and Vargo 1995, Geraghty et al. 2007). For example, some species of the genus *Formica* produce thatch mounds that enhance their freeze tolerance (Erpenbeck and Kirchner 1983, Heinze 1992). For other genera it is less clear what traits have allowed them to colonize and persist in high-elevation sites, though given that living at these sites appears difficult, it seems safe to assume that all of the relatively few lineages that persist there have evolved specific traits of one sort or another associated with cold tolerance.

Overdispersion in the phylogenies at low elevations is congruent with the notion that interspecific competition shapes the composition of local ant communities. Though interspecific competition has long been given primacy as the structuring agent in ant communities (Hölldobler and Wilson 1990, Andersen 1992, Deslippe and Savolainen 1995, Parr et al. 2005), our results suggest that competition may structure ant communities, but conditionally so, only in more favorable climatic conditions (Retana and Cerdá 2000). This is not to say that competition is unimportant in cold or other extreme

conditions, only that it is secondary to the effects of environmental or habitat filtering.

The overall trend was clustering at high elevations, but overdispersion at low elevation sites. But of course there was variation around this general trend: several of the individual ant communities examined that did not display significant phylogenetic structure were found at high elevation. One possible explanation for lack of phylogenetic structure at a few high elevation sites is that those sites included species that were poorly resolved on our phylogeny and so were biased in some way. However, the robustness of NRI across different phylogeny resolutions makes this seem unlikely. An alternative explanation is that the relative extent of phylogenetic structure varies due to factors additional to those considered here, such as additional climatic or environmental variables (such as the composition of plant communities) or due to local variation in climate not captured at the scale at which we sampled the climate. In addition, both environmental filtering and competition might simultaneously occur and obscure one another in the overall phylogenetic structure of a community (Helmus

Table 5. The results indicate that both the NRIs derived from genus-level phylogeny and from phylogeny without branch length estimates are highly correlated (besides Chiricahua Mts) with NRIs based on our phylogenies (Supplementary material Appendix 2). Please, see the text for discussion of the results.

	Genus level				Topology			
	F	DF	r	p	F	DF	r	p
Smoky Mts	3893	26	0.996	< 0.001	281.8	26	0.955	<0.001
Vorarlberg Mts	1219	16	0.999	< 0.001	41.29	16	0.838	<0.001
Chiricahua Mts	3.744	7	0.505	0.094	3.529	7	0.490	0.102

et al. 2007). Gradients in phylogenetic structure with environmental gradients are unlikely to ever be absolute. Rather, they reflect tendencies from which individual communities can deviate in many ways.

Our work adds to a growing number of studies that have examined phylogenetic structure (Emerson and Gillespie 2008, Graham and Fine 2008, Algar et al. 2009, Cavender-Bares et al. 2009, Vamosi et al. 2009). To our knowledge, however, only two studies to date have examined how phylogenetic structure varies along environmental gradients and neither has actually tested whether the niche conservatism assumed in filtering models existed. In the Andes, hummingbird communities studied by Graham et al. (2009) tended to be phylogenetically clustered at high elevation and overdispersed at low elevations, which agrees with the results we document here for ants. However, in another study conducted in the Rocky Mountains in Colorado, microbial communities were phylogenetically clustered at all elevations, whereas plant communities tended to be more overdispersed with increasing elevation (Bryant et al. 2008). One possibility for these contrasting results among taxa and studies is that different forces might act to shape the structure of communities composed of different taxa. After all, microbes, plants, hummingbirds, and ants all perceive their environment and interact with it in different ways; one taxon's extreme climate is another taxon's favorable climate. While the peaks of elevational gradients represent the coldest conditions in which ants are found (Hölldobler and Wilson 1990), they are not even close to the most extreme climates encountered by microbes, which can be found even at the center of snowflakes (Black 2008).

In sum, our results imply that the interplay between interspecific interactions, trait evolution, and temperature shapes the distribution of species among three gradients. We can also infer the critical temperature at which the importance of competitive interactions as a structuring agent fades and habitat filtering (stress) begins to dominate. At least for the temperate ecosystems considered here that temperature is $\sim 10^{\circ}\text{C}$ (indicated by a zero value of NRI). It is worth noting that this is the temperature in recent global analyses (Dunn et al. 2009) at which ant diversity drops dramatically, suggesting that the barriers to overwintering, harvesting sufficient food, or some combination thereof, are overcome by only a few lineages below this temperature. More consideration of why only a subset of ant lineages do well in conditions cooler than this threshold will be fundamental to understanding patterns in ant distribution, but also to understanding how ant communities may change as global temperatures change.

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